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

**Jatishwor Singh Irungbam [1], Martin Konvicka [2] and Zdenek Faltynek Fric [2,3,*]**

[1] Centrum Algatech, Institute of Microbiology, CAS, Novohradská 237—Opatovický Mlýn, CZ-37901 Třeboň, Czech Republic; jatishwor.irungbam@gmail.com
[2] Institute of Entomology, Biology Centre, CAS, Branisovská 1160/31, CZ-37005 České Budějovice, Czech Republic; konva@entu.cas.cz
[3] Faculty of Environmental Sciences. Czech University of Life Sciences, Kamycka 129, CZ-16500 Praha, Czech Republic
* Correspondence: fric@entu.cas.cz

**Abstract:** We analyzed elevational species richness gradients (“decline”, “increase”, “unimodal”, or “bimodal”) in the Himalayan range using data from 157 publications covering both plants and animals. Our study tested the hypothesis that unimodal gradients, explainable by the geometric mid-domain effect, dominate in the mountains, while decreasing or increasing gradients result from studies that only examined limited sections of the full altitudinal range. Multivariate canonical correspondence analysis was applied to associate gradient shapes with altitude ranges, geographic locations, and the taxa studied. Our results show that, across taxa, most Himalayan altitudinal gradients exhibit a unimodal shape, with diversity peaks at approximately 2500 m a.s.l. for plants and 2200 m a.s.l. for animals. The gradient shapes were primarily influenced by three interrelated predictors: vertical range, maximum elevation, and mean elevation. Studies from the world’s highest mountain range suggest that surveys encompassing substantial portions of the elevational range tend to produce hump-shaped gradients, while incomplete sampling leads to declining or increasing species richness patterns.

**Keywords:** altitudinal ecology; elevational species richness; Himalayan biodiversity; mid-domain effect; species diversity gradients

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## 1. Introduction

Variations in species richness, diversity, and community composition with increasing elevation represent a significant biogeographical gradient on Earth [1]. This gradient profoundly impacts biota, influencing both plant and animal morphology [2,3], physiology [4,5], activity patterns [6], reproduction modes [4,7], spatial distribution [8,9], and diversity and abundance [2]. Additionally, the high number of studies of elevational gradients allows for high reproducibility and comparison of patterns from a variety of habitats and latitudes [10,11]. Recent research by Gordon et al. [12] indicates that changes in biodiversity are often associated with human impacts, though the magnitude, timing, and sometimes the direction of these associations vary across continents, biomes, and sites. Studying biodiversity changes along elevational gradients provides valuable insights into ecological processes on small spatial scales, helping to disentangle historical and biogeographical influences across locations [2,13]. The study by Rana et al. [14] emphasizes that the evolutionary history of plant lineages significantly influences current species richness patterns and climatic conditions, such as temperature and precipitation, which plays a crucial role in determining species richness. Environmental heterogeneity also enhances the relationship between biodiversity and ecosystem functioning, where species richness serves as a more powerful driver of ecosystem function than species turnover [15].

Species richness along elevation gradients may exhibit three main patterns: (1) a decrease towards higher elevations, (2) an increase towards higher elevations, or (3) a unimodal (hump-shaped) pattern with a peak at mid-elevations (Figure 1) [16–20]. These patterns are influenced by a variety of factors, both biotic and abiotic factors which interact in a complex way to shape the patterns of species richness we observe in different ecosystems [21,22]. The decline in richness with elevation is often attributed to decreasing temperatures [23], variations in precipitation [24,25], and generally lower net primary productivity [26–28]. Conversely, an increase in richness at higher elevations can result from cold-adapted species thriving under these conditions [29,30]. Unimodal patterns are frequently linked to the geometry of mountain environments. If species' elevational preferences are randomly distributed and the number of species per elevational zone is influenced by the species–area relationship, the greatest overlap of species distributions occurs at mid-elevations, leading to a mid-domain effect [31–34]. Complementarily, if both high and low elevations host diverse biotas with distinct adaptations and evolutionary histories, mid-elevation zones may emerge as areas of peak diversity due to the overlap of these biotas [35,36]. Colwell et al. [37] demonstrated that geometric constraints and environmental favorability interact to shape species richness patterns and gradients of environmental favorability, and helps to explain why species richness peaks at mid-elevations. Another hypothesis to explain mid-elevational diversity peaks is centered on the water–energy dynamic [10,38]. Beck and Chey [39] proposed that diversity at higher elevations is constrained by ambient energy, while at lower elevations, water availability becomes the limiting factor. This hypothesis builds on previous findings indicating a shift from temperature to water as the primary limiting factor for diversity as latitude decreases, suggesting an indirect, trophic cascade effect [38]. Beck and Chey's [39] research on geometrid moths in Borneo supported the idea of energy limitation at high elevations but did not find evidence for water limitation at lower elevations. Similarly, Beck and Kitching [11] identified temperature as a key predictor of peak species richness for sphingid moths, with only weak support for water as a factor. In contrast, McCain [10], studying bats, and Hawkins et al. [38], examining plants, vertebrates, and invertebrates, found strong evidence that both water and energy are significant predictors of diversity patterns. Although there may not be a common pattern applicable to all sorts of organisms [40,41], it should be kept in mind that elevation gradient studies conducted so far differed in vertical spans surveyed, different diversity measures, and sampling methods. Nogués-Bravo et al. [42] observed a decisive effect of scale on the shape of the species richness pattern, so that studies covering complete elevational ranges of mountains returned unimodal, whereas those covering upper elevations only, returned decreasing patterns. Dani et al. [43] analyzed elevational gradients in plant species richness worldwide and also reported that diversity tends to peak at mid or lower elevations. The hump-shaped patterns were more prevalent in the very high mountains, with both hemispheres showing similar patterns. These patterns are shaped by topographical and climatic factors [44].

Given that a general unimodal pattern appears as a near-linear relationship on short gradients (Figure 1) [45], we predict that for a majority of taxa, the variation in shapes of elevational patterns observed (decrease, increase, unimodal, or bimodal) should be explicable by differences in study design, particularly by the elevation gradient lengths.

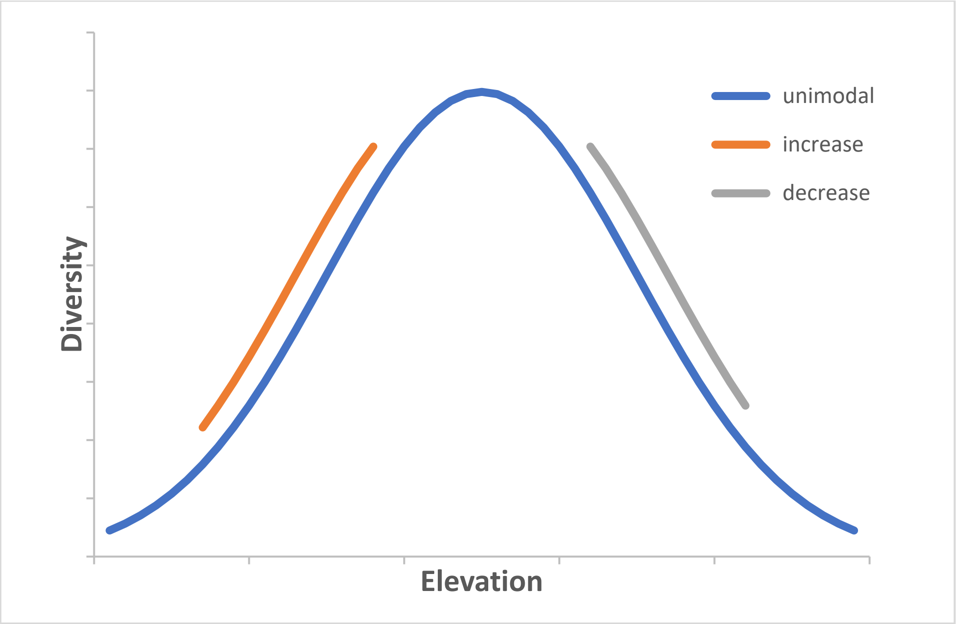

**Figure 1.** Illustration of our focal prediction regarding the shapes of elevational species richness/diversity gradients observed in elevation gradient studies. The shapes of gradients covering substantial parts of mountains vertical range, ideally from piedmonts to the summits, are unimodal. However, observations based on short sections of the gradient may appear nearly linear, showing increasing (lower elevations) or decreasing (upper elevations) species richness patterns. Inspired by Nogués-Bravo et al. [42].

To explore this hypothesis, we targeted the Himalayas, the World's highest mountain range, renowned for its vast and diverse ecosystems [41] and recognized as one of the most significant biodiversity hotspots. The Himalayan range, characterized by the greatest elevational gradient on Earth, harbors extremely rich and distinctive biodiversity [46,47]. Himalaya is a large mountain arc that extends for 2500 km from the Nanga Parbat Mountain (8125 m) and the Indus River Gorge in the northwest to the Namche Barwa Mountain (7756 m) and the Yarlungtsangpo–Brahmaputra River Gorge in the east [48]. Spanning from monsoon-affected tropical regions in the south to cold continental deserts in the north; these mountains serve as a natural divide between the Paleotropical and Holarctic floral realms (hereafter called "temperate" and "tropical" regions), as well as the Oriental and Palearctic faunal realms [49]. Owing to their unique biota, several biodiversity hotspots are recognized there (Himalaya, Mountains of Southwest China) [50]. Numerous studies describing the elevational gradients originated from the mountains, covering multiple taxonomic groups. Grytnes and Vetaas [51] observed that in the Nepalese Himalaya, the species richness of plants was lower at low and high altitude and observed highest species richness between 1500 and 2500 m. Vetaas and Grytnes [52] observed, also in the Nepalese Himalaya, that above 4000 m, the species richness of vascular plants decreases but the endemism increases. In the Bhabha valley of western Himalaya, Chawla et al. [53] also observed that species richness decreases along the higher elevational gradient and endemic plant species increases at higher altitudes. In the Gulmarg Wildlife Sanctuary of western Himalaya, Wani et al. [54] studied the pattern of β-diversity of plants along an elevation gradient ranging from 2200 to 3900 m and observed that herbaceous and tree richness showed a significant decrease with the increase in elevation; however, the richness of shrubs showed a bimodal pattern. These patterns were observed also in the eastern part of the Himalayas. Thorne et al. [55] reported peak species richness of tropical plant species at 900–1300 m and temperate plant species at higher altitudes of 2500–2900 m in Bhutan. Chettri et al. [56] observed that the peak species richness of reptiles up to 500–1000 m, while no reptiles existed above 3000 m. The lizards show the linear decline with the altitude and snakes followed a nonlinear relation peaking at 500–1000 m. In Sikkim, Acharya and Vijayan [57] recorded the butterfly species richness showing a unimodal pattern with the 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 pattern related to elevational gradient range, plus such characteristics of the studies as mean and maximum elevations of the gradients. We specifically hypothesized that the positions and lengths of the elevational gradients will influence their resulting shapes, so that long gradients will produce unimodal biodiversity responses, whereas short gradients in lower elevations will produce unimodally increasing trends, and short gradients in higher elevations will produce unimodally decreasing trends.

## 2. Material and Methods

### 2.1. Data Collection

We searched for publications on the species richness along the Himalayan elevational gradients for all taxa using the Google Scholar search engine, PubMed and Web of Science with "elevation (-al) gradient", "altitude (-inal) gradient", "Himalayan elevation", "Himalayan altitude", "species richness", "species diversity", "gradient analysis", and "species abundance" as keywords and then we searched bibliographies of the publications found through Google Scholar for further relevant studies [accessed December 2024]. Datasets were selected based on priority sampling criteria. We selected only those studies giving proper locations, with elevation/altitude, latitudes, and longitudes (when not provided, we searched for the localities on Google maps). We included only publications that reported both abundance (i.e., number of individuals) and either species richness (i.e., number of species within a defined region) or species diversity (a widely used index, e.g., Shannon's [58]). Studies had to sample all taxa of a focal group at a minimum of four elevation transects/points using consistent sampling methods and effort 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", "increase", "unimodal", or "bimodal" of species richness/diversity along elevational gradient), studied taxon (distinguishing amphibians, ants, birds, plants, angiosperms, 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., gradient length) (See Supplement (S1) for the details).

### 2.2. Data Analyses

We used the gradient shapes (4-states factor: "decline", "increase", "unimodal", or "bimodal") 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 Supplement S1 for the details). Primarily, we used the $\chi^2$ test in R [59] to search for a possible difference of numbers of individual gradient shapes per studied taxa.

Next, we employed multivariate Canonical Correspondence Analyses (CCA), which allows for testing the effects of various sets of predictors, including their collinearities and interactions [60], in Canoco 5 [61]. To assess the significance of the CCAs, we used 999 Monte Carlo permutations. In CCA analyses, gradient shapes constituted the multivariate response variable. We first tested for the effect of 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 predictors on the gradient shapes. Third, we used a forward selection procedure to build a Full model, based on a combination of predictors. Both single-term analyses and the Full model were calculated twice, excluding, and including studied taxa as a categorical covariate.

## 3. Results

In total, we gathered data from 157 publications, reporting 229 separate gradient studies with a good representation over the Himalayas region. The highest number of the gradient studies targeted plants, followed by birds and arthropods (Figure 2a). The average length of elevation range was 3325 ± 1870 SD m (minimum 300 m, maximum 7500 m), the mean midpoint elevation was at 3008 ± 979 SD m a.s.l., the lowest point was 0 m a.s.l., and the highest point was 8000 m a.s.l. Only a few of the studies covered almost complete elevation gradient (Figure 3).

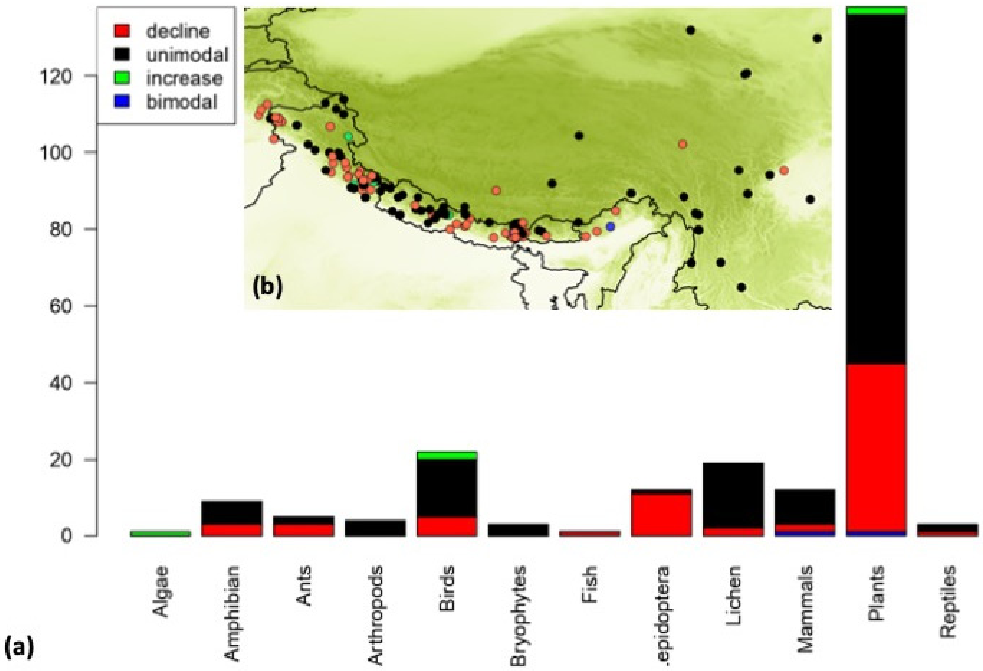

**Figure 2.** A representation of taxa studied (**a**) with relation to gradient shapes, $x$-axis represents the taxon studied and $y$-axis represents the number of gradients with the appropriate taxon and response and (**b**) geographic distribution of 157 elevation studies conducted in the Himalayan region (see Supplement S1 for details of each of study). Gradient shapes indicated by different colors.

Majority of the examined studies from the Himalayan region reported unimodal shapes (N = 146), followed by declines (N = 68) and increases (N = 5); three studies reported bimodal shape (Figure 2a,b). The taxa differed in proportional representation of gradient shapes ($\chi^2$ = 92.94, df = 33, $p$ < 0.001). For the most frequently studied taxa, mean peak was higher situated for plants (3126 m ± 984 SD, maximum: 5550 m) than for animals (2538 ± 913 SD), in which it was lower for birds (2735 m ± 895, maximum: 4250 m) than for all arthropods (2935 m ± 1218 SD, maximum: 5350 m). A comparison of peak elevations between plants and animals revealed significantly higher elevation of plants peaks (F = 8.18, df = 1, 227, $p$ = 0.005).

Single-term CCAs for each predictor (Table 1) showed that the gradient shape was significantly related to mean elevation, maximum and minimum elevation, elevation range, and longitude regardless of controlling or not controlling for studied taxa. Latitude was without effects, whereas minimum elevation had an effect only with taxonomy as the covariate.

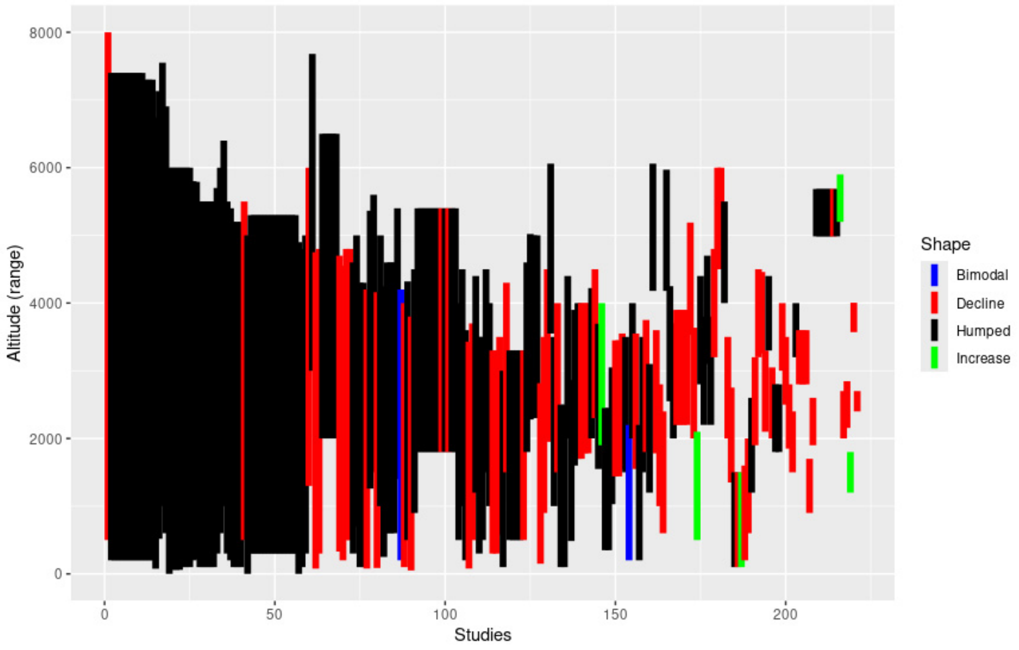

**Figure 3.** Distribution of elevation ranges across 157 studies, representing 229 elevational gradients in the Himalayan region, plotted in relation to altitude. Gradient shapes are indicated by different colors.

**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 a Holm correction.

| Variable. | Contribution When Alone (%) | Pseudo-F | *p* |
|---|---|---|---|
| **Taxon** | | | |
| | No covariable | | |
| Maximum elevation | 72.3 | 17.46 | 0.001 |
| Elevation range | 64.6 | 15.49 | 0.001 |
| Mean elevation | 23.3 | 5.35 | 0.001 |
| Longitude | 20.2 | 4.63 | 0.009 |
| Minimum elevation | 9.0 | 2.03 | 0.096 |
| Latitude | 3.5 | 0.80 | 0.476 |
| | Taxonomy as covariable | | |
| Maximum elevation | 13.6 | 14.29 | 0.001 |
| Elevation range | 10.7 | 14.01 | 0.001 |
| Mean elevation | 9.0 | 5.48 | 0.040 |
| Longitude | 3.5 | 6.70 | 0.002 |
| Minimum elevation | 2.8 | 3.94 | 0.009 |
| Latitude | 0.9 | 1.07 | 0.339 |

The forward selection from all predictors (Full model: explained variation 9.14%, first axis pseudo—F 10.8, pseudo—$p < 0.001$, all axes pseudo—F 11.4, pseudo—$p < 0.001$; full model with taxonomy covariable: explained variation 10.15%, first axis pseudo—F 6.9, pseudo—$p < 0.001$, all axes pseudo—F 8.1, pseudo—$p < 0.001$) returned maximum elevation, longitude, and in the case without covariable, also elevation range as predictors for the gradient shape responses (Figure 4).

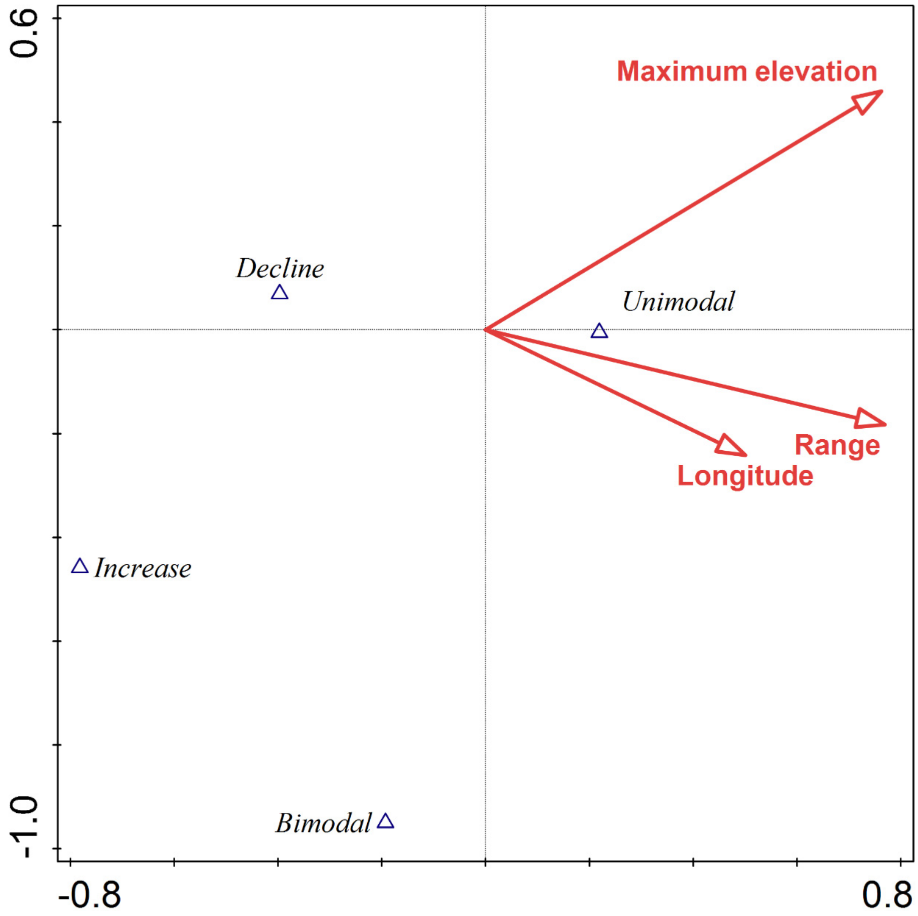

**Figure 4.** Canonical correspondence analysis biplot illustrating the effects of predictors significant in single-term analyses (cf. Table 1) on elevation gradient shapes (i.e., full model used for forward selection of variables). Maximum elevation, the sole predictor sufficient to explain the pattern, is shown in red.

Visualizing the predictors with significant effects showed that high values of maximum elevation, elevation range and longitude were positively intercorrelated, all pointing towards a unimodal gradient shape. On the contrary, short gradients (i.e., low values of elevational range) revealed either increasing or decreasing species richness/diversity, and low-elevated gradients (i.e., low values of maximum elevation) indicated an increase in species richness with altitude (Figure 4). These patterns were retained when treating studied taxa as covariates (Table 1).

## 4. Discussion

Across taxa, a great majority of elevational gradient studies in the Himalayan region returned a unimodal altitudinal pattern of species richness. This pattern was characteristic of gradients spanning a broad elevational range, while gradients with a short elevational range exhibited either a consistently increasing or decreasing species richness. 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 a unimodal response of species richness to elevation prevails in Himalayan biota, and those studies reporting decreasing or increasing species richness with altitude covered subsets of elevational range of the mountains. We concur with Nogués-Bravo et al. [42] that focusing exclusively on the upper portions of elevational gradients can lead to the appearance of decreasing species richness patterns. Additionally, we support Kessler et al. [62], who emphasized the importance of covering entire elevational gradients in global fern studies. Costa et al. [63] also highlights a bias in detecting species richness patterns along elevation gradients, largely influenced by factors such as the number of sampling units, the range covered, and the comprehensiveness of mountain sampling in a global meta-analysis of major terrestrial taxa.

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 2000–3500 m., 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). A high diversity of birds, insects, and many other groups in South Himalayan Mountain forests is a well-established fact, e.g., [64–66]. Only for plants, some of the diversity peaks (n = 31) reached the subalpine to alpine vegetation (>≈3000 m). The two highest-elevation richness peaks were reported by Baniya et al. [67] and Klimes [68] who nevertheless covered rather short and primarily alpine gradients (elevational ranges 4985–5685 and 4180–5970 m a.s.l., respectively). The other authors reporting plant diversity peaks in alpine elevations covered substantially longer gradients, spanning > 3000 m a.s.l. [53,54,68–76]. 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 in Himalayan (sub)alpine altitudes [77,78], or high alpha-diversity of some plant groups in high altitude environments, resulting in 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 have limited mobility and are non-cryptic, compared to the difficulties with sampling mobile and/or cryptic animals in harsh terrains of high elevations.

Unimodal species richness patterns [79–81] were also reported from other major mountain ranges, both temperate and tropical, the former including, e.g., plants in Norway [82], land snails in Europe [83], mammals in American Rocky Mountains [84], geometrid moths in Borneo [39], or beetles and moths in Korea [85]; and the latter, e.g., leaf litter invertebrates in Panama [16], ferns in Costa-Rica [86], sphingid moths in southeast Peru [87], or mammals of the Philippines [88]. Geometrid moths in mountains worldwide [89] also revealed unimodal patterns.

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 from the rule. Towards the upper extremes, these most likely include trees, limited by physical limits to their growth [90]; fish, limited in high altitudes by absence of sufficiently large water bodies [91]; 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 the mid-domain effect [92,93], they deserve to be further analyzed regarding underlaying physiological, ecological, or evolutionary mechanisms, which may vary among taxa, but also regions of the world. Hu et al. [94] demonstrated that the biotas of different functional or climatic guilds, along with their turnover and climatic data, can effectively explain the formation of the unimodal pattern. Furthermore, high altitude species overlapping in mid altitudes with lowland species could have originated from autochthonous high altitude radiations [95,96]; dispersed to the mountains from higher latitudes, perhaps during periods of cooler climate cf. [97,98], or derived from lowland biotas by endemic speciation [99]. In the Himalayas, the diversity of high altitudes is often of Palearctic/Holarctic origin, whereas lowland species are Oriental [100].

Cross-taxon analyses focusing 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 attitudinal 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 = 12) of the 157 papers considered here also reported original data. Without species-level data, understanding the unique composition of individual species communities along gradients and explaining the formation of the general unimodal pattern of species richness is impossible.

## 5. Conclusions

Using published information on elevational species richness gradients covering diverse taxa from the Himalayan Mountain range, we demonstrated that a vast majority of the gradients display unimodal responses to elevation, or mid-elevation diversity peaks. Gradients reporting a monotonous decrease or increase in species richness covered relatively short elevation ranges in the upper or lower parts of the mountains, respectively. The observation that plant species richness peaks at higher elevations than animal richness indicates that much work is still needed to understand biological mechanisms generating the unimodal gradients. For this, researchers should publish not only information on species richness, but also lists of the species recorded.

**Supplementary Materials:** The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d17030215/s1, Supplement S1. A spreadsheet summarizing publications and separate gradient studies, used in our study testing potential predictors of the pattern related to elevational gradient range. List "Alt_Himalayas" shows the data, list "References" the publications details.

**Author Contributions:** Conceptualization, J.S.I., M.K. and Z.F.F.; Data curation, J.S.I. and Z.F.F.; Formal analysis, Z.F.F.; Funding acquisition, M.K. and Z.F.F.; Investigation, J.S.I. Methodology, J.S.I. and Z.F.F.; Project administration, Z.F.F.; Resources, J.S.I. and Z.F.F.; Validation, Z.F.F.; Visualization, M.K. and Z.F.F.; Writing—original draft, J.S.I., M.K. and Z.F.F.; Writing—review and editing, J.S.I., M.K. and Z.F.F. All authors have read and agreed to the published version of the manuscript.

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## References

1. Hutchinson, G.E. Homage to Santa Rosalia or Why are there so many kinds of animals? *Am. Nat.* **1959**, *93*, 145–159. [CrossRef]
2. Hodkinson, I.D. Terrestrial insects along elevation gradients: Species and community responses to altitude. *Biol. Rev.* **2005**, *80*, 489–513. [CrossRef] [PubMed]

3. Smith, R.J.; Hines, A.; Richmond, S.; Merrick, M.; Drew, A.; Fargo, R. Altitudinal Variation in Body Size and Population Density of *Nicrophorus investigator* (Coleoptera: Silphidae). *Environ. Entomol.* **2020**, *29*, 290–298. [CrossRef]
4. Laiolo, P.; Obeso, J.R. Life-History Responses to the Altitudinal Gradient. In *High Mountain Conservation in a Changing World. Advances in Global Change Research*; Catalan, J., Ninot, J., Aniz, M., Eds.; Springer: Cham, Switzerland, 2017; Volume 62. [CrossRef]
5. Vrba, P.; Nedvěd, O.; Zahradníčková, H.; Konvička, M. More complex than expected: Cold hardiness and the concentration of cryoprotectants in overwintering larvae of five *Erebia* butterflies (Lepidoptera: Nymphalidae). *Eur. J. Entomol.* **2017**, *114*, 470–480. [CrossRef]
6. Camacho, L.; Avilés, L. Decreasing predator density and activity explain declining predation of insect prey along elevational gradients. *Am. Nat.* **2019**, *194*, 334–343. [CrossRef]
7. Zhao, Z.; Du, G.; Zhou, X.; Wang, M.; Ren, Q. Variations with altitude in reproductive traits and resource allocation of three Tibetan species of Ranunculaceae. *Aust. J. Bot.* **2006**, *54*, 691–700. [CrossRef]
8. Scheffers, B.R.; Phillips, B.L.; Laurance, W.F.; Sodhi, N.S.; Diesmos, A.; Williams, S.E. Increasing arboreality with altitude: A novel biogeographic dimension. *Proc. R. Soc. Lond. B Biol. Sci.* **2013**, *280*, 20131581. [CrossRef]
9. Wang, J.; Zhang, B.; Yao, Y. Pattern of the Upper Limit of Montane Deciduous Broad-Leaved Forests and Its Geographical Interpretation in the East Monsoon Realm of China. *Forests* **2021**, *12*, 1225. [CrossRef]
10. McCain, M.C. Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Glob. Ecol. Biogeogr.* **2007**, *16*, 1–13. [CrossRef]
11. Beck, J.; Kitching, I.J. Drivers of moth species richness on tropical altitudinal gradients: A cross-regional comparison. *Glob. Ecol. Biogeogr.* **2009**, *18*, 361–371. [CrossRef]
12. Gordon, J.D.; Fagan, B.; Milner, N.; Thomas, C.D. Thomas Floristic diversity and its relationships with human land use varied regionally during the Holocene. *Nat. Ecol. Evol.* **2024**, *8*, 1459–1471. [CrossRef] [PubMed]
13. Rasmann, S.; Pellissier, L.; Defossez, E.; Jactel, H.; Kunstler, G. Climate-driven change in plant-insect interactions along elevation gradients. *Funct. Ecol.* **2014**, *28*, 46–54. [CrossRef]
14. Rana, S.K.; Gross, K.; Price, T.D. Drivers of elevational richness peaks, evaluated for trees in the east Himalaya. *Ecology* **2019**, *100*, e02548. [CrossRef]
15. Albrecht, J.; Peters, M.K.; Becker, J.N.; Behler, C.; Classen, A.; Ensslin, A.; Ferger, S.W.; Gebert, F.; Gerschlauer, F.; Helbig-Bonitz, M.; et al. Species richness is more important for ecosystem functioning than species turnover along an elevational gradient. *Nat. Ecol. Evol.* **2021**, *5*, 1582–1593. [CrossRef]
16. Olson, D.M. The Distribution of Leaf Litter Invertebrates Along a Neotropical Altitudinal Gradient. *J. Trop. Ecol.* **1994**, *10*, 129–150. [CrossRef]
17. Rahbek, C. The altitudinal gradient of species richness: A uniform pattern? *Ecography* **1995**, *18*, 200–205. [CrossRef]
18. McCain, C.M. Global analysis of bird elevational diversity. *Glob. Ecol. Biogeogr.* **2009**, *18*, 346–360. [CrossRef]
19. Beck, J.; Liedtke, H.C.; Widler, S.; Altermatt, F.; Loader, S.P.; Hagmann, R.; Lang, S.; Fiedler, K. Patterns or mechanisms? Bergmann's and Rapoport's rule in moths along an elevational gradient. *Community Ecol.* **2016**, *17*, 137–148. [CrossRef]
20. Quintero, I.; Jetz, W. Global elevational diversity and diversification of birds. *Nature* **2018**, *555*, 246–250. [CrossRef]
21. Casazza, G.; Zappa, E.; Mariotti, M.G.; Médail, F.; Minuto, L. Ecological and historical factors affecting distribution pattern and richness of endemic plant species: The case of the Maritime and Ligurian Alps hotspot. *Divers. Distrib.* **2008**, *14*, 47–58. [CrossRef]
22. Hufnagel, L.; Mics, F. Introductory Chapter: Factors That Affect Biodiversity and Species Richness of Ecosystems—A Review. In *Biodiversity of Ecosystems*; Hufnagel, L., Ed.; IntechOpen: London, UK, 2022; pp. 3–17. [CrossRef]
23. Birrell, J.H.; Shah, A.A.; Hotaling, S.; Giersch, J.J.; Williamson, C.E.; Jacobsen, D.; Woods, H.A. Insects in high-elevation streams: Life in extreme environments imperiled by climate change. *Glob. Change Biol.* **2020**, *26*, 5667–6684. [CrossRef] [PubMed]
24. Menéndez, R. How are insects responding to global warming? *Tijdschr. Entomol.* **2007**, *150*, 355–365.
25. Robinet, C.; Roques, A. Direct impacts of recent climate warming on insect populations. *Integr. Zool.* **2010**, *5*, 132–142. [CrossRef] [PubMed]
26. Ding, T.-S.; Yuan, H.-W.; Geng, S.; Lin, Y.-S.; Lee, P.-F. Energy flux, body size and density in relation to bird species richness along an elevational gradient in Taiwan. *Glob. Ecol. Biogeogr.* **2005**, *14*, 299–306. [CrossRef]
27. Malhi, Y.; Girardin, C.A.J.; Goldsmith, G.R.; Doughty, C.E.; Salinas, N.; Metcalfe, D.B.; Huasco, W.H.; Silva-Espejo, J.E.; del Aguilla-Pasquell, J.; Amezquita, F.F.; et al. The variation of productivity and its allocation along a tropical elevation gradient: A whole carbon budget perspective. *New Phytol.* **2017**, *214*, 1019–1032. [CrossRef]
28. Chen, T.; Peng, L.; Liu, S.; Wang, Q. Spatio-temporal pattern of net primary productivity in Hengduan Mountains area, China: Impacts of climate change and human activities. *Chin. Geogr. Sci.* **2017**, *27*, 948–962. [CrossRef]
29. Konvicka, M.; Benes, J.; Cizek, O.; Kuras, T.; Kleckova, I. Has the currently warming climate affected populations of the mountain ringlet butterfly, *Erebia epiphron* (Lepidoptera: Nymphalidae), in low-elevation mountains? *Eur. J. Entomol.* **2016**, *113*, 295–301. [CrossRef]

30. Storz, J.F. High-Altitude Adaptation: Mechanistic Insights from Integrated Genomics and Physiology. *Mol. Biol. Evol.* **2021**, *38*, 2677–2691. [CrossRef]
31. Stevens, G.C. The Elevational Gradient in Altitudinal Range: An Extension of Rapoport's Latitudinal Rule to Altitude. *Am. Nat.* **1992**, *140*, 893–911. [CrossRef]
32. Laiolo, P.; Pato, J.; Obeso, J.R. Ecological and evolutionary drivers of the elevational gradient of diversity. *Ecol. Lett.* **2018**, *21*, 1022–1032. [CrossRef]
33. Khatiwada, J.R.; Zhao, T.; Chen, Y.; Wang, B.; Xie, F.; Cannatella, D.C.; Jiang, J. Amphibian community structure along elevation gradients in eastern Nepal Himalaya. *BMC Ecol.* **2019**, *19*, 19. [CrossRef] [PubMed]
34. Moradi, H.; Fattorini, S.; Oldeland, J. Influence of elevation on the species–area relationship. *J. Biogeogr.* **2020**, *47*, 2029–2041. [CrossRef]
35. Li, M.; Feng, J. Biogeographical Interpretation of Elevational Patterns of Genus Diversity of Seed Plants in Nepal. *PLoS ONE* **2015**, *10*, e0140992. [CrossRef]
36. Gebrehiwot, K.; Demissew, S.; Woldu, Z.; Fekadu, M.; Desalegn, T.; Teferi, E. Elevational changes in vascular plants richness, diversity, and distribution pattern in Abune Yosef mountain range, Northern Ethiopia. *Plant Divers.* **2019**, *41*, 220–228. [CrossRef]
37. Colwell, R.K.; Gotelli, N.J.; Ashton, L.A.; Beck, J.; Brehm, G.; Fayle, T.M.; Fiedler, K.; Forister, M.L.; Kessler, M.; Kitching, R.L.; et al. Midpoint attractors and species richness: Modelling the interaction between environmental drivers and geometric constraints. *Ecol. Lett.* **2016**, *19*, 1009–1022. [CrossRef]
38. Hawkins, B.A.; Field, R.; Cornell, H.V.; Currie, D.J.; Gue'gan, J.F.; Kaufman, D.M.; Kerr, J.T.; Mittelbach, G.G.; Oberdorff, T.; O'Brien, E.M.; et al. Energy, water, and broad-scale geographic patterns of species richness. *Ecology* **2003**, *84*, 3105–3117. [CrossRef]
39. Beck, J.; Chey, V.K. Explaining the elevation diversity pattern of geometrid moths from Borneo: A test of five hypotheses. *J. Biogeogr.* **2008**, *35*, 1452–1464. [CrossRef]
40. Guo, Q.; Kelt, D.A.; Sun, Z.; Liu, H.; Hu, L.; Ren, H.; Wen, J. Global variation in elevational diversity patterns. *Sci. Rep.* **2013**, *3*, 3007. [CrossRef]
41. McCain, C.M.; Beck, J. Species turnover in vertebrate communities along elevational gradients is idiosyncratic and unrelated to species richness. *Glob. Ecol. Biogeogr.* **2016**, *25*, 299–310. [CrossRef]
42. Nogués-Bravo, D.; Araújo, M.B.; Romdal, T.; Rahbek, C. Scale effects and human impact on the elevational species richness gradients. *Nature* **2008**, *453*, 216–219. [CrossRef]
43. Dani, R.S.; Divakar, P.K.; Baniya, C.B. Diversity and composition of plants species along elevational gradient: Research trends. *Biodivers. Conserv.* **2023**, *32*, 2961–2980. [CrossRef]
44. Irl, S.D.H.; Harter, D.E.V.; Steinbauer, M.J.; Gallego, P.D.; Fernández-Palacios, J.M.; Jentsch, A.; Beierkuhnlein, C. Climate vs. topography—Spatial patterns of plant species diversity and endemism on a high-elevation island. *J. Ecol.* **2015**, *103*, 1621–1633. [CrossRef]
45. Ter Braak, C.J.F.; Prentice, I.C. A theory of gradient analysis. *Adv. Ecol. Res.* **1988**, *18*, 271–317. [CrossRef]
46. Semwal, R.L.; Nautiyal, S.; Sen, K.K.; Rana, U.; Maikhuri, R.K.; Rao, K.S.; Saxena, K.G. Patterns and ecological implications of agricultural land-use changes: A case study from central Himalaya, India. *Agric. Ecosyst. Environ.* **2004**, *102*, 81–92. [CrossRef]
47. Pandit, M.K. *Life in the Himalaya—An Ecosystem at Risk*; Harvard University Press: Cambridge, MA, USA, 2017.
48. Treloar, P.J.; Searle, M.P. (Eds.) *Himalayan Tectonics: A Modern Synthesis*; Geological Society, London, Special Publications: London, UK, 2019; Volume 483, pp. 1–17. [CrossRef]
49. Lomolino, M.V.; Riddle, B.; Whittaker, R. *Biogeography: Biological Diversity Across Space and Time*, 5th ed.; Sinauer Associates: Sunderland, MA, USA, 2016; 784p.
50. Myers, N.; Mittermeier, R.A.; Mittermeier, C.G.; da Fonseca, G.A.B.; Kent, J. Biodiversity hotspots for conservation priorities. *Nature* **2000**, *403*, 853–858. [CrossRef]
51. Grytnes, J.A.; Vetaas, O.R. Species richness and altitude: A comparison between null models and interpolated plant species richness along the Himalayan altitudinal gradient, Nepal. *Am. Nat.* **2002**, *159*, 294–304. [CrossRef]
52. Vetaas, O.R.; Grytnes, J.A. Distribution of vascular plant species richness and endemic richness along the Himalayan elevation gradient in Nepal. *Glob. Ecol. Biogeogr.* **2002**, *11*, 291–301. [CrossRef]
53. Chawla, A.; Rajkumar, S.; Singh, K.N.; Lal, B.; Singh, R.D. Plant Species Diversity along an Altitudinal Gradient of Bhabha Valley in Western Himalaya. *J. Mt. Sci.* **2008**, *5*, 157–177. [CrossRef]
54. Wani, Z.A.; Khan, S.; Bhat, J.A.; Malik, A.H.; Alyas, T.; Pant, S.; Siddiqui, S.; Moustafa, M.; Ahmad, A.E. Pattern of β-Diversity and Plant Species Richness along Vertical Gradient in Northwest Himalaya, India. *Biology* **2022**, *11*, 1064. [CrossRef]
55. Thorne, J.H.; Choe, H.; Dorji, L.; Yangden, K.; Wangdi, D.; Phuntsho, Y.; Beardsley, K. Species richness and turnover patterns for tropical and temperate plants on the elevation gradient of the eastern Himalayan Mountains. *Front. Ecol. Evol.* **2022**, *10*, 942759. [CrossRef]
56. Chettri, B.; Bhupathy, S.; Acharya, B.K. Distribution pattern of reptiles along an eastern Himalayan altitude gradient. India. *Acta Oecol.* **2010**, *36*, 16–22. [CrossRef]

57. Acharya, B.K.; Vijayan, L. Butterfly diversity along the altitude gradient of Eastern Himalaya, India. *Ecol. Res.* **2015**, *30*, 909–919. [CrossRef]
58. Magurran, A.E.; McGill, B.J. *Biological Diversity: Frontiers in Measurement and Assessment*; Oxford University Press: Oxford, UK, 2011; 368p.
59. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2020. Available online: https://www.R-project.org/ (accessed on 2 November 2020).
60. Ter Braak, C.J.F.; Šmilauer, P. *CANOCO Reference Manual and User's Guide to Canoco for Windows*; Microcomputer Power: Ithaca, NY, USA, 1998; 352p.
61. Šmilauer, P.; Leps, J. *Multivariate Analysis of Ecological Data Using CANOCO 5*; Cambridge University Press: Cambridge, UK, 2014.
62. Kessler, M.; Kluge, J.; Hemp, A.; Ohlemüller, R. A global comparative analysis of elevational species richness patterns of ferns. *Glob. Ecol. Biogeogr.* **2011**, *20*, 868–880. [CrossRef]
63. Costa, F.V.d.; Viana-Júnior, A.B.; Aguilar, R.; Silveira, F.A.O.; Cornelissen, T.G. Biodiversity and elevation gradients: Insights on sampling biases across worldwide mountains. *J. Biogeogr.* **2023**, *50*, 1879–1889. [CrossRef]
64. Chandra, K.; Kumar, V.; Singh, N.; Raha, A.; Sanyal, A.K. *Assemblages of Lepidoptera in Indian Himalaya Through Long Term Monitoring Plots*; Zoological Survey of India: Kolkata, India, 2019; 457p.
65. Paudel, P.K.; Šipoš, J. Conservation status affects elevational gradient in bird diversity in the Himalaya: A new perspective. *Glob. Ecol. Conserv.* **2014**, *2*, 338–348. [CrossRef]
66. Ghimire, A.; Rokaya, M.B.; Timsina, B.; Bílá, K.; Shrestha, U.B.; Chalise, M.K.; Kindlmann, P. Diversity of birds recorded at different altitudes in central Nepal Himalayas. *Ecol. Indic.* **2021**, *127*, 107730. [CrossRef]
67. Baniya, C.B.; Solhøy, T.; Gauslaa, Y.; Palmer, M.W. Richness and Composition of Vascular Plants and Cryptogams along a High Elevational Gradient on Buddha Mountain, Central Tibet. *Folia Geobot.* **2012**, *47*, 135–151. [CrossRef]
68. Klimes, L. Life-forms and clonality of vascular plants along an altitudinal gradient in E Ladakh (NW Himalayas). *Basic Appl. Ecol.* **2003**, *4*, 317–328. [CrossRef]
69. Manish, K.; Pandit, M.K.; Telwala, Y.; Nautiyal, D.C.; Koh, L.P.; Tiwari, S. Altitudinal plant species richness patterns and their drivers across non-endemics, endemics and growth forms in the Eastern Himalaya. *J. Plant Res.* **2017**, *130*, 829–844. [CrossRef]
70. Liang, J.; Ding, Z.; Lie, G.; Zhou, Z.; Singh, P.K.; Zhang, Z.; Hu, H. Species richness patterns of vascular plants and their drivers along an elevational gradient in the central Himalayas. *Glob. Ecol. Conserv.* **2020**, *24*, e01279. [CrossRef]
71. Macek, M.; Dvorský, M.; Klimeš, A.; Wild, J.; Doležal, J.; Kopecký, M. Midpoint attractor models resolve the mid-elevation peak in Himalayan plant species richness. *Ecography* **2021**, *44*, 1665–1677. [CrossRef]
72. Kala, C.P.; Mathur, V.B. Patterns of plant species distribution in the Trans-Himalayan region of Ladakh, India. *J. Veg. Sci.* **2002**, *13*, 751–754. [CrossRef]
73. Dvorský, M.; Doležal, J.; de Bello, F.; Klimešová, J.; Klimeš, L. Vegetation types of East Ladakh: Species and growth form composition along main environmental gradients. *Appl. Veg. Sci.* **2011**, *14*, 132–147. [CrossRef]
74. Klimešová, J.; Doležal, J.; Dvorský, M.; de Bello, F.; Klimeš, L. Clonal growth forms in eastern Ladakh, Western Himalayas: Classification and habitat preferences. *Folia Geobot.* **2011**, *46*, 191–217. [CrossRef]
75. Namgail, T.; Rawat, G.S.; Mishra, C.; vaan Wieren, S.E.; Prins, H.H.T. Biomass and diversity of dry alpine plant communities along altitudinal gradients in the Himalayas. *J. Plant Res.* **2012**, *125*, 93–101. [CrossRef]
76. Jahan, R. Altitudinal distribution and spatial pattern of species richness of the high mountain flora: A case study on Ladakh (Himalaya). *Jahangirnagar Rev. Part II Soc. Sci.* **2021**, *XLV*, 99–106.
77. Favre, A.; Michalak, I.; Chen, C.-H.; Wang, J.-C.; Pringle, J.S.; Matuszak, S.; Sun, H.; Yuan, Y.-M.; Struwe, L.; Muellner-Riehl, A.N. Out-of-Tibet: The spatio-temporal evolution of *Gentiana* (Gentianaceae). *J. Biogeogr.* **2016**, *43*, 1967–1978. [CrossRef]
78. Ebersbach, J.; Schnitzler, J.; Favre, A.; Muellner-Riehl, A.N. Evolutionary radiations in the species-rich mountain genus *Saxifraga* L. *BMC Ecol. Evol.* **2017**, *17*, 119. [CrossRef]
79. Colwell, R.K.; Hurtt, G.C. Non biological gradients in species richness and a spurious Rapoport's effect. *Am. Nat.* **1994**, *144*, 570–595. [CrossRef]
80. Colwell, R.K.; Mao, C.X.; Chang, J. Interpolating, Extrapolating, and Comparing incidence-based species accumulation curves. *Ecology* **2004**, *85*, 2717–2727. [CrossRef]
81. Fischer, A.; Blaschke, M.; Bässler, C. Altitudinal gradients in biodiversity research: The state of the art and future perspectives under climate change aspects. *Wald. Landschaftsforschung Und Naturschutz* **2011**, *11*, 35–47.
82. Grytnes, J.A. Species-richness patterns of vascular plants along seven altitudinal transects in Norway. *Ecography* **2003**, *26*, 291–300. [CrossRef]
83. Hausdorf, B. Latitudinal and altitudinal diversity patterns and Rapoport effects in north-west European land snails and their causes. *Biol. J. Linn. Soc.* **2006**, *87*, 309–323. [CrossRef]
84. Rowe, R.J. Environmental and geometric drivers of small mammal diversity along elevational gradients in Utah. *Ecography* **2009**, *32*, 411–422. [CrossRef]

85. Choi, S.-W.; Thein, P.P. Distribution breadth and species turnover of night-flying beetles and moths on different mainland and island mountains. *Ecol. Res.* **2018**, *33*, 237–247. [CrossRef]
86. Kluge, J.; Kessler, M.; Dunn, R.R. What drives elevational patterns of diversity? A test of geometric constraints climate and species pool effects for pteridophytes on an elevational gradient in Costa Rica. *Glob. Ecol. Biogeogr.* **2006**, *15*, 358–371. [CrossRef]
87. Sublett, C.A.; Cook, J.L.; Janovec, J.P. Species richness and community composition of sphingid moths (Lepidoptera: Sphingidae) along an elevational gradient in southeastern Peru. *Zoologia* **2019**, *36*, e32938. [CrossRef]
88. Heaney, L.R. Small Mammal Diversity along Elevational Gradients in the Philippines: An Assessment of Patterns and Hypotheses. *Glob. Ecol. Biogeogr.* **2001**, *10*, 15–39. [CrossRef]
89. Beck, J.; McCain, C.M.; Axmacher, J.C.; Ashton, L.A.; Bärtschi, F.; Brehm, G.; Choi, S.-W.; Cizek, O.; Colwell, R.K.; Fiedler, K.; et al. Elevational species richness gradients in a hyperdiverse insect taxon: A global meta-study on geometrid moths. *Glob. Ecol. Biogeogr.* **2017**, *26*, 412–424. [CrossRef]
90. Koch, G.W.; Sillett, S.C.; Jennings, G.M.; Davis, S.D. The limit to tree height. *Nature* **2004**, *428*, 851–854. [CrossRef]
91. Jacobsen, D. Low oxygen pressure as a driving factor for the altitudinal decline in taxon richness of stream macroinvertebrates. *Oecologia* **2008**, *154*, 795–807. [CrossRef] [PubMed]
92. McCain, C.M. The mid-domain effect applied to elevational gradients: Species richness of small mammals in Costa Rica. *J. Biogeogr.* **2004**, *31*, 19–31. [CrossRef]
93. Dunn, R.R.; McCain, C.M.; Sanders, N.J. When Does Diversity Fit Null Model Predictions? Scale and Range Size Mediate the Mid-Domain Effect. *Glob. Ecol. Biogeogr.* **2007**, *16*, 305–312. [CrossRef]
94. Hu, Y.; Ding, Z.; Jiang, Z.; Quan, Q.; Guo, K.; Tian, L.; Hu, H.; Gibson, L. Birds in the Himalayas: What drives beta diversity patterns along an elevational gradient? *Ecol. Evol.* **2018**, *8*, 11704–11716. [CrossRef]
95. Wiens, J. The niche, biogeography and species interactions. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **2011**, *366*, 2336–2350. [CrossRef]
96. Heads, M. Passive uplift of plant and animal populations during mountain-building. *Cladistics* **2019**, *35*, 550–572. [CrossRef]
97. Varga, Z.S.; Schmitt, T. Types of oreal and oreotundral disjunctions in the western Palearctic. *Biol. J. Linn. Soc.* **2008**, *93*, 415–430. [CrossRef]
98. Louy, D.; Habel, J.C.; Abadjiev, S.; Rákosy, L.; Varga, Z.; Rödder, D.; Schmitt, T. Molecules and models indicate diverging evolutionary effects from parallel altitudinal range shifts in two mountain Ringlet butterflies. *Biol. J. Linn. Soc.* **2014**, *112*, 569–583. [CrossRef]
99. Nicolas, A.H.; Morenob, J.S.; Ortiz-Movliav, C.; Palacio, R.D. Biogeographic regions and events of isolation and diversification of the endemic biota of the tropical Andes. *Proc. Natl. Acad. Sci. USA* **2018**, *115*, 7985–7990. [CrossRef]
100. Kindlmann, P. *Himalayan Biodiversity in the Changing World*; Springer Science & Business Media: Berlin/Heidelberg, Germany, 2012; 226p.