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RESEARCH ARTICLE

Gymnosperm species richness patterns along the elevational gradient and its comparison with other plant taxonomic groups in the Himalayas

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Abstract.

Phylogenetic constraints on ecophysiological adaptations and specific resource requirements are likely to explain why some taxonomic and functional groups exhibit different richness patterns along climatic gradients. We used interpolated species elevational distribution data and climatic data to describe gymnosperm species richness variation along elevational and climatic gradients in the Himalayas. We compared the climatic and elevational distributions of gymnosperms to those previously found for bryophytes, ferns, and angiosperm tree lineages to understand the respective drivers of species richness. Our study location was divided into three regions: Eastern; Central; and Western Himalayas. In each region, the sum of gymnosperm species richness was calculated over every 100-m elevational band. Using linear regression, we analyzed the relationship between species' elevational mid-point and species' elevational range size to test the Rapoport's rule for gymnosperms in the Himalayas. Generalized linear models were used to test if potential evapotranspiration, growing degree days, and the number of rainy days could predict the observed patterns of gymnosperm species richness. We used the non-linear least squares method to examine if species richness optima differed among the four taxa. We found supporting evidence for the elevational Rapoport's rule in the distribution of gymnosperms, and a unimodal pattern in gymnosperm species richness with elevation, with the highest species richness observed at ca. 3000 m. We also found a unimodal pattern of gymnosperm species richness along both the potential evapotranspiration and growing degree day gradients, while the relationship between species richness and the number of rainy days per year was non-significant. Gymnosperm species richness peaked at higher elevations than for any other plant functional group. Our results are consistent with the view that differences in response of contrasting plant taxonomic groups with elevation can be explained by differences in energy requirements and competitive interactions.

Highlights:

- Different plant functional lineages should be considered separately when attempting to understand basic patterns of plant species diversity and distributions along environmental gradients.

- The factors determining range sizes likely vary among plant functional/taxonomic groups.

- The different functional plant lineages in the central Himalayas exhibit a vertical zonation of maximum species richness.

- Gymnosperm species richness peak at higher elevations, lower mean annual PET values, and at shorter mean annual growing degree days than found for bryophyte, fern, or angiosperm tree lineages.

- Gymnosperm communities exhibited their highest diversity at mid-elevation but exhibited patterns in range sizes predicted by Rapoport's rule.

Introduction

The latitudinal diversity gradient, i.e., the increase in species richness from polar to equatorial regions, a conspicuous feature of global biogeography, has long intrigued biogeographers (Davidowitz and Rosenzweig 1998, Hawkins et al. 2003a, Willig et al. 2003, Qian and Ricklefs 2007, Weiser et al. 2018). Several hypotheses that attempt to explain the latitudinal diversity gradient involve the direct or indirect role of climate in mediating biotic interactions (Pianka 1966, Janzen 1967, Hawkins et al. 2003b, Usinowicz et al. 2017). For instance, climate has been suggested to be an important factor influencing interspecific competition across latitudes (Usinowicz et al. 2017), with its influence mediated by species' intrinsic climatic tolerances (Janzen 1967, Perez et al. 2016). In general, relatively few species tolerate the climatic extremes at higher latitudes and elevations, whereas climatic conditions in the tropical lowlands are less limiting (Huston 1994). Consequently, fewer species can occur at higher latitudes, but they can occupy broader climatic niches due to the lower interspecific competition (Pianka 1989). Conversely, tropical species finely partition resources due to higher interspecific competition, which subsequently results in higher species diversity (Connell 1978). Thus, one way that the interaction between climate and competition is thought to manifest is through species' range size distributions, which also depend on species' intrinsic tolerance to climatic fluctuations.

Rapoport's rule posits that the breadth of species' climatic tolerances broadens as climate seasonality becomes more variable at higher latitudes (Stevens 1989). Since species richness and range sizes are fundamental aspects of ecology, their relationship with latitudinal gradient –as hypothesized by Rapoport's rule– has garnered considerable attention, but mixed support. Inconsistent results among taxonomic groups and the localized nature of the predicted patterns have fueled debate on the status of Rapoport's rule (Rohde 1996, Gaston et al. 1998). However, departures from the hypothesized positive relationship between latitude (or elevation) and species range size, as predicted by Rapoport's rule, may simply result from non-unidirectional climatic gradients within a species range (Pintor et al. 2015). It is noted that latitudinal and elevational gradients in species richness patterns may be explained by similar factors (Currie 1991, Rohde 1992, Grytnes and Vetaas 2002, Kreft and Jetz 2007, De Frenne et al. 2013, Guo et al. 2013, Lee et al. 2013). Different species and functional groups may vary in the degree to which they exhibit Rapoport's rule because they possess unique behavioral or ecophysiological adapations that allow them to decouple their metabolic processes from climatic conditions (Bond 1989, Feng et al. 2016, Michaletz et al. 2016). For example, some plants are capable of elevating their leaf temperatures above ambient air tempeaures (Meinzer and Goldstein 1985) or lowering them (Smith 1978) to facilitate optimal tissue temperatures for photosynthesis.

Indeed, phylogenetic constraints on ecophysiological traits and specific resource requirements are likely to explain why some groups of species exhibit different patterns of richness across coarse climatic gradients (Peters et al. 2016). Within the Himalayan mountain range, different aspects of water–energy dynamics, i.e., a function of maximized water and optimized energy (heat/light), were found to differentially predict species' richness (Bhattarai and Vetaas 2003, Vetaas et al. 2019). Yet, water–energy dynamics could not directly explain the elevational distributions in herbaceous (i.e., forbs, grasses, and herbaceous climbers) species richness (Bhattarai and Vetaas 2003). This supports the notion that patterns and predictors of species richness along elevation gradients may differ among taxa or functional groups. Conversely, at very coarse scales, species richness in temperate regions is thought to be regulated by tolerance to environmental stress and energy input to an ecosystem, while tropical studies emphasize the importance of moisture and related factors (Xu et al. 2016), and competition for resources and space (Wright 2002).

Despite years of study in the Himalayas, fundamental biogeographic patterns, such as the relationship between species richness and elevation, remain unknown for several taxonomic and functional groups. While such patterns are known for angiosperms, ferns, and bryophytes (Bhattarai and Vetaas 2003, Bhattarai et al. 2004, Bhattarai and Vetaas 2006, Grau et al. 2007), such relationships have not yet been studied for gymnosperms. Yet, gymnosperms are important components of terrestrial ecosystems and are among the oldest and largest of all plants (Fragniere et al. 2015). They exhibit traits that allow them to tolerate some of the coldest and driest environments on Earth (Kozlowski et al. 2015). Furthermore, comparing patterns in gymnosperm diversity to patterns in diversity of other plant functional groups can enhance our ability to explain the mechanisms that drive patterns of species distributions across climatic gradients (Grau et al. 2007).

In this study, we used interpolated species elevational distribution data and climatic variables to answer three major questions:

1) How does gymnosperm species richness vary along elevational and climatic gradients in the Himalayas?

2) Do the distributions of richness along climatic and elevational gradients differ among bryophytes, ferns, gymnosperms, and angiosperms?

3) Do gymnosperms follow the distributional patterns posited by Rapoport's rule?

Methods

Study area

Our study area extends ca. 3000 km (70–105°E, 40–25°N) across the northern portion of the Indian subcontinent and encompasses parts of Pakistan, India, Nepal, and Bhutan (Fig. 1). The Himalayan climate is characterized by a dry period during winter, from January to April, and a rainy season during summer, from June to September. A cloud base forms between 1400 m and 2000 m (Bhattarai et al. 2004) and the
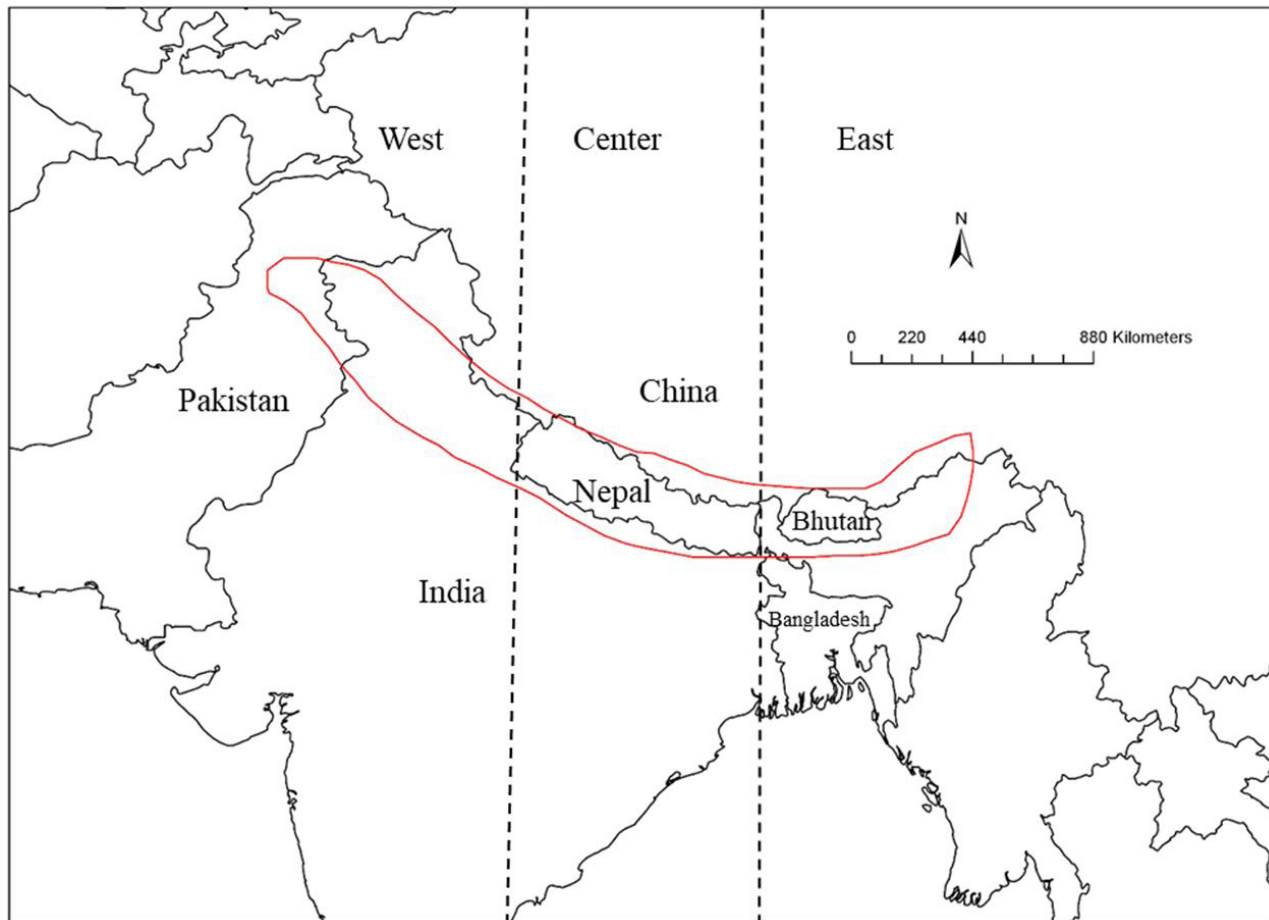
Figure 1. The Himalayan arc (red color) extending from the Nanga Parbat in the west (India) to Bhutan through Namche Barwha (India) in the east and Nepal Himalayas in the middle (map modified from Zurich and Karan, 1999). The Himalayas are divided into three regions: western (west to Nepal); central (Nepal); and eastern (east to Nepal).

elevational temperature gradient follows an adiabatic lapse rate of 0.51ºC per 100 m (Bhattarai and Vetaas 2003). Moisture from the Bay of Bengal causes the heaviest precipitation and monsoonal rains to occur in the eastern Himalayas (Rees and Collins 2006). This east-to-west precipitation gradient influences patterns of vegetation across the whole study area.

Floristic inventories indicate that Himalayan plant communities vary longitudinally across the eastern (India and Bhutan, located approximately from Sikkim to Assam), central (Nepal), and western (located from Kummaun, India, and westward) phytogeographic zones (Banerji 1963, Rees and Collins 2006). Therefore, we divided our study area into three regions: the eastern Himalayas (northeastern India and Bhutan; longitudinal range 89-105º E); the central Himalayas (Nepal, 80-89º E); and the western Himalayas (northwestern India: 70-80º E).

Data sources and species richness calculation

To determine gymnosperm species richness in the Himalayas, we used available checklists based on floristic explorations, herbarium specimens, and several scientific publications from various neighboring countries because there is no published gymnosperm flora for

these Himalayan regions (Table 1). As gymnosperm data sources included the records based on extensive botanical surveys covering whole Himalayas (eastern, central, and western) and national checklists (e.g., Press et al. 2000) prepared from herbarium specimens deposited in major herbaria of Himalayan plants; our data represent the most comprehensive distributional records for gymnosperms in this part of the world. Our gymnosperm species data generally covers the three floristic regions listed above. We only included species occurring between 200 and 4300 m a.s.l. because no gymnosperm species in the eastern or central region are typically found outside of this range. Comparative data for ferns, bryophytes, and angiosperm trees in the central Himalayas were also taken using the same sources, complemented by the data used in earlier scientific publications (Bhattarai et al. 2003, 2004, 2006, Grau et al. 2007).

To examine the relationship between species richness and elevation, we binned each species distribution along the elevational gradient, where each bin represented a 100-meter elevational band. We used a total of 41 bins to cover the entire studied elevational gradient from 200 to 4300 m. The number of species present in each elevation band was calculated

Table 1. Summary of species data sources for gymnosperm and other functional group species in Himalayas.

Region	Country	Citation
Central	Nepal	(Hara et al.1978-1982, Hara 1966)
Central	Nepal	(Press et al. 2000)
Central	Nepal	Department of Plant Resources, Government of Nepal, Godavari, Nepal
Eastern	India, Bhutan	(Ōhashi 1975)
Eastern	India	(Nair 1977)
Eastern	India, Bhutan	(Grierson and Long 1983)
Eastern	India	(Kanjilal et al. 1940)
Western	India	(Osmaston 1927)
Western	India	(Gupta 1928, Singh and Kachroo 1987, Sharma and Jamwal 1988)
Western	India	(Chowdhery and Wadhwa 1984)
Western	India	(Dhaliwal and Sharma, 1999)
Central	Nepal	(Press et al. 2000, Bhattarai and Vetaas 2006)
Central	Nepal	(Bhattarai et al. 2004)
Central	Nepal	(Kattel 2002)
Central	Nepal	(Kattel and Adhikari 1992)

using an established interpolation method (Vetaas and Grytnes 2002, Bhattarai and Vetaas 2006, Grau et al. 2007). This method assumes that each species has a continuous distribution even though a particular species might not have been recorded from each 100-m elevation band. We defined species richness as the total number of species present within each 100-m elevation band.

The data we used derives from extensive collections, surveys, checklists, and several publications of Himalayan flora. While we assume the interpolation method used in our study should reflect the natural distribution of the species and be appropriate for most of the species, we acknowledge that some species may not have continuous elevational distributions (i.e., clumped, disjunct, or otherwise non-normal elevational distributions). Within our dataset there are only 10 or less elevational bands (each band of 100-m) for which there are no records for nine species in the central Himalayas, 15 or less elevational bands for which there are no data for 14 species in the eastern Himalayas, and 15 or less elevational bands for which there are no data for 18 species in the western Himalayas. Systematic species distributional and abundance data that could be used to better understand elevational distributions and determine species' abundance-weighted range centers are not yet available.

Climatic variables

To understand the climatic drivers of species richness in the Himalayas, we used climatic data from 97 weather stations located from 72 to 4100 m a.s.l. in the central Himalayas, with records covering the period 1971–1996 (Department of Hydrology and Meteorology, Government of Nepal). We calculated, for each 100-m elevational band, long-term averages for annual potential evapotranspiration (PET), the annual cumulated number of growing degree days above 5°C, and the total number of rainy days per year – three

important bioclimatic variables related to water–energy dynamics (Woodward 1987) in the central region of the Himalayas. Among these three variables, PET, in mm.yr^{-1}, is an estimate of the potential amount of water released through surface evaporation and transpiration from homogeneous covered vegetation that is well supplied with water (Currie 1991). Potential evapotranspiration is fundamental to water-budget analyses, and it was calculated using the formula from Holdridge et al. (1971): PET = annual mean biotemperature × 58.93. To calculate annual mean biotemperature, negative temperatures were scaled up to zero before calculating the monthly mean temperatures throughout the year (Holdridge et al. 1971). Plant growth typically occurs when temperatures exceed 5°C (Woodward 1987). Therefore, for each 100-m elevation band, we calculated growing days as the number of days per year when daily mean air temperatures exceeded 5°C within that band (Bhattarai et al. 2004). The annual number of rainy days per elevation band was calculated by summing the number of days per year with observed rainfall and then computing the mean over the 25 years covering the study period (1971–1996). Since these climatic data were based on the central Himalayas (Nepal), our investigation on species richness patterns against climatic variables was based on the central region only.

Statistical analysis

We used a generalized additive model (GAM) (Hastie and Chambers 2017) to examine the relationship between gymnosperm species richness and elevation across our three study regions. In general, GAM allows species distribution with respect to climate to determine the shape of the response curves instead of being limited by the assumption of symmetric distribution in parametric regression (Crawley 1993), as it makes no a priori assumptions about the type of relationship being modelled. To test for the "region" effect on gymnosperm species richness along the elevational

gradient, we used the factor variable "region", with three levels (western, central, and eastern), as a main effect in an analysis of covariance (Ricklefs and White 2004).

Then, for gymnosperms as well as for angiosperm trees, ferns, and bryophytes – for comparison purposes – we investigated the relationships between species richness and each of the three above-mentioned climatic variables and elevation. Note that we ran this comparative analysis among taxonomic groups only for the central region where we could get reliable climatic data per 100-m elevational band. We used univariate generalized linear models (GLM) with a Poisson error distribution (McCullagh 2019) and a log-link function to properly assess the relationship between species richness and each of the four studied predictor variables available for the central region: annual mean PET; annual mean growing degree days; the average number of rainy days per year; and elevation. We compared the Poisson-family model to a Gaussian-family model with an identity-link function and assessed the proper error distribution with diagnostic Q-Q plots of the residuals (Hastie and Chambers 2017). The error distributions in both model families were almost indistinguishable from a normal distribution. But we chose the Poisson-family model because the response variable (species richness) consisted of count data (Crawley 2012). Each univariate model was compared to a more complex model including a second-order polynomial term for the focal predictor variable. We used a F-test to check the significance of the difference between these nested models, as this is more robust than the chi square-test when data are over-dispersed (Crawley 2012). All statistical analyses were conducted using R v3.4.3 (R Team 2017).

We used the non-linear least squares (nls) function in R (R Team 2017) to examine if the richness and climatic optima differed among the four functional plant lineages we investigated for the central Himalayas. We randomly resampled each of the four studied environmental variables (PET, growing degree days, number of rainy days, and elevation) 1000 times to generate an estimate of the mean optimum richness for each functional lineage, including a 95% confidence interval. For each iteration we predicted richness as a function of a given environmental variable following the formula for a Gaussian function. The confidence interval for the optimum richness was calculated as the range of values between the lower 2.5 and upper 97.5 percentiles of all 1000 resampled iterations for each environmental variable per functional lineage. These confidence intervals allowed us to check for overlapping richness optima among functional lineages. Richness values for each functional group was log transformed for visual purposes only.

To test for the Rapoport's rule in gymnosperm distribution, we calculated the elevational range and mid-point elevation of each gymnosperm species for all three studied regions (western, central, and eastern). Elevation range was calculated by subtracting the lowest elevation from the highest elevation at which each species was reported. Elevation midpoints were calculated as the mean (corresponding to the median value here) of the highest and the lowest elevational occurrences observed for each species. We used a linear regression model to test for the Rapoport's rule (i.e., the positive relationship between species' elevational mid-point and species' elevational range).

Results

Altogether, there were 53 gymnosperm species reported from the whole Himalayas, of which 30 species were reported from the eastern Himalayas, 29 from the central Himalayas, and 27 from the western Himalayas. Altogether, 33 species were found in more than one region.

In the Himalayas, gymnosperm species richness had a unimodal hump-shaped relationship with elevation, although the maximum gymnosperm species richness tended to be skewed toward higher elevations within the elevational range covered by gymnosperms. Maximum gymnosperm species richness occurred at ca. 3141 m across the study area (Fig. 2). In the eastern and central Himalayas, species richness peaked at 3300 m, while it peaked at 3000 m in the western Himalayas. Yet, the analysis of covariance (region and elevation) showed no significant differences between regions in the location of maximum gymnosperm species richness along the elevational gradient (Table 2).

In the central region, gymnosperm species richness showed significant unimodal relationships with mean annual PET and mean annual growing degree days (Table 3, Fig. 3). In contrast, gymnosperm species richness was unrelated to the average number of rainy days per year (Fig. 4). Similar unimodal patterns between species richness and climatic variables were observed for bryophytes, ferns, and angiosperm trees. However, each functional/taxonomic plant lineage exhibited maximum species richness at different climatic ranges (95% confidence intervals do not overlap, Table 4, Fig. 3), which we term the particular group's climatic optima. For gymnosperms, maximum species richness peaked at a mean annual PET value of 528 mm and at a mean annual growing day of 192 days. Compared to gymnosperms, maximum species richness in other functional plant lineages were observed at lower elevations (below 3000 m) with greater moisture and greater growing degree days (Table 4). For instance, maximum species richness peaked at mean annual PET values of 605 mm, 880 mm and 1073 mm for bryophytes, ferns, and angiosperms trees, respectively (Table 4, Fig. 3). Similarly, maximum species richness peaked at mean annual growing degree days values of 205, 272, and more than 317 days for bryophytes, ferns, and angiosperm trees, respectively (Table 4, Fig. 3).

We found a significant positive linear correlation between mid-point elevation and elevational range of gymnosperms for all three regions (eastern: r=0.58, p-value<0.01; central: r=0.71, p-value<0.01; and western: r=0.65, p-value<0.01) (Fig. 5), as the Rapoport's elevation rule predicts.
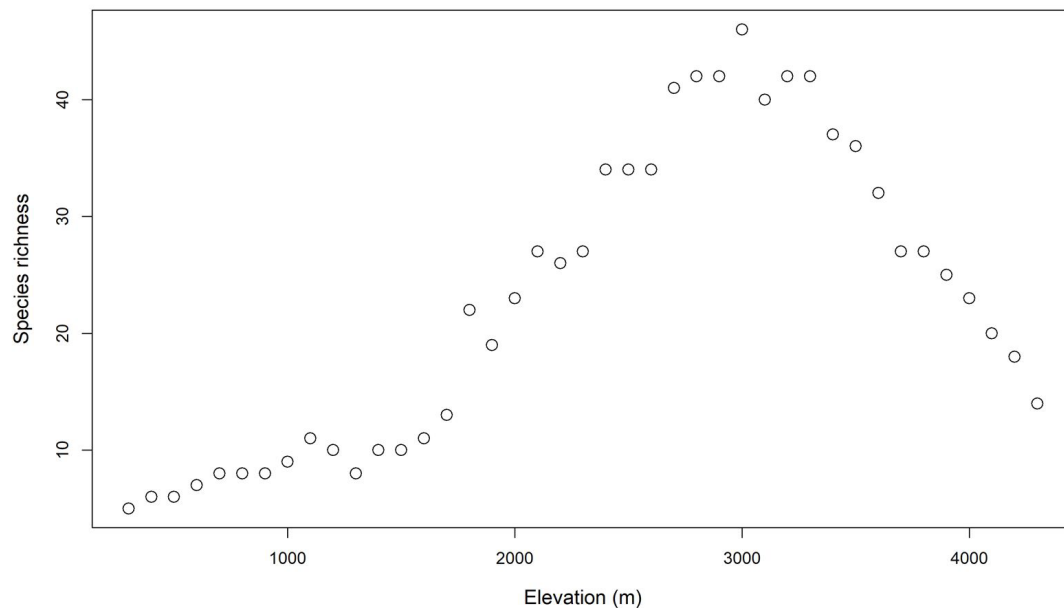
Figure 2. Relationship between gymnosperm species richness (combined for all three regions, i.e., eastern, central, and western) and elevation gradient in the Himalayas. The elevation gradient was divided into 43 bins. Each data point represents interpolated richness for each 100-m elevational band where we counted the total number of species occurring in each bin.

Table 2. Covariance analysis results for gymnosperm species richness patterns along the elevational gradient in the whole Himalayas, region (3 regions) was used as covariate in the model.

Factor	DF	F-value	P-value
Elevation	1	83.95	**<0.001**
Region	2	2.26	0.10
Elevation*Region	2	0.81	0.44
Residuals	117		

Table 3. Summary of univariate generalized linear model analysis of each functional lineage in the central Himalayas when related to elevation and each climatic variable (PET, number of growing days and rainy days). Order 1 and 2 indicate the linear and polynomial order, respectively. The deviance explained indicates the percentage of total deviance.

Taxonomic groups	Climatic Var.	order	D.f.	%-dev. Explained	P-value
Bryophytes	Elevation	2	38	88.62	P<0.001
	PET	2	38	95.75	P<0.001
	Growing days	2	38	79.02	P<0.001
	Rainy days				ns
Gymnosperms	Elevation	2	38	64.24	P<0.01
	PET	2	38	87.45	P<0.001
	Growing days	2	38	93.72	P=0
	Rainy days				ns
Ferns	Elevation	2	38	78.75	P<0.01
	PET	2	38	97.78	P<0.001
	Growing days	2	38	83.94	P<0.001
	Rainy days	1	39	19.32	P<0.01
Angiosperm trees	Elevation	2	38	81.61	P<0.001
	PET	2	38	89.42	P<0.001
	Growing days	2	38	84.96	P<0.001
	Rainy days	1	39	12.98	P<0.05

Climatic var. = Climatic variables, D.f. = Degree of freedom, dev. Explained = Deviance explained
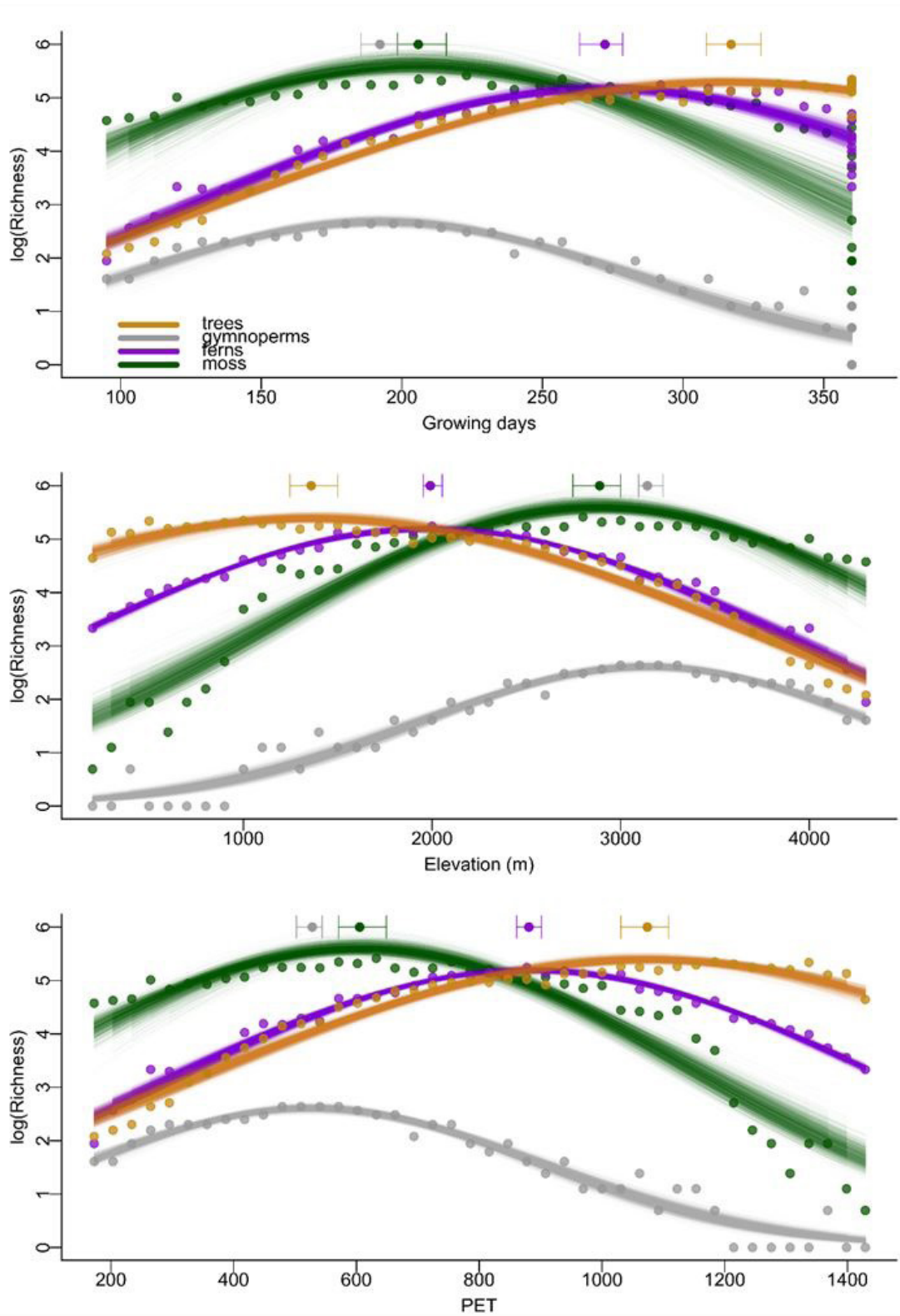
Figure 3. Species richness optima (number of growing degree days, elevation, and a thermal energy expressed as Holdrige's PET, i.e., mm water evaporated by increase of 1°C) for each plant functional lineage in the central Himalayas. "Trees" refers to angiosperm trees only. The elevation gradient was divided into 43 bins. Each data point represents interpolated richness for each 100-m elevational band. Units for growing day, elevation and PET are number of days, meter, and millimeter, respectively. Colored points at the top of each graph show the optimum and 95 per cent interval of richness for each condition.

Table 4. Results from non-linear least squares analysis for the central Himalayas showing optimum mean and confident interval of three factors (elevation, PET, and number of growing days) for each plant functional lineage. We randomly resampled our data with replacement 1000 times for each combination of species and environmental variable to determine the conditions that promote optimal conditions for each functional lineage.

| Group	Factor	Mean Optimum	Confident Interval	
			Lower	Upper
Bryophytes	Elevation	2888	2746	3000
Ferns	Elevation	1990	1953	2053
Gymnosperms	Elevation	3141	3095	3224
Angiosperm trees	Elevation	1359	1246	1500
Bryophytes	PET	605	571	648
Fern	PET	880	861	901
Gymnosperm	PET	528	502	544
Angiosperm tree	PET	1073	1030	1108
Bryophytes	Growing Day	205	198	215
Fern	Growing Day	272	263	278
Gymnosperm	Growing Day	192	185	198
Angiosperm tree	Growing Day	317	308	327
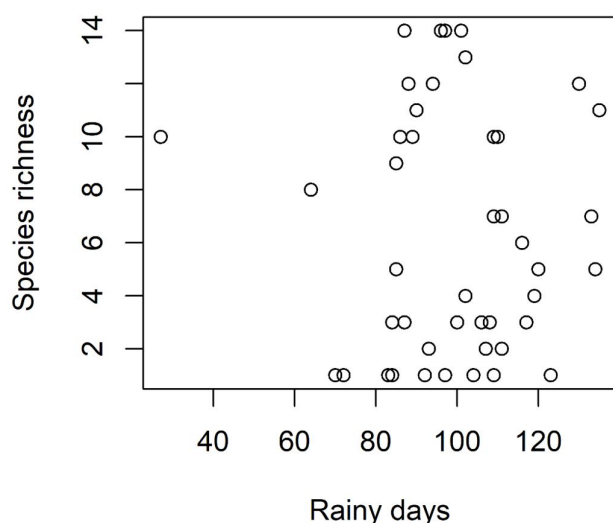
Figure 4. Relationship between gymnosperm species richness and the average number of rainy days per year in the central Himalayas. The elevation gradient was divided into 43 bins. Each data point represents interpolated richness for each 100-m elevational band where we counted the total number of species occurring in each bin.

Discussion

We found that gymnosperm species richness peaked at higher elevations, lower mean annual PET values, and at shorter mean annual growing degree days than any other functional plant lineage. Furthermore, our results indicate that each functional group's maximum species richness occurred at different elevations and climatic conditions. Our data are consistent with the idea that the distributions of Himalayan plant functional lineages may be determined by the combined effects
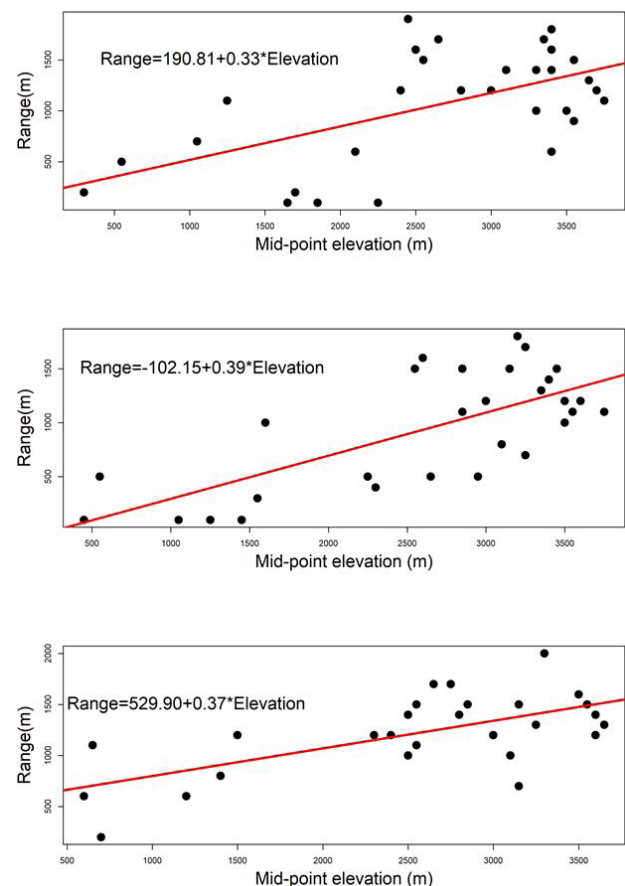

Figure 5. Relationship between gymnosperm elevational range (m) and mid-point elevation (m) in the eastern (top, 30 species, r=0.58, p-value<0.01), central (middle, 29 species, r=0.71, p-value<0.01), and western (bottom, 27 species, r=0.65, p-value<0.01) Himalayas. The line was fitted using ordinary least square linear regression.

of greater competition levels at low elevations and greater physiological tolerances at high elevations. Finally, the distribution of gymnosperms along the elevational gradient conforms to the predictions of the elevational variant of Rapoport's rule.

Species richness patterns along elevation gradient

Many taxonomic groups exhibit a unimodal pattern in species richness along elevational gradients (Guo et al. 2013, Subedi et al. 2015, Kluge et al. 2017, Guo et al. 2018), and we observed a similar pattern for Himalayan gymnosperms. There are numerous explanations that have been proposed to explain this elevational richness pattern, but our results highlight the importance of climatic tolerances in explaining gymnosperm distribution in the Himalayas. A previous study showed a strong increase in adaptations to drought by gymnosperms with increasing elevation (Li et al. 2004). For example, gymnosperms may achieve drought tolerance or avoidance due to low water demand facilitated in part by their narrow and small leaves, low specific leaf area, and high wood density (Fonseca et al. 2000, Searson et al. 2004, Poorter and Markesteijn 2008). In addition, gymnosperms may be less prone to drought-induced embolism due to their general lack of vessel elements, which are present in the majority of angiosperms (Sperry et al. 2006). The lack of vessel elements in gymnosperms is also thought to limit hydraulic conductivity, which promotes the larger leaf sizes of angiosperms and limits leaf size in gymnosperms (Lusk et al. 2012). Leaf size is also an important thermoregulatory trait, and the relatively small leaves of gymnosperms may prevent excessive night-time radiative heat loss that may lead to freezing damage in large-leaved angiosperms (Wright et al. 2017). The majority of gymnosperm species in the Himalayas are conifers, which have small tracheids with low cavitation potential (Hacke et al. 2015).

The different functional plant lineages we studied in the central Himalayas exhibited a vertical zonation of maximum species richness. Previous studies have demonstrated that species' range-limits at high elevations are set by abiotic tolerances, while biotic interactions, like competition, may define low-elevation range limits (Kreft and Jetz 2007). Assuming these rules that govern range-limits are true, herbaceous species whose ranges extend up to 6500 m may be more cold-tolerant than tree species, whose ranges do not extend beyond 4300 m (Bhattarai and Vetaas 2006). Because of their statures and closer aerodynamic coupling to air circulation, trees may experience critically lower temperatures than smaller plants at any elevation (Korner 2012). Yet, among all of the functional lineages we studied, we observed that maximum species richness for gymnosperms occurred at lower values of mean annual PET, lower values of mean annual growing degree days, and at highest elevation. The occurrence of Himalayan gymnosperms in areas of low mean annual PET values suggests low productivity or marginal growing conditions, which is consistent with hypotheses regarding gymnosperm ecology (Bond 1989).

Gymnosperms often form tree lines in mountainous regions around the world, which are likely caused by freezing damage, desiccation, and mechanical damage by wind, snow, or ice that limits growth and reduces survival (Sveinbjornsson 2000). Gymnosperm species richness also peaks at the lowest number of growing days compared to the other functional plant lineages we studied, further supporting the idea that gymnosperms are tolerant or capable of physiologically mitigating the adverse effects of marginal environmental conditions (Brodribb et al. 2012, Fragniere et al. 2015). On the other hand, the number of rainy days is known to have a positive effect on the species richness of other functional plant lineages in the central region but had no discernable effect on gymnosperm richness (Bhattarai and Vetaas 2003, Bhattarai et al. 2004, Bhattarai and Vetaas 2006). This indicates that the pattern of gymnosperm species distribution may not follow the moisture gradient. Rather, a majority of these species may be outcompeted in optimal growing conditions by other groups thus forcing gymnosperms to elevations where wind and ice blasting can destroy leaf cuticles and lead to drought stress (Li et al. 2004). In addition, colder soils and air temperatures also reduce the water uptake ability of the root system and induce drought stress (Magnani and Borghetti 1995). On top of this, the very thin soils and steep slopes at higher elevations may significantly reduce the availability of water to trees.

Our observation that gymnosperms' species richness peaks in the most environmentally marginal elevations is in agreement with current gymnosperm distribution from other areas of the world (Brodribb et al. 2012, Fragniere et al. 2015). Analyses of the global distribution of gymnosperms demonstrated that 50% (506 species) of all extant gymnosperms occurs in the tropics (Brodribb et al. 2012, Fragniere et al. 2015). Although gymnosperms can grow in warm and moist environment such as tropical and sub-tropical regions (Fragniere et al. 2015), they are usually outcompeted by angiosperms in such environments (Bond 1989, Coomes et al. 2005). Angiosperms are likely to be better competitors than gymnosperms because of angiosperms' higher photosynthetic rates and growth rates – at least at low elevations (Bond 1989, Coomes et al. 2005). Consistent with this hypothesis, our results show that gymnosperm species richness optima and angiosperm richness optima occur at the highest and lowest elevations, respectively. If climate or land-use change shifts the reduced water availability, conditions may become favorable for gymnosperms to shift their distributions downslope. Conversely, increases in temperature and greater water availability at high elevations could lead to upslope shifts in competitively superior angiosperms.

In general, species richness and habitat areas are positively correlated, such that larger habitat areas have higher diversity and smaller habitat areas have lower diversity. In mountainous systems, terrestrial surface area tends to decrease with the increase in elevation, and species richness would be expected to decline accordingly, but we observed that richness tended to

increase with elevation for gymnosperms and mosses up to very high elevation. Although this counter-intuitive result could stem from our methodological approach of binning ranges size by 100-m band intervals, thus artificially inflating our estimates of species richness, it is also likely that this pattern reflects the poorer competitive ability of gymnosperms and their greater tolerance for lower energy environments compared with angiosperm trees.

Rapoport's elevation rule

Rapoport's rule has been refuted in studies throughout the world, including the Himalayas (Ribas and Schoereder 2006 Grau et al. 2007, Feng et al. 2016). For instance, the distributions of Himalayan angiosperm tree species did not support Rapoport's rule since species were observed to have small range sizes at both ends of the gradient and large ranges at middle elevations (Bhattarai and Vetaas 2006). Moreover, Himalayan bryophytes are known to exhibit distributional patterns distinct from other groups, as their range sizes did not increase linearly with elevation but did increase at very high elevations (Grau et al. 2007). However, the elevational variant of Rapoport's rule was supported by our data on gymnosperm distributions, and this indicates that the factors determining range sizes likely vary among plant groups. Factors that may cause different plant lineages to exhibit different patterns of distribution along elevational gradients may include lineages' capacities to become locally adapted, their competitive abilities, and climatic tolerances (Futuyma and Moreno 1988, Wright 2002).

In general, both biotic and abiotic conditions jointly influence species' distributions (Jetz and Rahbek 2002, Field et al. 2005, Kreft and Jetz 2007). For instance, the sensitivity of most tropical species to drought and frost limits their distribution outside tropical areas (Currie et al. 2004). Yet, species occurring in climatically stable tropical environments are hypothesized to be stronger competitors, in part, due to their narrower niche breadths (including climatic niche breadths) than species from more variable environments (Pianka 1966, Janzen 1967, Perez et al. 2016). On the other hand, species occurring at high elevations experience greater climatic variation (Oommen and Shanker 2005, Wang et al. 2007, Feng et al. 2016). Therefore, both physiological traits and biotic interactions are likely to play an important role in determining different lineages' distributional limits along climatic gradients (Soberón 2007). Ultimately, our results provide evidence that different plant functional lineages should be considered separately when attempting to understand basic patterns of plant species diversity and distributions.

One expectation of the Rapoport's rule is that the small ranges of low-elevation species should result in higher diversity in low elevation communities due to niche-packing compared to communities at higher elevations. We observed that gymnosperm communities exhibited their highest diversity at mid-elevations, yet still exhibited changes in range size as predicted by Rapoport's rule. This apparent disparity between theory and observation can likely be resolved by considering other functional plant lineages that co-occur with gymnosperms and contribute to community assembly processes. Furthermore, we suggest that drought and cold tolerances allow gymnosperm species to overcome moisture and temperature gradients that do not favor growth for most plant groups, and may explain the pattern in gymnosperm distribution that is consistent with the Rapoport's rule.

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