

# Plant species richness across the Himalaya driven by evolutionary history and current climate

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**Citation:** Rana, S. K., T. D. Price, and H. Qian. 2019. Plant species richness across the Himalaya driven by evolutionary history and current climate. *Ecosphere* 10(11):e02945. 10.1002/ecs2.2945

**Abstract.** The Himalaya, the world's largest mountain chain, spans a wide variety of climates. Further, different locations have historically experienced climatic perturbations to different degrees. This makes it the ideal region to assess roles of contemporary climate, diversification (speciation minus extinction), and dispersal barriers in affecting local species richness. Based on a review of all available Himalayan floras, we determined that 8765 native angiosperm species are presently documented and recorded their location and elevational distributions. We compared species richness and measures of phylogenetic structure in 100-m elevational bands for all species combined and for three major life-forms separately (trees, shrubs, and herbs) across the Himalaya. Species richness declines threefold from the east to the northwest of the Himalaya. Along elevational gradients, tree richness monotonically declines in the northwest, but peaks at ~1000 m in the east. Shrubs and herbs peak in richness at mid-elevations (~2000 m). Mean temperature and annual precipitation together explain ~60% of the variation in species richness. The general phylogenetic pattern observed in this study is that phylogenetic clustering (i.e., more closely related species on fewer long branches) increases from low to high elevations, but with a dip at mid-elevations (2000–3000 m), which may result from a mixing of distinct floras, but is not associated with exceptionally high richness. High clustering at higher elevations (3000–4500 m) and in the drier northwest suggests ongoing diversification dynamics limit richness in these harsher environments. The effects of diversification dynamics appear to be smaller than those of contemporary climate in limiting buildup of species numbers.

**Key words:** angiosperms; cradles; elevational gradient; environmental filtering; Himalaya; museums; phylogeny.

**Received** 4 June 2019; revised 19 September 2019; accepted 8 October 2019. Corresponding Editor: Songlin Fei.

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## INTRODUCTION

Speciation, extinction, and dispersal—the last including both movement to a new location and successfully establishing there—together account for the number of species present in a location (Roy and Goldberg 2007, Wiens 2011, White 2016). These three historical processes work differently across different regions or climatic regimes. Even locations with similar numbers of species may contain many old lineages

(museums) or relatively few old lineages each subtending many young species (cradles; Stebbins 1974, Chown and Gaston 2000), reflecting different histories of dispersal and diversification (Roy and Goldberg 2007), but such historical processes may also be an important reason for differences in species numbers across the world. Regions experiencing low extinction, high speciation, and high immigration are expected to have more species than those with the opposite processes. For example, in temperate regions,

climate fluctuations over millions of years, coupled with difficulties of evolving adaptation to deal with a freezing climate, may result in only few lineages successfully entering these challenging conditions, implying many more species could be accommodated. In contrast to historical effects, the number of species present in a location may be largely a function of present-day climate (Currie et al. 2004), irrespective of past history. For example, the number of species able to coexist in a temperate locality may be less than in a tropical locality, whereby each location is close to an equilibrium state. The relative roles of non-equilibrium (historical) vs. equilibrium (ecological limits on coexistence) processes as determinants of species numbers continue to be debated (Harmon and Harrison 2015, Rabosky and Hurlbert 2015). In plants, evidence for contributions from non-equilibrium historical processes to local diversity is strong (Qian and Ricklefs 2000, Ricklefs and He 2016).

The Himalayan region encompasses a large fraction of global climate diversity, enabling a comparison of the history of species accumulation among climates across a geographically cohesive area. It straddles the freezing boundary, with higher elevations snowbound. Further, the lowlands receive about three times more precipitation in the subtropical east than the northwest (Anders et al. 2006, Bookhagen and Burbank 2010, Fick and Hijmans 2017). Distinct zonation in plant richness, despite relatively easy access for plants from wet and warm regions in the eastern low elevations, to both low elevations in the northwest and high elevations in the east suggests that climatic controls, rather than geographical barriers, importantly affect establishment of plants. This gives the opportunity for multiple ancient tropical lineages to be retained at higher elevations or in the western drier locations, even if the position of these climatic regimes has moved geographically over time, thereby resulting in a pattern of phylogenetic over-dispersion, consistent with the museum hypothesis (as observed for trees at high elevations in tropical regions; Qian and Ricklefs 2016). Alternatively, higher elevations and the northwest especially have been subject to more climatic upheavals over millions of years, giving opportunities for few lineages to invade and diversify, resulting in phylogenetic clustering, consistent with the cradle hypothesis (as observed for trees

at high latitudes; Qian and Ricklefs 2016), and more indicative of non-equilibrium conditions. In this paper, we examine these alternative hypotheses based on a compilation of all angiosperms (i.e., not only trees, but also shrubs and herbs) in the Himalaya and ask how each may contribute to variation in species richness.

Historically, the Himalayan region is likely to have been associated with high elevations and rugged topography from at least 45 million years ago (mya) and probably the beginning of the Paleogene, predating the initial collision of India with Asia (currently estimated to be about 55 mya; Wang et al. 2010), as reviewed by Spicer (2017). Therefore, any mixing of floras from the Indian plate (part of Gondwana) and the Eurasian plate (part of Laurasia) is likely to have deep roots (Qian et al. 2019), and mountain building be of lesser importance than climate change in affecting species richness. Indeed, climate fluctuations have clearly affected plant speciation, extinction, and dispersal in the Himalaya (Manish and Pandit 2018). Accelerated cooling at the Eocene–Oligocene boundary at 34 mya led to a large floral and faunal turnover across the world, including Asia (Buerki et al. 2013, Sun et al. 2014, Pound and Salzmann 2017). More recently, between 8.5 and 6 mya, drying and global cooling across more temperate regions (Herbert et al. 2016) was associated with a shift from forest to grassland in the western Himalaya (Badgley et al. 2008) and apparently importantly affected both plant dispersal and speciation at higher elevations in the Himalaya and southern China (Zhao et al. 2016, Xing and Ree 2017, Deng et al. 2018). On the other hand, pollen records imply that lowlands in the east were relatively stable climatically over the past 15 million years (warm and wet throughout the year; Khan et al. 2019). Finally, over the past 2 million years, particularly during glacial maxima, forests were likely to have been greatly reduced in the northwestern Himalaya, restricting many species of the Himalaya to more climatically stable and tropical regions to the east (Owen et al. 2002, Mehrotra et al. 2005, Vögeli et al. 2017, Srivastava et al. 2018). In summary, the northwestern Himalaya appears to have suffered more climatic fluctuations over the past millions of years, as well as greater directional trends in both cooling and drying, than the more tropical east. These

are patterns consistent with temperate and tropical history globally, which has resulted in a steepening of climatic gradients across latitudes at least over the past 15 million years (Herbert et al. 2016). The pattern of climate change sets up conditions for the temperate regions of the Himalaya to contain relatively few species as a non-equilibrium consequence of past history.

In this paper, we evaluate the history of present-day angiosperm species assemblages across the entire Himalaya, focusing on contributions from evolutionary history and current climate to richness patterns. We have four specific goals:

1. To build the first comprehensive assessment of the distribution of angiosperm species across the Himalaya. For plants, the eastern Himalaya is thought to be one of the most species-rich locations in the world, declining toward the northwest (Kreft and Jetz 2007), as is the case in well-studied animal groups (Orme et al. 2005, Price et al. 2011, Jenkins et al. 2013). For plants, this inference has been based on interpolation across a few sites (Kreft and Jetz 2007).
2. To evaluate correlates of present-day species richness patterns with climatic variables and potential interactions among life-forms (trees, shrubs, herbs).
3. To evaluate the evolutionary history of angiosperm assembly across climates and regions by assessing phylogenetic structure, notably phylogenetic clustering (i.e., coexistence of closely related species belonging to relatively few lineages) vs. over-dispersion (i.e., coexistence of distantly related lineages, each of which has shown relatively little radiation).
4. To compare patterns in different life-forms (trees, shrubs, and herbs) to ask how and why they differ and how one life-form may influence another in affecting phylogenetic clustering and species richness.

## MATERIALS AND METHODS

### *Species assemblage data*

Current knowledge on distributions of Himalayan angiosperms is documented in regional floras, which have not been previously compiled

into a single database. Here, we consulted 31 different floras comprising a total of 43 volumes (a list of data sources is in Appendix S1). These floras covered either individual Indian Himalayan states, Bhutan, Nepal, or more local areas within these larger regions. We assessed all species listed in these floras against the updated list of botanical names available from [www.theplantlist.com](http://www.theplantlist.com) (The Plant List 2013), which resulted in the elimination of >3000 synonyms. We removed 1593 species considered to be aliens, according to either the floras or online plant distribution databases. This left a total of 8765 angiosperm species belonging to 1912 genera in 210 families (Data S1). Each species was assigned a life-form (i.e., herb, shrub, tree, liana). Given current state of knowledge and the way the floras have been compiled, geographical ranges can only be assigned coarsely to one of six distinct regions, which are, from east to west, as follows: Arunachal Pradesh, Bhutan plus Sikkim and adjoining hill districts of West Bengal (henceforth the Bhutan region), Nepal, Uttarakhand, Himachal Pradesh, and Jammu and Kashmir (Fig. 1a). Each region spans an elevational gradient from about 400 m in the northwest and 100 m in the east, up to permanent snow. Note that our analysis reflects the state of knowledge of Himalayan plant distributions, and hence, the regional pools are of necessity defined by political boundaries, because that reflects the way floras have been compiled. A possible issue is the impact of human disturbance, especially recent disturbance, on species distributions. This may be more of a problem when analyses are based on sampling of local sites (Carpenter 2005, Shoener et al. 2018, Rana et al. 2019). Here, we base our analysis on compilations of entire regions based on compiled records over more than 100 yr. The extent to which upper and lower limits have been affected by human transport or habitat conversion is unknown, but we assume it is likely to apply to a relatively small proportion of the almost 9000 species we study.

We compiled species elevational ranges for each region separately based on the minimum and maximum elevations reported in all floras for that specific region. In some cases, a species elevational range was not reported in one region and then we substituted the elevational range from the adjacent region. Although many of the

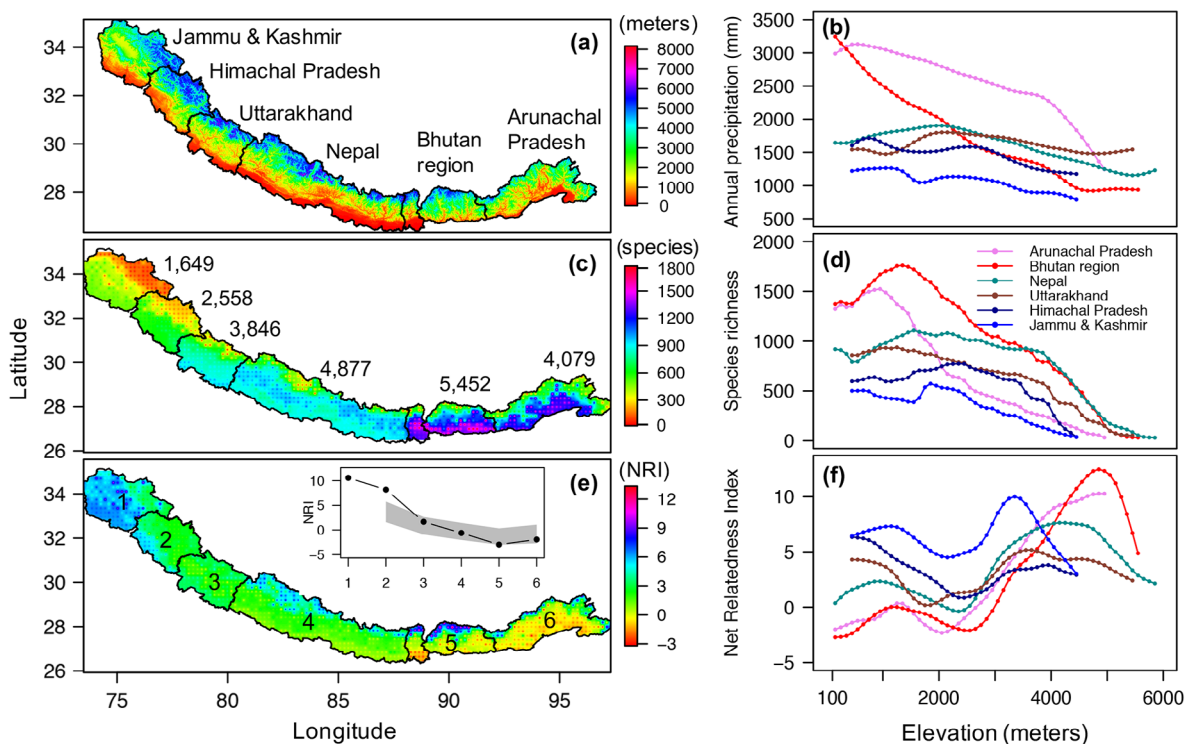


Fig. 1. (a) Digital elevation model of the Himalaya with boundaries of the six regions over which information is collapsed. (b) Elevational pattern of annual precipitation, from the CHELSA dataset (Karger et al. 2017). (c) Species richness map for all angiosperms; the total in each region is given above the region. (d) Elevational patterns of species richness. (e) Net relatedness index (NRI) map; the inset graph shows total NRI in each region, with the shaded bands indicating the 2.5th and 97.5th percentiles based on resampling of 1649 species (the number in Jammu and Kashmir) 1000 times without replacement. (f) Elevational patterns of NRI. The species and NRI maps are smoothed by the inverse distance weight spatial interpolation technique (Lu and Wong 2008) based on the values assigned to 1140 grids at  $0.2^\circ$  resolution.

floras include species from low elevations, the actual area of low elevation spanned by each of the six regions is relatively small. Because of this and limited sampling, many species have ranges that extend lower than are recorded in the floras, which specifically describe species in the Himalayan states (Grytnes and Vetaas 2002, Rana et al. 2019). To correct for this, we cross-checked all species for their presence in the Indian plains based on information in online plant databases (Appendix S1) and modified the lowest ranges of the species accordingly. We divided each of the six regions into 100-m elevational bands. For each band in each region, a species was considered present if its elevational range at least partly overlapped the band, and a presence/absence matrix was built. We retained all bands which

had at least 30 species for further analysis. This resulted in a total of 296 bands.

#### Phylogenetic analysis

We used the most inclusive, updated, and time-calibrated phylogeny of seed plants (acronym GBOTB; Smith and Brown 2018) as a backbone and applied the V.PhyloMaker function (Jin and Qian 2019) in R (R Core Team 2018) on the focal checklist of 8765 native angiosperm species to generate a species-level phylogenetic tree. A total of 3485 species were present in the backbone tree, which is 40% of all the native species documented for the Himalaya. All 210 families and 1700 of the 1912 genera were present on the backbone tree, and another 106 are closely related to genera present in the backbone tree

and were attached to these genera as sisters. Thus, 94.5% of the genera and all families in this study were resolved in the phylogeny. The remaining species and genera were added as soft polytomies at the base of respective genus or family to which they belong.

We used three metrics to quantify phylogenetic structure of each assemblage (i.e., a 100-m elevational band within one of the six regions). We focus on the net relatedness index (NRI). This index is derived from the average distance between all pairs of species in an assemblage (the mean phylogenetic distance), which Oliveira et al. (2016) showed by simulation to be relatively invariant to species richness. Net relatedness index is the standardized version of the mean phylogenetic distance, which subtracts the expected value and divides by the standard deviation, based on random draws of species across the entire phylogeny, and then reverses the sign (Webb et al. 2002). Hence, NRI is a richness-standardized index. A positive value for NRI implies clustering (i.e., few, recently diversified lineages), whereas a negative value implies over-dispersion (i.e., many ancient lineages, each of which is relatively little diversified). We calculated NRI using the R package *PhyloMeasures* (Tsirogiannis and Sandel 2016). We used the complete Himalayan flora as the species pool and a uniform null model against which to assess significance of the statistic. This considers species are drawn with equal probability from the entire pool to build up the same richness as the focal assemblage. To ask if the phylogenetic measures are driven by patterns of richness rather than a property of region per se, we took the number of species in least speciose region (Jammu and Kashmir, 1649 species) as a baseline. For each of the other regions, we drew 1000 samples of 1649 species randomly selected from each regional species pool without replacement and computed the 2.5th and 97.5th percentiles on the NRI statistic generated from these samples. A similar statistic is NTI (nearest taxon index), which is based on the average distance between each species and its closest relative. We found NRI and NTI to give similar results and report only NRI here.

Phylogenetic diversity (PD) is the total branch length connecting all species in the assemblage and hence combines both richness and branch length into a single statistic (Faith 1992).

Phylogenetic diversity can be standardized as the phylogenetic diversity index (PDI) by subtracting the mean value and dividing by the standard deviation, based on random draws across the phylogeny. Thus, PDI is a richness-standardized index, which is negatively correlated with NRI in the data (Appendix S2: Table S1). We calculated PDI in the R package *PhyloMeasures* (Tsirogiannis and Sandel 2016) with a uniform null model and the complete Himalayan flora as the species pool. We used PDI as a measure of phylogenetic richness. For our third statistic, we obtained stem ages of all families according to a global phylogeny of Smith and Brown (2018). The mean family age of each assemblage was calculated as the sum of family ages of all species in the assemblage divided by the number of species in the assemblage. Low values for mean family ages roughly correspond to high clustering (Appendix S2: Table S1). Because NRI measures phylogenetic relatedness across the whole phylogeny under question (i.e., based on mean pairwise distance) whereas PDI is a tip-weighted phylogenetic index (Mazel et al. 2016) and mean family age does not account for age variation among genera within a family, our main analyses were based on NRI.

We assessed elevational species richness and NRI separately for three different life-forms (i.e., trees, shrubs, and herbs). We did not analyze lianas in this way because of their low species richness and absence in many assemblages. For each life-form, we based the NRI calculations on the Himalayan phylogeny pruned to contain just the life-form in question ( $N = 1083$  tree species, 1256 shrub species, 5904 herb species).

#### *Climate data*

Annual mean temperature and annual precipitation are considered the most important climate variables that determine plant distributions (Whittaker 1975). Thus, we used these two climate variables in this study. Minimum temperature is potentially a more important influence on a species persistence than the annual mean but is captured by the mean (mean temperature is correlated with both minimum temperature of coldest month and quarter;  $r = 0.99$  for both variables). However, temperature range, a measure of seasonality, is weakly correlated with mean temperature ( $r = 0.27$ ). We did not include

it in our analyses, because similar ranges are found in dry low-elevation locations that never freeze, as well as in wet high-elevation locations that regularly freeze, and in the northwest mid-elevations, they are the least variable (Appendix S2: Fig. S1). Climate data were obtained from two datasets, CHELSA version 1.2 (<http://chelsa-climate.org>, Karger et al. 2017) and WorldClim version 2.0 (<http://www.worldclim.org>, Fick and Hijmans 2017). These datasets have been generated differently, CHELSA on the basis of climate modeling (e.g., effects of topography on precipitation) and WorldClim using interpolation between climate stations. We used the coordinates of all pixels at 90 m resolution DEM (<http://srtm.csi.cgiar.org>) to extract annual mean temperature (Bio1) and annual precipitation (Bio12) for the six Himalayan regions and, separately for both datasets, calculated average values for every 100-m elevational band in each region. Both datasets are consistent in showing a more or less continuous decline in average precipitation with elevation in the east, and a low-elevation plateau in the west (Fig. 1b for CHELSA, Price et al. 2011, Rana et al. 2019 for WorldClim), but CHELSA precipitation is more variable at a given elevation (see Fig. S5 in Rana et al. 2019). Both datasets gave similar results. We report those from CHELSA in the main text and provide supplemental figures for analyses based on WorldClim.

### Structural equation models

Arunachal Pradesh was omitted from all analyses, because we infer it to be poorly sampled. We used structural equation models (Kline 2015) to disentangle effects of current climate and evolutionary history on patterns of species richness. The models we employed are concerned only with linear effects, despite the presence of hump-shaped richness patterns along elevation in some cases. We take this approach because a priori hypotheses for the effects of climate, history, and competitors all assume monotonic increases or decreases with each variable, at least over the range present in our dataset (Rana et al. 2019). For example, under a historical hypothesis, more phylogenetically clustered communities are expected to be associated with lower species richness, and under a climate hypothesis, more species are expected to be found in warmer

temperatures once precipitation is controlled for. Kluge et al. (2017) suggested a quadratic relationship with temperature might explain plant species richness patterns across an elevational gradient in Bhutan, but the mechanism by which this might arise is unclear, and in general, warm wet areas have more species globally (Kreft and Jetz 2007, Ricklefs and He 2016). Note that even with linear models, hump-shaped patterns may result from combinations of variables working in opposite directions along gradients, if they interact.

We recorded longitude on a scale of 1 in the east (Bhutan region) to 5 in the west (Jammu and Kashmir). Ideally, one would wish to separate climate from elevation and longitude, because physical barriers may influence movement and hence potentially richness patterns. However, longitude and topography together explain 99% of the variance in annual mean temperature (Appendix S2: Fig. S1). This means temperature cannot be statistically separated from the combined effect of elevation and longitude. Hence, when evaluating elevation and longitude as contributors to the pattern, we included precipitation, but not temperature, in the model. For climate specifically, we built two models. The first is that precipitation and temperature alone affect species numbers, and the second is that precipitation and temperature affect phylogenetic clustering and that precipitation, temperature, and phylogenetic clustering all affect species numbers.

Before running the models, we transformed all variables to have unit variance. All bands with at least 30 species were included ( $N = 247$  bands). Akaike's information criterion values are commonly used to evaluate alternative models, but it is difficult to obtain the appropriate degrees of freedom in computing the likelihood, given adjacency along elevational gradients, and lumping longitude into five bins. Hence, we focus on total variation explained ( $R^2$ , effect size). We used the R package lavaan (Rosseel 2012) for these analyses. Similar procedures were followed separately for trees, shrubs, and herbs, except that we added putative dominant life-forms as an independent variable (i.e., we included trees as a predictor of shrubs, and trees and shrubs as predictors of herbs). In these cases, we restricted the analyses to elevational bands containing at least 5 species of the focal life-form.

## RESULTS

### *Species richness*

Species richness in the Himalaya varies along elevational, latitudinal, and longitudinal gradients (Fig. 1c, d). The Bhutan region in the east has the highest documented richness (5452 species), which decreases monotonically more than threefold to the northwest (1649 species in Jammu and Kashmir). However, the easternmost region, Arunachal Pradesh, has fewer species recorded than the Bhutan region (4079). We believe this reflects under-sampling, given it is more than twice the size of the Bhutan region and is apparently more tropical in climate. This inference is supported by its high value of PDI, implying older lineages have been sampled, but close relatives have not (Appendix S2: Fig. S2a, inset). Along elevational gradients, species richness peaks between 1000 and 2000 m in the eastern Himalaya but follows a more or less low-elevation plateau up to 3000 m in the northwest (Fig. 1d).

### *Phylogenetic structure measures*

Phylogenetic clustering increases from east to northwest across regions (Fig. 1e, f). High clustering in Jammu and Kashmir is confirmed with an analysis based on 1000 random subsamples without replacement taken from each region to match the numbers in Jammu and Kashmir (Fig. 1e, inset). Across elevational gradients, proceeding from the base, NRI shows a bimodal pattern, with a pattern of over-dispersion at mid-elevations, that is, ~2000 m (Fig. 1f; Appendix S2: Fig. S3), and relatively more clustering above and below. The highest phylogenetic clustering of all is around the treeline both in Jammu and Kashmir (~3400 m) and in Bhutan (~4500 m; Fig. 1f, Appendix S2: Fig. S3). The very highest elevations with less than 100 species (>4000 m in Jammu and Kashmir, >5000 m in Bhutan) show a decline in clustering.

Spatial patterns of PDI are broadly consistent with those of NRI (Appendix S2: Figs. S2b and S4). Phylogenetic diversity index is lowest above treeline, and hence reaches a minimum at higher elevations in the east (Appendix S2: Fig. S4), at essentially the same points where NRI is especially high. Mean family age shows a somewhat different pattern, being more or less uniform in

the west to about 3000 m, but high in the east, declining to northwest values only by about 3000 m (Appendix S2: Fig. S2d).

### *Phylogenetic structure and current climate as predictors of species richness*

Because of the apparent under-sampling in Arunachal Pradesh, we restrict subsequent analyses to the five regions from the Bhutan region westward. Longitude and elevation together explain 77% of the variance in species richness. Adding precipitation to the model increases the variance explained by 5% (Fig. 2a). Temperature and precipitation alone explain 73% of the variance in species richness, with precipitation having the greater effect (Fig. 2b). Assemblages in dry and, to a lesser extent, cold environments contain few species.

Elevation and longitude explain only 29% of the variance in NRI (Fig. 2c), whereas precipitation on its own explains 53% of the variance in NRI (Fig. 2d). Species assemblages in dry environments are more phylogenetically clustered. Net relatedness index affects species richness in the way expected if historical non-equilibrium effects have been important, because more clustered communities, that is, those consisting of relatively few old lineages, are associated with low richness (Appendix S2: Table S1, Fig. S5), even after climate effects are accounted for (Appendix S2: Fig. S2). However, the standardized path coefficient is low (−0.12) and the historical effect explains a smaller fraction of the variance in species richness when the climate variables are accounted for than does climate when NRI is accounted for (Appendix S2: Fig. S2d).

### *Differences among plant life-forms*

We first compared the Bhutan region and Jammu and Kashmir, because these regions are relatively well sampled and lie at the extremes (the other regions are described in Appendix S2: Figs. S6, S7). Note, however, that patterns in Jammu and Kashmir are somewhat affected by the Vale of Kashmir, covering ~4000 km<sup>2</sup> at ~1500 m (Fig. 1a). In both regions, shrubs tend to peak in richness just beyond the tree richness peak, and herb richness shows a slowing rate of decline toward treeline (Fig. 3a, b). Considered separately, all life-forms have a higher NRI in the

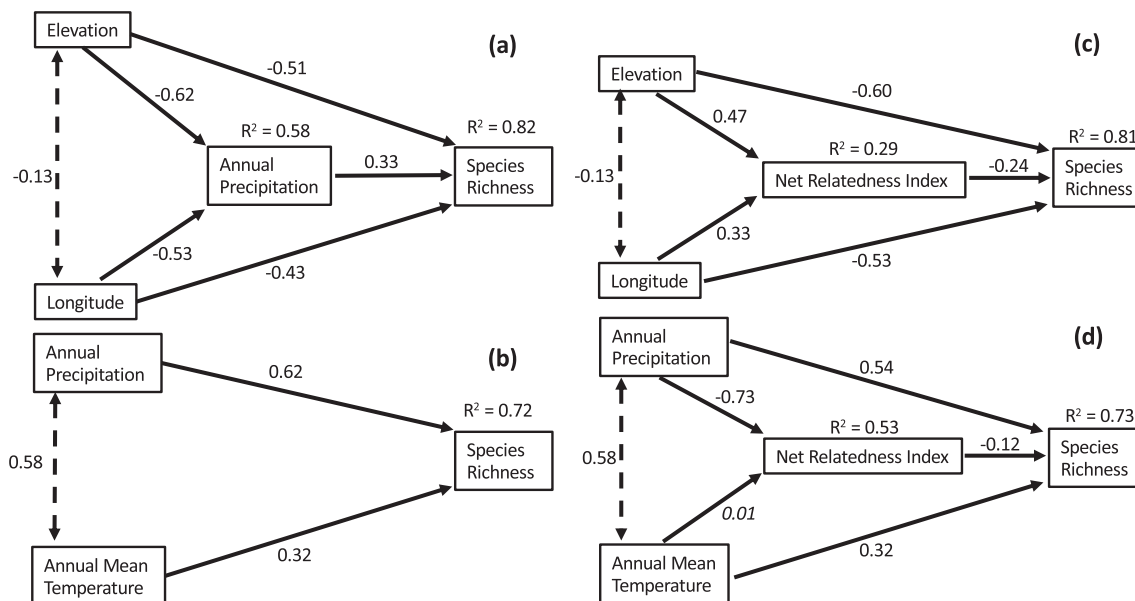


Fig. 2. Structural equation models showing effects of climate (data from CHELSA; Karger et al. 2017) and geography on species richness and the net relatedness index for the region from Bhutan through Jammu and Kashmir in the Himalaya. Only elevational bands with at least 30 species in total are included ( $N = 247$ ).

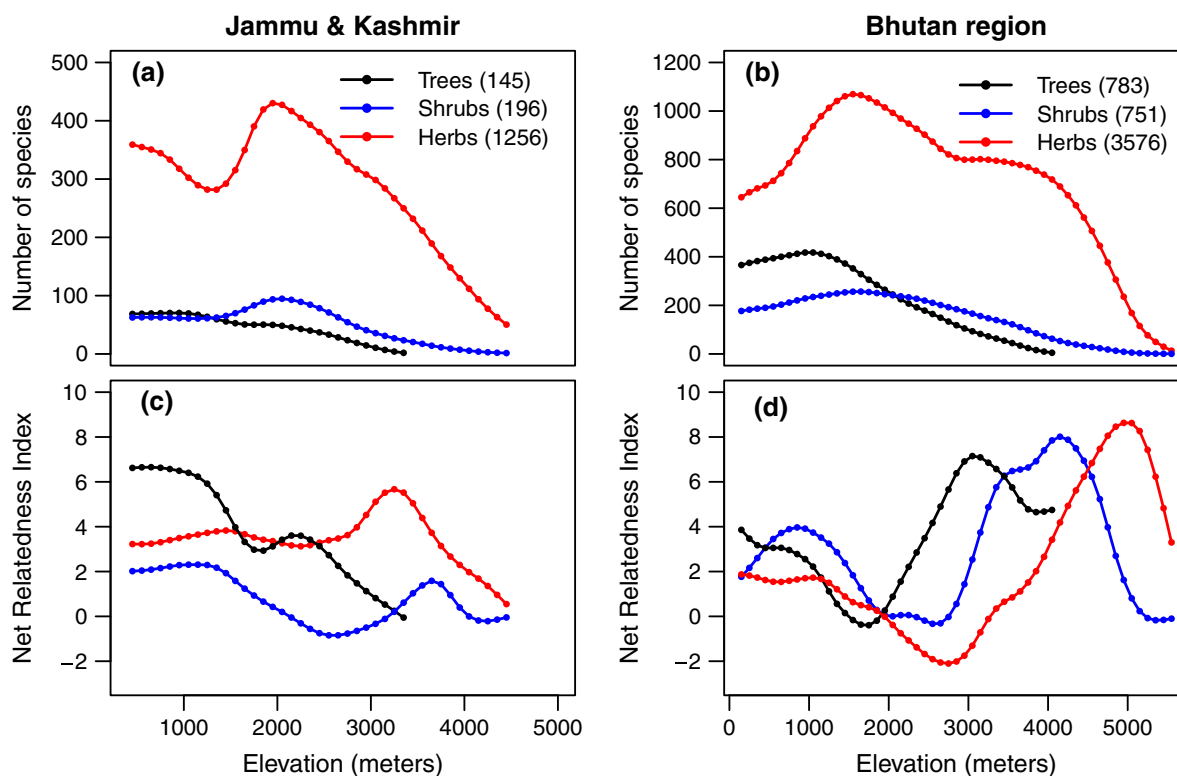


Fig. 3. Species richness and the net relatedness index along the elevational gradients in the Bhutan region and Jammu and Kashmir for three different life-forms, that is, trees (black), shrubs (blue), and herbs (red). Only elevational bands with at least five species are shown.



northwest than in the east; that is, they are more phylogenetically clustered overall (Fig. 3; Appendix S2: Fig. S7). Net relatedness index across elevations for each life-form roughly matches that of angiosperms in total (compare lower panels of Fig. 3 with Fig. 1f), although the positions of turnover vary. Specifically, shrubs, herbs, and trees all tend to be over-dispersed at middle elevations (1500–2800 m depending on group and region). For each life-form except trees in Jammu and Kashmir, clustering increases as one goes to higher elevations and reaches a maximum between 3000 and 5000 m. At even higher elevations, as species richness declines to below about 50–100 (again depending on group and region), assemblages become less clustered. At these elevations, species:genus ratios are low (Appendix S2: Figs. S8, S9).

Including all five regions from Bhutan (in the east) to Jammu and Kashmir (in the west) in structural equation models, within all life-forms, precipitation and temperature are both correlated positively with richness (Figs. 4, 5a, b), as is the case for all groups combined (Fig. 2). However, trees appear to facilitate shrubs, and shrubs facilitate herbs, once climate is accounted for (Fig. 5c). Trees have a negative effect on herbs ( $r = -0.41$ ). In summary, after controlling for climate, in locations with many tree species we tend to find more shrub species, but relatively fewer herb species.

Variance in NRI explained by climate is lower than in the combined dataset (trees, 34%; shrubs, 1%; herbs, 21%) but in the same direction; that is, more clustered assemblages have fewer species (Figs. 4, 5; Appendix S2: Fig. S5).

### DISCUSSION

Our data show that the eastern Himalaya contains approximately three times more species than the northwestern Himalaya, consistent with inferences from a global assessment (Kreft and Jetz 2007). The threefold difference is especially apparent at lower and higher elevations (e.g., at 300 and 2500 m, which both have about 700 species in the northwest and 2000 species in the east; see Fig. 1d), but increases to an almost fourfold difference at mid-elevations (1000–2000 m), because of a species richness peak in the east at these elevations. Among different life-forms, trees show a fivefold decline from the east (Bhutan) to the northwest (Jammu and Kashmir), whereas shrubs and herbs both show a threefold decline. Possibly this reflects poor documentation and incomplete knowledge of shrubs and herbs in the eastern Himalaya. Clearly, Arunachal Pradesh is under-sampled, and we may expect under-sampling to be less of an issue for trees than for other life-forms. For the majority of the analyses, we have not included Arunachal Pradesh. We first consider

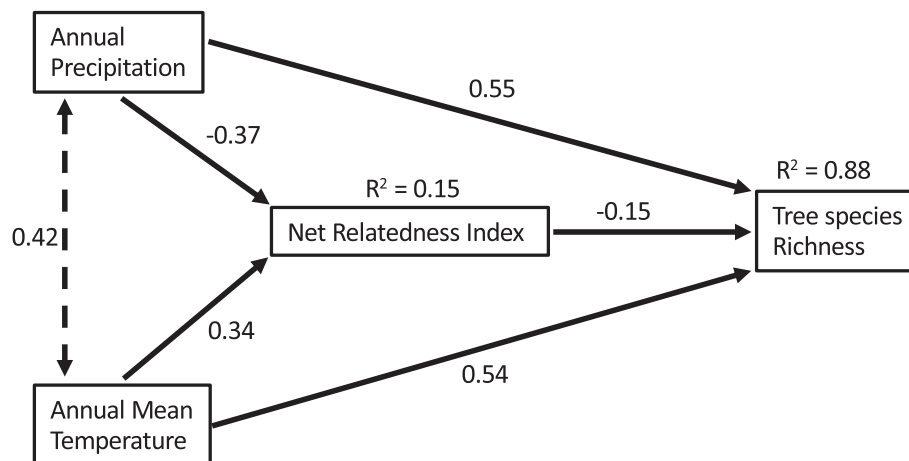


Fig. 4. Structural equation model showing the effects of climate (data from CHELSA; Karger et al. 2017) on tree species richness and net relatedness index for the region from Bhutan through Jammu and Kashmir in the Himalaya. Only elevational bands with at least five tree species were included in the analysis ( $N = 179$ ).

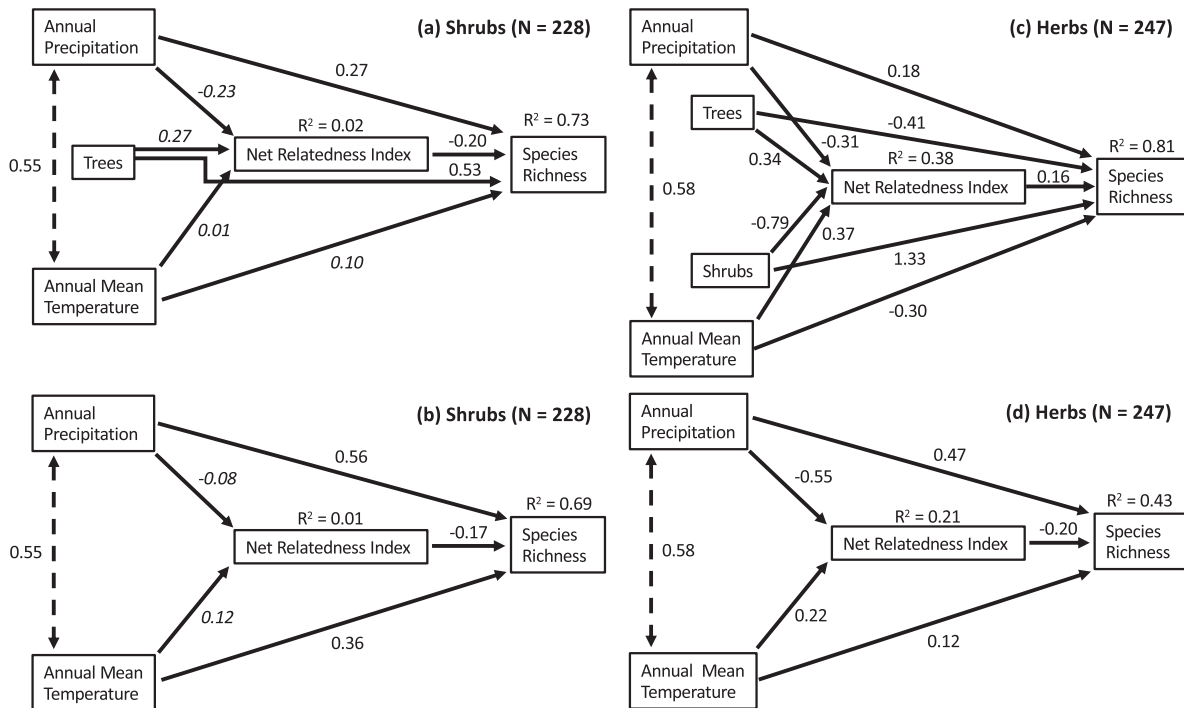


Fig. 5. Structural equation model showing the effects of climate (data from CHELSA; Karger et al. 2017) on species richness and net relatedness index of shrubs and herbs for the region from Bhutan through Jammu and Kashmir in the Himalaya. Only elevational bands with at least five species of the given life-form were included (shrubs:  $N = 228$ ; herbs:  $N = 247$ ).

present-day determinants of richness and, second, how historical processes of diversification and dispersal might contribute to richness patterns.

**Climate and competition**

Spatial variation in total angiosperm richness is well predicted by climate. Warm, wet areas generally contain more species than cold, dry areas. However, all life-forms, except for trees in the northwest, show richness peaks at mid-elevations in both the east and the northwest (Fig. 3). The patterns are less pronounced in the northwest, where instead richness might be considered to be a plateau from the lowest elevations to above 2000 m, more or less corresponding to precipitation. The largest mid-elevation richness peak is that of herbs in the Bhutan region, with 400 more species inferred to be present at 1800 m than at the mountain base, and we focus on this pattern. The base is thought to be both warmer and wetter, and might therefore a priori

be expected to have high species richness. Various artifacts, such as under-sampling at range edges (Grytnes and Vetaas 2002, Karger et al. 2011), seem unlikely to account for such a large difference, especially as we checked each species for its occurrence in the plains of India.

The herb mid-elevation peak in the Bhutan region may reflect the location that can accommodate more herbs than elsewhere, as a consequence of both abiotic and biotic present-day conditions. One obvious reason for this could be that trees at lower elevations dominate herbs and shrubs, for example, by shading, which acts to reduce species richness in these groups. While such asymmetric competitive effects may be a factor, previous studies have found mean tree height and density to vary idiosyncratically along the elevational gradient and not be correlated with tree species richness (Rana et al. 2019, their Fig. S13), and foliage density (i.e., the number of leaves that would be intersected by a pole extending from the ground up) to be roughly the

same from the lowest elevations up to 2000 m (Price et al. 2011). Further, when climate effects are controlled for, we could find little evidence that tree species richness is negatively correlated with herb and shrub richness (Fig. 5). Indeed, tree richness appears to be a facilitator of shrub richness, and shrub richness, a facilitator of herb richness. Seemingly contradicting this finding, fieldwork in the eastern Himalaya has shown that in small plots, herbs peak at the point where shrubs decline (Bhatta et al. 2018); we also found that the decline in herbs shallows at this point (Fig. 3). In our dataset, the positive correlations between trees and shrubs, and between shrubs and herbs, may reflect underlying associations with benign conditions not captured by the climatic variables we studied, but alternative hypotheses based in dispersal and diversification are also possible (see below). Once shrubs and climate are both included in the model, trees do have a negative effect on herbs (Fig. 5c), consistent with competitive effects.

#### Phylogenetic patterns

Yan et al. (2013) presented an analysis of the adjacent Qinghai–Tibetan Plateau, most of which lies above 4000 m, but they included a section adjacent to northeast India that extends below 1000 m. They found a general increase in clustering with elevation, but at a slower rate at mid-elevations. By contrast, Shooner et al. (2018) found a weak tendency for trees sampled on 500- to 5000-m<sup>2</sup> plots in Arunachal Pradesh to be more phylogenetically clustered at low elevations. Our findings may reconcile these observations because we show clustering does not monotonically increase from the lowest to highest elevations. First, across all gradients for all angiosperms, in both the east and northwest, middle elevations (1500–2500 m) tend to be more phylogenetically over-dispersed (less clustered) than just above or below. This is approximately the case within each life-form. Notably in the east, each life-form shows the greatest over-dispersion at mid-elevations: 1700 m (trees), 2700 m (shrubs), and 2800 m (herbs). The pattern may be accounted for by dispersal and/or diversification dynamics. Dispersal of distinct floras from above and below (i.e., mixing) should elevate phylogenetic clustering (e.g., see Fritz and Rahbek 2012 for a similar argument with

respect to global patterns in Amphibians). For trees, the highest over-dispersion (1700 m) is at about the line of regular freezing (White et al. 2019), associated with a steep decline in the number of species that belong to primarily tropical genera (Rana et al. 2019). For herbs and shrubs, we suggest this may reflect contributions of families above treeline (~4000 m) that contain representative species extending down to 2700 m.

Apart from mixing, diversification dynamics should affect metrics of clustering. For all angiosperms combined, the lowest values for NRI anywhere in the Himalaya are at the lowest elevations in the east (see red line in Fig. 1f). As reviewed in the introduction, according to climate reconstructions the lowest elevations in the east have been climatically stable over millions of years. The over-dispersed pattern is consistent with a long period of accumulation and little turnover at the low elevations in the east. The most phylogenetically clustered assemblage anywhere is also in the east, at about 4400 m, which is close to treeline. Relatively few old lineages are present at these locations, and they subtend many species (e.g., *Rhododendron*; Xing and Ree 2017), with diversification likely as a response to climate upheavals over millions of years, as well as associated range fragmentation. High elevations in the Himalaya experience temperate climates, continuously connected by land to high latitudes, so these findings are consistent with the findings of high phylogenetic clustering of trees at high latitudes (Qian and Ricklefs 2016). Furthermore, ongoing turnover in harsh environments may explain the relatively high clustering in the drier northwest when compared to the east.

At the very highest elevations, where species numbers fall below 100, a pattern of relative over-dispersion reappears. Lineages appear to have persisted through climate upheavals, perhaps expected given an inferred long presence of exceptionally high elevations in the region (Spicer 2017), but this has been associated with low recent speciation rates, at least among species comprising a local assemblage. In summary, a possible explanation for the general increase in phylogenetic clustering toward treeline reflects increasing fluctuations in climate over time, with many opportunities for speciation and extinction, that the blip creating phylogenetic over-dispersion at mid-elevations is the consequence

of mixing of different floras, and low clustering at the base and very highest elevations reflects low turnover in more stable environments.

#### *Present-day vs. historical influences on species richness*

In equilibrium models, different climate regimes accommodate different numbers of species, whereas in non-equilibrium models, dispersal and diversification dynamics differ because of differences in climatic history and geographical differences in accessibility. The difficulty in separating these alternatives, which applies more widely across the globe (Rabosky and Hurlbert 2015), is that regions inferred to have been historically subject to exceptional species loss are correlated with present-day harsh climates, including in our case the drier northwest and higher elevations: When the world cools down or dries out, these regions become exceptionally inhospitable.

In our case, species-poor locations indeed contain assemblages that are relatively more phylogenetically clustered than elsewhere, which is consistent with non-equilibrium diversification dynamics as a cause of low richness (the correlation of NRI with species richness is  $r = -0.64$ ; Appendix S2: Table S1), but NRI also correlates with temperature ( $r = -0.43$ ) and precipitation ( $r = -0.73$ ) and, hence, the correlation of NRI with richness may arise because cooler and drier locations can accommodate fewer species than warmer and wetter ones, illustrating the difficulty highlighted by Rabosky and Hurlbert (2015). Nevertheless, structural equation models demonstrate that once climate is accounted for, both across all angiosperms and within each life-form separately, NRI is weakly negatively associated with species richness (Fig. 5a–c). Together these results imply some role for history in determining not only the phylogenetic structure of an assemblage, but also the number of species in it. That in turn supports the idea that climatically harsh regions are further from any sort of equilibrium because of high extinction and limited dispersal into these climatic zones, with speciation in an ongoing process of recovery.

#### CONCLUSIONS

Our results confirm the general finding that harsh environments with relatively few species

tend to be phylogenetically clustered, attributable to the ability of relatively few lineages to cross various climatic barriers (Qian et al. 2013, 2016, Patrick and Stevens 2016). This applies equally to trees, shrubs, and herbs. The extent to which species richness in these environments is limited by patterns of extinction, recolonization, and speciation or is a consequence of a limited carrying capacity (Marks et al. 2016) remains unclear, but it seems likely that both contribute. The importance of current climate conditions on species richness patterns within each life-form, and the relatively low contribution that NRI makes to overall richness patterns suggest an important upper limit on species richness is set by general harshness of the environment.

#### ACKNOWLEDGMENTS

We thank Songlin Fei and two anonymous reviewers for helpful comments. S.K.R. was supported during the study by National Mission on Himalayan Studies Fellowship program (Grant No.: GBPI/NMHS/HF/RA/2015-16) funded by the Ministry of Environment, Forest and Climate Change, Government of India. We thank G.S Rawat for his support during this study.

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### DATA AVAILABILITY

All data sources are shown in Appendix S1, and the complete dataset is available in Data S1.

### SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2945/full>