Do Shapes of Elevational Gradients of Species Richness Depend on the Vertical Range Studied? The Case of the Himalayas

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Abstract

We retrieved shapes of elevational species richness gradients (unimodal, decreasing, increasing) from 64 publications, studying Himalayan elevation patterns. We covered both plants and animals, and tested the hypothesis that unimodal gradients, explicable by the geometric mid-domain effect, prevail in the mountains, whereas decreasing or increasing gradients result from studying only short sections of entire altitudinal ranges. Multivariate canonical correspondence analysis was used to relate gradient shapes to their altitude ranges, geography positions, and taxa studied. Across taxa, most of the Himalayan altitudinal gradient display a unimodal shape, with a peak of diversity situated at ca 2500 m a.s.l. for plants, and 2200 m a.s.l. for animals. The gradient shapes were attributable to three intercorrelated predictors: vertical range, maximum elevation, and mean elevation of the gradients. Studies covering sufficiently broad altitudinal range returned unimodal gradients. Studies from the Earth's highest mountain range reveal that surveys covering substantial parts of the elevational range of the mountains result in unimodal elevational gradients, whereas declining or increasing species richness gradients result from incomplete elevation range sampling.

Introduction

Changing species richness, diversity, and community composition with increasing elevation represents a major biogeography gradient on the Earth. It has large effects on biota, as it shapes both plant and animal morphology^{1,2}, physiology³, activity patterns⁴, reproduction modes⁵, spatial distribution^{6,7}, and diversity and abundance¹. In this context, the study of biodiversity changes along elevational gradients has offered many opportunities to understand efficiently the processes involved over small spatial scales, while preventing confusion between historical and biogeographical effects between localities^{1,8}.

Species richness along elevation gradient may: 1) decrease towards higher elevations, or 2) follow a unimodal (hump-shaped) pattern with a peak around middle elevations, or 3) increase towards higher elevations (Figure 1)⁹⁻¹¹. Decreasing richness with elevation is mechanistically attributable to decreasing temperatures¹² or changing precipitation^{13,14}, and generally lower net primary productivity¹⁵⁻¹⁷. In turn, increasing richness reflects the reverse of these mechanisms for cold-adapted species^{18,19}. Unimodal patterns are most frequently attributed to the geometry of mountain environments. If species preferences for particular elevations are distributed randomly, and the number of species per elevational band is affected by the species area relationship, the overlaps of species elevational distribution will be highest in a central elevation, resulting in a mid-domain effect²⁰⁻²². Complementarily, if the high and low elevations host diverse biotas with special adaptations and different evolutionary histories, an overlap zone in mid-elevations may appear as hosting diversity peaks^{23,24}.

Although there may not be a common pattern applicable to all sorts of organisms, it should be kept in mind that elevation gradient studies conducted so far differed in the vertical spans surveyed, different diversity measures, and sampling methods. Nogués-Bravo et al.²⁵ observed a decisive effect of scale on

the shape of species richness patterns, so that studies covering complete elevational ranges of mountains returned unimodal, whereas those only covering upper elevations returned decreasing patterns. Given that a general unimodal pattern appears as a near-linear relationship on short gradients (Figure 1)²⁶, we predict that for a majority of taxa, the variation in shapes of elevational patterns observed (decrease, increase, or unimodal) should be attributed by differences in study design, particularly by elevation gradient length.

To explore this hypothesis, we targeted the Himalayas, the Earth's highest mountain range. These mountains reach from tropic areas affected by monsoon cycles in the south to cold continental deserts in the north, and divide Paleo tropics and Holarctic floral, or Oriental and Palearctic faunal, realms²⁷. Owing to their unique biota, several biodiversity hotspots are recognized there (the Himalayas, mountains of southwest China)²⁸. Numerous studies describing the elevational gradients originated from the mountains, covering multiple taxonomic groups. Grytnes & Vetaas²⁹ observed that in the Nepalese Himalayas, the species richness of plants was less at low and high altitudes and observed highest species richness between 1500 and 2500 m and decreases as the altitude increased. Vetaas & Grytnes³⁰ observed that above 4000 m, the species richness of vascular plants decreases, but the endemism of the species increases in the Nepalese Himalayas. In the Bhabha Valley of the western Himalayas, Chawla et al.³¹ also observed that species richness decreases along the higher elevational gradient and endemic plant species richness increases at higher altitudes. These patterns were observed also in the eastern part of the Himalayas. Chettri et al.³² observed peak species richness of reptiles up to 500–1000 m, while no reptiles existed above 3000 m. Lizards showed a linear decline with the altitude, while snakes followed a nonlinear relation peak at 500–1000 m. In Sikkim, Acharya & Vijayan³³ recorded that butterfly species richness shows a unimodal pattern highest species richness at 1000 m and sharp decline of species richness up to 3000 m.

We collected published elevational studies and tested potential predictors of the patterns related to elevational gradient range, plus such characteristics of the studies as mean and maximum elevations of the gradients.

Results

In total, we gathered data from 64 publications, reporting 90 separate gradient studies (Supplement S1) with a good representation over the Himalayan region. The highest number of gradient studies targeted plants, followed by birds and arthropods (Figure 2a). Average length of the elevation range was 3393 ± 1607 SD m (minimum 600 m, maximum 7200 m), the mean midpoint elevation was at 2680 ± 743 SD m a.s.l., the lowest point was 0 m a.s.l., and the highest point was 7550 m a.s.l. Only a few of the studies covered almost the complete elevation gradient (Figure 3).

The majority of the examined studies from the Himalayan region showed unimodal shapes ($N = 63$), followed by declines (24), and increases (3) (Figures 2a, b). The taxa did not differ in proportional

representation of gradient shapes ($\chi^2 = 23.89$, $df = 18$, $p = 0.159$). For the most frequently studied taxa, **mean peak** was higher situated for plants (2490 m $\pm$ 864 SD, maximum: 4625 m) than for animals (2174 $\pm$ 601 SD), in which it was higher for birds (2300 m $\pm$ 619 SD, maximum: 3000 m) than for arthropods (2140 m $\pm$ 488 SD, maximum: 2540 m). A comparison of peak elevations between plants and animals revealed a marginally significantly higher elevation of plants peaks ($t = 1.80$, $df = 61$, $P = 0.08$).

Single-term CCAs for each predictor (Table 1) showed that the gradient shape was significantly related to mean elevation, maximum elevation, and elevation range, regardless of controlling or not controlling for studied taxa. Longitude was marginally significant, minimum elevation and latitude were without effects. The forward selection from all predictors (Full model: explained variation 15.54%, first axis pseudo-F 3.2, pseudo-P < 0.001, all axes pseudo-F 3.9, pseudo-P < 0.001; Full model with taxonomy covariable: explained variation 19.57%, first axis pseudo-F 3.1, pseudo-P < 0.001, all axes pseudo-F 4.6, pseudo-P < 0.001) returned maximum elevation as a sufficient sole predictor for the gradient shape responses (Figure 4).

Table 1

Result of single-term canonical correspondence analyses relating elevational gradient shapes to variables describing the gradient, ordered by the amount of explained variability. Maximum elevation, the strongest predictor of gradient shapes, was returned as the single predictor also in forward selection based on all variables with significant single effect. The right column with p values is adjusted for Holm correction.

Variable	Variability explained (%)	pseudo-F	P	P(adj)
No covariable				
Maximum elevation	12.2	12.2	0.001	0.006
Elevation range	10.5	10.3	0.001	0.006
Mean elevation	6.4	6.0	0.006	0.024
Longitude	2.7	2.5	0.09	0.27
Minimum elevation	1.6	1.4	0.249	0.498
Latitude	0.8	0.7	0.497	0.498
Taxonomy as covariable				
Maximum elevation	13.6	12.3	0.001	0.006
Elevation range	10.7	9.4	0.001	0.006
Mean elevation	9.0	7.7	0.004	0.016
Longitude	3.5	2.8	0.07	0.21
Minimum elevation	2.8	2.2	0.112	0.224
Latitude	0.9	0.7	0.506	0.506

Visualizing the predictors with significant effects showed that high values of maximum elevation, mean elevation, and elevational range were positively intercorrelated³⁴, all pointing towards unimodal gradient shape. On the contrary, short gradients (i.e., low values of elevational range) with low maximum and mean elevations revealed either increasing or decreasing species richness/diversity, and low-elevated gradients (i.e., low values of mean and maximum elevation) indicated increase of species richness with altitude (Figure 3). These patterns were retained when treating studied taxa as covariates (Table 1).

Discussion

Across taxa, a great majority of elevational gradient studies in the Himalayan region returned a unimodal altitudinal pattern of species richness. This was typical for gradients covering a broad elevational range, whereas monotonously increasing or decreasing species richness applied for those covering short elevational ranges. In addition, monotonous increases were associated with low mean and maximum gradients' elevations, whereas monotonous decreases were associated with those with high mean elevations. These observations support our original hypotheses that unimodal response of species richness to elevation prevail in Himalayan biota, and those studies reporting decreasing or increasing species richness with altitude covered subsets of the elevational range of the mountains. We agree with the observation of Nogués-Bravo et al.²⁵ that studying only upper parts of elevational gradients results in apparently decreasing pattern species richness patterns, and with Kessler et al.³⁵, who insisted on the necessity to cover entire elevational gradients in a global study of ferns.

Our Himalayan analysis supports the prevalence of unimodality for a broad range of taxa in a major mountain range. For the most frequently studied taxa, the species richness peaks were situated in 2000–3000 meters, i.e., in the altitudinal belt of deciduous broadleaf forests (southern Himalayan slopes oriented towards Oriental tropics) or coniferous forests (NE and N slopes, oriented towards Palearctic temperate zones). The high diversity of birds, insects, and many other groups in South Himalayan Mountain forests is a well-established fact^{36,37}. Only for plants, some of the diversity peaks ($n = 8$) reached the subalpine to alpine vegetation ($>\approx 3000$ m). The two highest-elevation richness peaks were reported by Klimes³⁸ and Bhattarai et al.³⁹, who nevertheless covered rather short and primarily alpine gradients (elevational ranges 4180–5970 and 2800–4400 m a.s.l., respectively). The other authors reporting plant diversity peaks in alpine elevations covered substantially longer gradients, spanning >3000 altitudinal meters^{31–41}. These observations suggest that at least in some parts of the mountains, diversity peaks of Himalayan plants may be located above those of animals. This may reflect the radiation of some plant groups at Himalayan (sub)alpine altitudes^{42,43}, or high alpha-diversity of some plant groups in high altitude environments, resulting into highly situated plant diversity peaks. Alternatively, the apparently higher-elevated diversity peaks reported for plants may be due to considerably easier sampling of plants, which are immobile and non-cryptic, compared to difficulties with sampling mobile and/or cryptic animals in harsh terrains of high elevations.

Unimodal species richness patterns^{44,45} was also reported from other major mountain ranges, both temperate and tropical, the former temperate including, e.g., plants in Norway⁴⁶, land snails in Europe⁴⁷, mammals in the American Rocky Mountains⁴⁸, or beetles and moths in Korea⁴⁹; and the latter tropical including, e.g., leaf litter invertebrates in Panama⁹, ferns in Costa Rica⁵⁰, moths in tropical mountains world-wide¹¹, or mammals in the Philippines⁵¹.

Reversing the argument that sampling long elevational gradients results, almost invariably, in unimodal elevational species richness patterns, leads to the conjecture that the uniformly increasing or decreasing richness patterns are results of incomplete vertical sampling. If so, the monotonously decreasing or increasing gradients do not require additional biological explanation. Still, groups whose distribution towards elevational extremes is truncated by their biology likely represent exceptions to the rule. Towards the upper extreme, these most likely include trees, limited by physical limits to their growth⁵²; fish, limited in high altitudes by absence of sufficiently large water bodies⁵³; and perhaps other ectothermic vertebrates. Groups truncated towards lower elevational limits might include weakly competitive organisms, such as lichens or orchids.

Although the unimodal patterns fit the geometry-derived null hypothesis of mid-domain effect⁵⁴, they deserve to be further analyzed regarding underlying physiological, ecological, or evolutionary mechanisms, which may vary among taxa, but also regions of the world. Hu et al.⁵⁵ showed that biotas of various functional or climatic guilds and their turnover may effectively, together with climatic data, explain the unimodal pattern shape. Furthermore, high altitude species overlapping in mid-altitudes with lowland species could have originated by autochthonous high-altitude radiations⁵⁶; dispersed to the mountains from higher latitudes, perhaps during periods of cooler climate (cf.^{57,58}); or derived from lowland biotas by endemic speciation⁵⁹. In the Himalayas, the diversity of high altitudes is often of Palearctic/Holarctic origin, whereas lowland species are Oriental⁶⁰.

Cross-taxon analyses aiming on deciphering the mechanisms behind the unimodal patterns are highly desirable, but the data at hand do not allow them at this moment. The necessary conditions would be complete species lists for the altitudinal points surveyed, together with abundances. Such data would allow relating life history traits of species inhabiting different altitudes to their phylogeny and abiotic conditions. Only a small fraction ($n = 3$) of the 64 papers considered here reported original data. Without species-level data, it is impossible to understand the peculiarities of composition of individual species communities along the gradients and to explain how the general unimodal pattern of species richness is built.

Methods

Data collection. We searched for publications on species richness along the Himalayan elevational gradients for all taxa using the Google Scholar and Web of Science search engines with “elevational gradient”, “altitudinal gradient”, “Himalayan elevation”, and “Himalayan altitude” as keywords, then

searched bibliographies of the publications found through Google Scholar for further relevant studies [accessed December 2020]. We only included publications that reported both abundance (i.e., number of individuals), and either species richness (i.e., the number of species within a defined region) or species diversity (a broadly used diversity index, e.g., Shannon's), for all taxa of a focal group, sampled at a minimum of four elevation transects/points and that had equal sampling effort with identical sampling methods at each elevation. If several taxa were used in a single study, we kept the taxa as separate gradient studies. For each study, we extracted a type of the gradient shape ("decline", "unimodal", and "increase" of species richness/diversity along the elevational gradient), studied taxa (distinguishing amphibians, ants, birds, bryophytes, fish, Lepidoptera, lichens, mammals, and reptiles), geographic coordinates (latitude, longitude), and information on elevation used in a study (minimum, mean, and maximum elevation, and elevation range, i.e., the length of the gradient) (See Supplement S1 for details).

Data analyses. We used the gradient shapes (3-states factor: "decline", "unimodal", or "increase") extracted from the studies as a response variable, and recorded variables describing the gradients (studied taxa, longitude, latitude, minimum elevation, mean elevation, maximum elevation, and elevation range) as potential predictors (See S1 for details). Primarily, we used the χ^2 test in R⁶¹ to search for a possible difference of numbers of individual gradient shapes per studied taxa. Then, we employed multivariate Canonical Correspondence Analyses (CCA), which allows testing of various sets of predictors, including their collinearity and variance partitioning, calculated in Canoco 5⁶². First, we tested for the effect of the studied taxon (categorical predictor) on the gradient shapes. Second, we used a set of single-term analyses to inspect the effect of each of the variables on the gradient shapes. Third, we used a forward selection procedure to build a Full model. Both single-term analyses and the complex model were calculated twice, excluding, and including studied taxa category as a covariate.

Declarations

Authors Contributions

J.S.I. and Z.F.F. designed the work, acquired the data, and drafted the manuscript. Z.F.F. calculated the data, statistical analysis and prepares the figures used in the manuscript. J.S.I., Z.F.F., A.B.S. and M.K. contributed equally to the production and interpretation of results. All authors critically reviewed the manuscript and approved this version to be published.

Competing interests

The authors declare no competing interests.

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Figures

Figure 1

Illustration of our focal prediction regarding the shapes of elevational species richness/diversity gradients observed in elevation gradient studies. If the shapes of gradients covering substantial parts of mountains' vertical range, ideally from piedmonts to the summits, are unimodal, then observations based on short sections of the gradient will appear as near-linear, returning increasing (lower elevations) or decreasing (upper elevations) species richness patterns. Inspired by Nogués-Bravo et al. ²⁵.

Figure 2

A representation of taxa studied (a) with relation to gradient shapes and (b) geographic distribution of 90 elevation studies done in the Himalayan region (see S1 for details of each of study). Gradient shapes indicated by different colors.

Figure 3

Distribution of elevation ranges of the 90 elevation gradient studies done in the Himalayan region in relation to altitude. Gradient shapes are again indicated by different colors.

Figure 4

Canonical correspondence analysis biplot illustrating the effects of predictors significant in single-term analyses (cf. Table 1) on elevation gradient shapes (i.e., full model used for forward selection of variables). Maximum elevation, the sole predictor sufficient to explain the pattern, is shown in red.

Supplementary Files

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