

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/323229049>

# Scale sensitivity of the relationship between alpha and gamma diversity along an alpine elevation gradient in central Nepal

Article in *Journal of Biogeography* · February 2018

DOI: 10.1111/jbi.13188

CITATIONS

41

READS

233

3 authors:



**Kuber P Bhatta**

University of Bergen

47 PUBLICATIONS 465 CITATIONS

SEE PROFILE



**John Arvid Grytnes**

University of Bergen

210 PUBLICATIONS 13,328 CITATIONS

SEE PROFILE



**Ole R. Vetaas**

University of Bergen

135 PUBLICATIONS 5,776 CITATIONS

SEE PROFILE

# Scale sensitivity of the relationship between alpha and gamma diversity along an alpine elevation gradient in central Nepal

Kuber Prasad Bhatta<sup>1</sup>  | John-Arvid Grytnes<sup>2</sup> | Ole Reidar Vetaas<sup>1</sup> 

<sup>1</sup>Department of Geography, University of Bergen, Bergen, Norway

<sup>2</sup>Department of Biology, University of Bergen, Bergen, Norway

## Correspondence

Kuber Prasad Bhatta, Department of Geography, University of Bergen, Bergen, Norway.

Email: kuber.bhatta@uib.no

## Funding information

Meltzer Research Fund (Meltzer - prosjektstipend), Grant/Award Number: 10885

Editor: Holger Kreft

## Abstract

**Aim:** Components of scale, such as grain, focus and extent, influence the spatial patterns of alpha and gamma diversity and the relationships between them. We explored these scale relations by testing whether the gamma diversity and alpha diversity along an elevation gradient were related independent of scale and whether the elevational patterns of herbaceous and woody species richness were dependent on scale.

**Location:** Langtang National Park, Nepal.

**Methods:** We estimated alpha diversity (plot richness) for woody and herbaceous plant species along an alpine elevation gradient (3,900–5,000 m a.s.l.) in nested plots of 1 m<sup>2</sup>, 16 m<sup>2</sup> and 100 m<sup>2</sup> and gamma diversity (regional richness) from published sources. Generalized linear modelling was used to analyse alpha and gamma diversity and their correspondence at different grain sizes.

**Results:** Elevational trends of gamma and alpha diversity were significantly correlated for both woody and herbaceous species at all grain sizes. The concordance increased with increasing grain size and area for gamma diversity estimation, particularly for the monotonously decreasing elevational gamma and alpha diversity patterns of woody species. The hump-shaped patterns of elevational gamma and alpha diversity for herbaceous species were also significantly correlated, but the concordance between the alpha diversity of herbaceous species and local gamma diversity was stronger. Elevational patterns of alpha diversity were coarsely consistent across grain sizes, although the patterns became more pronounced at larger grain sizes.

**Main conclusions:** The correspondence of elevational gamma and alpha diversity was largely scale invariant, implying that elevational and possibly other geographical diversity patterns can reliably be studied at different spatial scales. Nonetheless, the alpha diversity pattern was the least pronounced at fine grain size, particularly for woody life-forms. This finding suggests that for large-scale patterns such as elevational gradients at regional or continental scales, coarse grain sizes and large areas for gamma estimation are more appropriate.

## KEYWORDS

alpha diversity, elevation gradient, gamma diversity, generalized linear model, grain, plot richness, spatial scale, species richness

## 1 | INTRODUCTION

The exploration of species richness gradients is a major theme in biogeography, ecology and conservation science (Gotelli & Colwell, 2001; Kessler, Kluge, Hemp, & Ohlemüller, 2011). Species richness as currently perceived is naturally scale-dependent, and the patterns of richness and their explanatory factors vary over spatial scales (Karger et al., 2011; Nogués-Bravo, Araújo, Romdal, & Rahbek, 2008; Rowe, Heaney, & Rickart, 2015). However, evident systematic differences in the patterns and perceptions among the richness studies at different spatial scales imply that differences also exist in the methods of study and the nature of the quantified data (Kessler et al., 2009). Whether discrepancies in observed patterns are scale-related or due to variation in the methods used is often difficult to determine. Maintaining consistency among the methodologies of species richness studies to develop a more complete understanding of the spatial patterns of species richness is therefore a major challenge (Karger et al., 2011).

Although the species–area relationship is one of the best-documented patterns among species richness studies (Lomolino, Riddle, Whittaker, & Brown, 2010; Scheiner et al., 2011), the grain size sensitivity of richness patterns along environmental gradients continues to generate concern (e.g. Belmaker & Jetz, 2011; Nogués-Bravo et al., 2008; Rahbek & Graves, 2001; Rowe et al., 2015; Tuomisto et al., 2016). Previous studies on species richness have also illustrated an effect of scale on both the degree of nonlinearity in richness patterns (e.g. Karger et al., 2011; Nogués-Bravo et al., 2008; Rowe et al., 2015; Tuomisto et al., 2016) and gamma–alpha diversity relationships (e.g. Gering & Crist, 2002; Michalet et al., 2015; Szava-Kovats, Ronk, & Pärtel, 2013). The direct species–area relationship asserts that species richness in a region is directly influenced by its area because larger areas have more species (Rosenzweig, 1995). Therefore, as the area of a region increases, its species richness also increases; rapidly at first, and then more slowly as area increases (Lomolino, 2000). However, in addition to the direct effect of area, gamma diversity (here, the total species richness of an entire elevational zone, *sensu* Lomolino, 2001) may influence the alpha diversity or plot richness (the number of species recorded within a sample plot) via an indirect effect of area (Romdal & Grytnes, 2007). This is because the gamma diversity of larger areas would include more species and alpha diversity in this condition can be perceived as dynamic samples drawn from regional diversity. Therefore, a relation is expected between the patterns of gamma diversity and plot richness for a region (Rosenzweig & Ziv, 1999).

However, the classical tests of local versus regional diversity relationships reveal contrasting linear or curvilinear patterns; furthermore, the reliability of most of the tests and their interpretations have been questioned (Cornell & Harrison, 2014). Moreover, for plants, the scale sensitivity of richness patterns may vary considerably according to the life-form of the plant species due to variations in their functional characteristics and the scale sensitivity of their

environmental determinants (see Bhattarai & Vetaas, 2003; Qian, 2013; Rowe et al., 2015; Wang, Fang, Sanders, White, & Tang, 2009). Thus, whether a linear or curvilinear relationship between local and regional richness is consistent across different grain sizes, areas from which gamma diversity is estimated, and plant life-forms remains unclear. Additionally, the use of extrapolated data sets from different sources in most of the cross-scale richness studies makes these studies prone to inconsistencies in the sampling techniques, sampling effort, area and proportion of the gradient and spatial heterogeneity of the sample plots. To date, empirical assessments based on a standard methodology and precisely comparable data at a fine grain scale are very few (but see Grytnes, 2003; Grytnes & Birks, 2003). Therefore, to explore these relationships, precisely comparable empirical data sets and standardized techniques are required, and an explicit correlation between gamma diversity and the plot richness of different plant life-forms at different spatial scales must be established.

The above-mentioned scale-related concerns of species richness are highly significant along any environmental gradient. However, the large differences in climate that occur over short geographical distances along an elevation gradient in mountain regions make elevation gradients particularly suitable for studies on climate-driven richness patterns (Grytnes & McCain, 2007). Therefore, the elevational gradient is convenient also for the study of the scale sensitivity of richness patterns. Because of the large variation in species composition over a short distance, grain size may significantly influence the estimation of alpha diversity patterns in alpine areas and hence the strength of the relationship between alpha and gamma diversity. We used an alpine elevation gradient in the central Himalaya, where species composition varies extensively over short distances and where scale-influenced variations in richness patterns are thus expected to be highly evident. To analyse the scale sensitivity of species richness, we varied different scale variables such as grain size (size of the sampling unit), focus (total area sampled in each 100-m elevation band) and area for gamma diversity estimation (i.e. regional versus local gamma diversity).

We analysed the influence of grain size and area for gamma diversity estimation on the correspondence between elevational patterns of gamma and alpha diversity. We also assessed the elevational pattern of empirical species richness for different plant life-forms at different grain sizes while maintaining a consistent sampling strategy, proportion of the elevation gradient and extent of sampling area for different grain sizes. The elevational richness data of different scales and plant life-forms were directly tested against one another in this study. Therefore, the findings of this study have significant implications for understanding the biodiversity patterns and processes of the high-elevation Himalaya and their drivers at different spatio-temporal scales. This information can ultimately contribute to the sustainable management of regional biodiversity. Moreover, the study reveals whether the species data of a different scale can be compared or synthesized for a region, which is crucial for studies concerning spatio-temporal changes in the patterns of biodiversity.



The main questions we posed were the following: How does scale (grain size, focus and area for gamma diversity estimation) influence the elevational gamma–alpha diversity relationship of different plant life-forms? And does the elevational pattern of alpine-plant species richness vary across grain sizes? The elevation ranges of flowering plant species of Nepal have been widely used for the interpolation of regional species richness (e.g. Bhattarai & Vetaas, 2006), where the elevation range of a species is partitioned into 100-m vertical bands and the species is assumed to be present in each 100-m band between its upper and lower limits. Interpolated plant species richness for Nepal reveals a hump-shaped elevational pattern for herbs with the maximum richness between 4,000 and 4,100 m a.s.l. and a pattern of linear decline for woody species. Therefore, we a priori interpreted the gamma diversity along the alpine elevation gradient as hypotheses regarding the alpha diversity patterns as follows: (1) a significant linear relationship occurs between elevational alpha and gamma diversity at all grain sizes, at all areas of gamma diversity estimation, and for both life-forms. If this relationship is verified, we hypothesize that (2) a hump-shaped relationship occurs between herbaceous species richness and elevation and that a monotonic decreasing trend in woody species richness occurs along the elevation gradient in the alpine zone, (3) irrespective of grain size.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

We conducted sampling along an alpine elevation gradient in Langtang National Park, central Nepal, from July to October 2014. The sample plots were placed along two mountain slopes: Yala Mountain (Site-1) (28°12' N, 85°35' E) between 4,000 and 5,000 m a.s.l. and Pansang Mountain (Site-2) (28°10' N, 85°23' E) between 3,900 and 4,400 m a.s.l. (Figure 1a–c). The Pansang-Yala range is part of the central Himalaya and is within a zone of subalpine/cool to alpine/cold climate, with ~650 mm of annual precipitation and frequent snowfall throughout the winter months (Bhatta, Rokaya, & Münzbergová, 2015; Miehe et al., 2015). Average monthly temperatures recorded at the nearest weather station (Kyanjing weather station/no. 1031.3, 3,920 m a.s.l.; ~3–5 km from the sampling locations) range from –6.13–3.63°C (winter) to 6.44–11.43°C (summer) (unpublished data from Department of Meteorology and Hydrology, Nepal from 1988–2010).

The vegetation of the area consists of subalpine (upper montane) and alpine associations (Miehe et al., 2015). The forest limit in the study area is at approximately 3,800 m a.s.l., and the tree line ecotone extends approximately from 3,800 to 3,900 m a.s.l. The subalpine vegetation (ca. 3,000–4,000 m a.s.l.) is characterized by the predominance of *Abies spectabilis*, *Betula utilis* and *Rhododendron campanulatum*. On the drier slopes, junipers are associated with the shrubby rhododendrons. Alpine vegetation between ca. 4,000 and 4,300 m a.s.l. consists of dwarf shrubs such as *Ephedra gerardiana*, *Rhododendron lepidotum* and *R. setosum*, and herbs in the genera

*Anemone*, *Pedicularis* and *Primula*. The upper alpine zone between ca. 4,300 and 5,000 m consists of alpine meadows dominated by graminoids. Settlements are in the valley bottoms from 2,800 to 3,900 m, and pastoralism, agriculture and tourism are the primary forms of livelihood (Bhatta et al., 2015).

### 2.2 | Field sampling

We sampled 123 nested plots along eight transects of different lengths between 3,900 and 5,000 m a.s.l. to include the maximum possible habitat and plant species diversity along the two mountain slopes (Figure 1c, Table S1 in Appendix S1). We followed a systematic sampling strategy along the transects (cf. Bhatta, Chaudhary, & Vetaas, 2012), and depending upon the availability of suitable space, we placed 3–5 nested plots (each of three different grain sizes: 1 m<sup>2</sup>, 16 m<sup>2</sup> and 100 m<sup>2</sup>) at a distance of 30–50 m in each 100-m elevation band along each transect (Figure 1d). We recorded vascular plant species in each plot and measured the elevation (m a.s.l.) of each sample plot using a GPS reader (Garmin eTrex® 10, Garmin Corporation, New Taipei City, Taiwan, China). Further details of the field sampling and the list of the recorded species are given in the supporting material (Text S1 and Table S2 in Appendix S1).

### 2.3 | Data analyses

#### 2.3.1 | Gamma diversity estimation

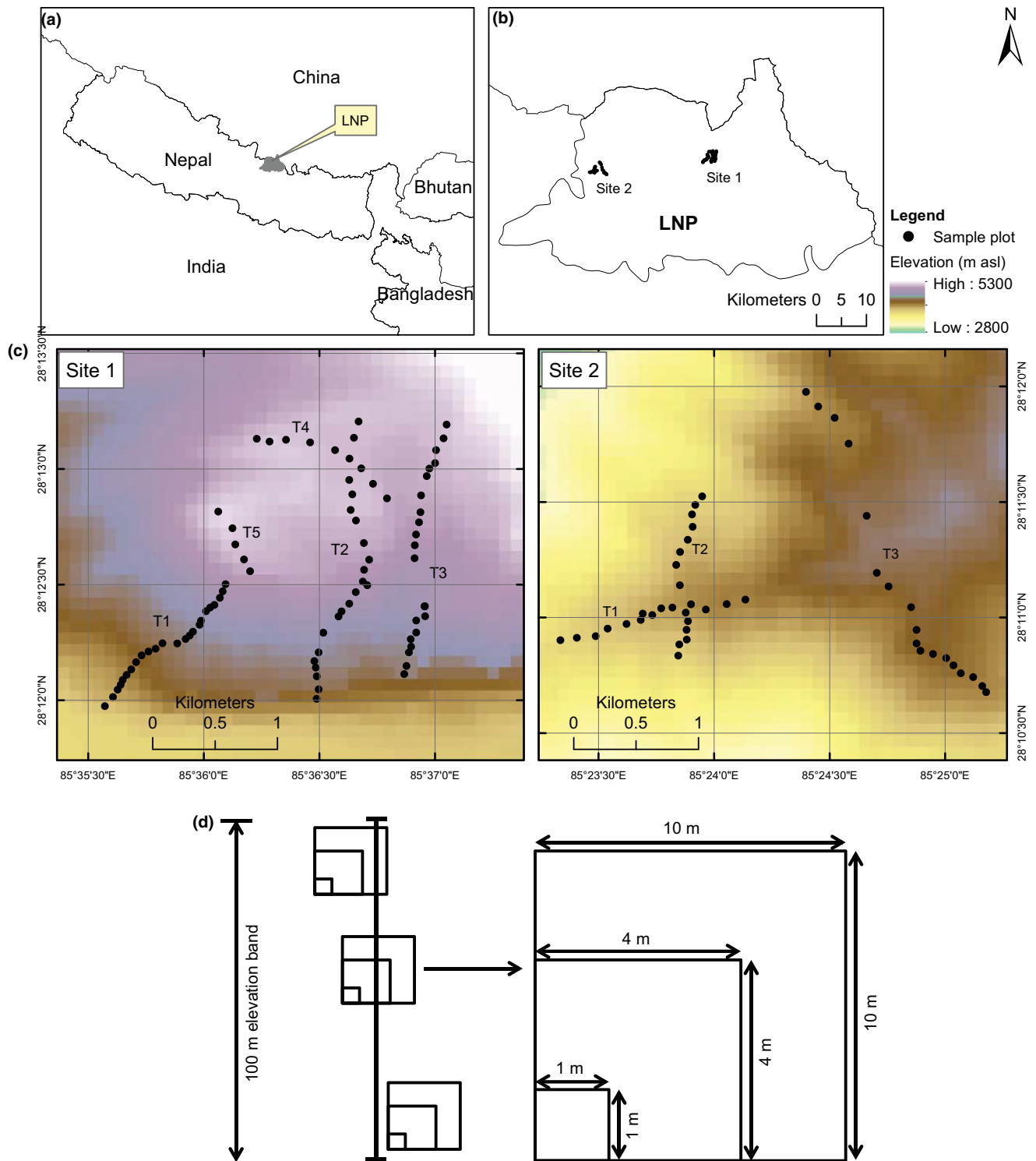
Regional elevational gamma diversity (sensu Lomolino, 2001) of a particular 100-m elevation band was estimated by calculating the interpolated richness (using species ranges from Press, Shrestha, & Sutton, 2000) for that band in central Nepal. Furthermore, we regarded the alpha diversity of the largest focus (cumulative plot richness of the 100 m<sup>2</sup> grain size in each 100-m elevation band) as the local gamma diversity.

#### 2.3.2 | Beta diversity (nestedness) estimation along an elevation gradient

We calculated the “nestedness” component of beta diversity (beta-nestedness) for the regional (gamma) and local (alpha) richness in each 100-m elevation band along the elevation gradients using the “betapart” package (Baselga & Orme, 2012) in R version 3.4.1 (R Core Team, 2017). Nestedness is the dissimilarity in species composition derived from the site-to-site species loss (Baselga & Orme, 2012).

#### 2.3.3 | Elevational gamma–alpha diversity relationship

To analyse whether alpha diversity of the different grain sizes corresponded consistently with gamma diversity, we regarded the plot richness at different grain sizes as the response and the regional and local gamma diversity as predictor variables in a generalized linear



**FIGURE 1** Study area with sampling locations and sampling scheme. (a) Outline map of Nepal with study area marked. (b) Location of the sampling sites. (c) Location of the transects. (d) Sketch of the sampling design for each 100-m elevation band. (a)–(c) replicated from Bhatta, Grytnes, and Vetaas (2018)

model (GLM). We used explained deviance (%) for each regression model across grain sizes as a measure of the goodness-of-fit. We treated the fit of a regression model as the power of the gamma diversity in explaining the plot-based alpha diversity pattern. We classified the species into two life-forms (herbs and woody species) and performed the same analysis separately for each group to

determine whether the correspondence between alpha and gamma diversity varied between the plant life-forms.

To test the statistical significance of the random effects of grain size and life-form on the elevational gamma–alpha relationship, we treated elevational gamma richness as a fixed effect and grain size and life-form as the random effects in a generalized linear mixed

model (GLMM) via Monte Carlo likelihood approximation ("glmm" package: Knudson, 2017). We also developed GLMs that included the two- and three-way interactions among grain size, life-forms and gamma richness to test whether the relationship between elevational gamma and alpha richness is influenced by grain size or plant life-form (Table S1 in Appendix S2). We performed all analyses using R.

### 2.3.4 | Elevational alpha diversity patterns across grain sizes

First, we applied a GLMM to test whether locality (sampling site and transect locality), grain size and plant life-form had effects on the observed elevational patterns of plot richness. For this test, we treated plot richness as the response variable, interactions of elevation, grain size and life-form as the fixed effect, and the locality variables as random effects. The random effect of site was not significant, whereas transect locality was marginally significant (Table S2a in Appendix S2). The transects were located at different elevations and were of insufficient length to be analysed separately for the elevational pattern of alpine species richness. Therefore, we pooled the data sets of all the transects in both sites for further analyses. An analysis of the fixed effects in GLMM revealed a significant interaction among grain size, life-form and elevation. Therefore, we analysed the elevational patterns of the two life-forms separately to reveal the grain size- and life-form-specific differences among the patterns.

We also performed a GLM to analyse the elevational patterns of plot richness of each life-form at different grain sizes. The regression models were fitted up to the third order polynomial and tested (chi-square test) against the null model and against one another to determine their significance in minimizing the residual deviance. Finally, the best model, i.e. the model that most significantly reduced the residual deviance compared with the competing models, was used for pattern interpretation. Because the predictor variable (elevation)

was the same for all the nested grain sizes, we regarded the explained deviance of each model as the explanatory power of the elevation gradient for the richness patterns and the comparisons across grain sizes. All regression analyses were performed in R.

## 3 | RESULTS

We recorded 190 (174 herbaceous and 16 woody), 234 (214 herbaceous and 20 woody) and 269 (243 herbaceous and 26 woody) species of vascular plants from 123 sample plots of 1 m<sup>2</sup>, 16 m<sup>2</sup> and 100 m<sup>2</sup> respectively (Table S2 in Appendix S1).

### 3.1 | Alpha–gamma diversity relationship

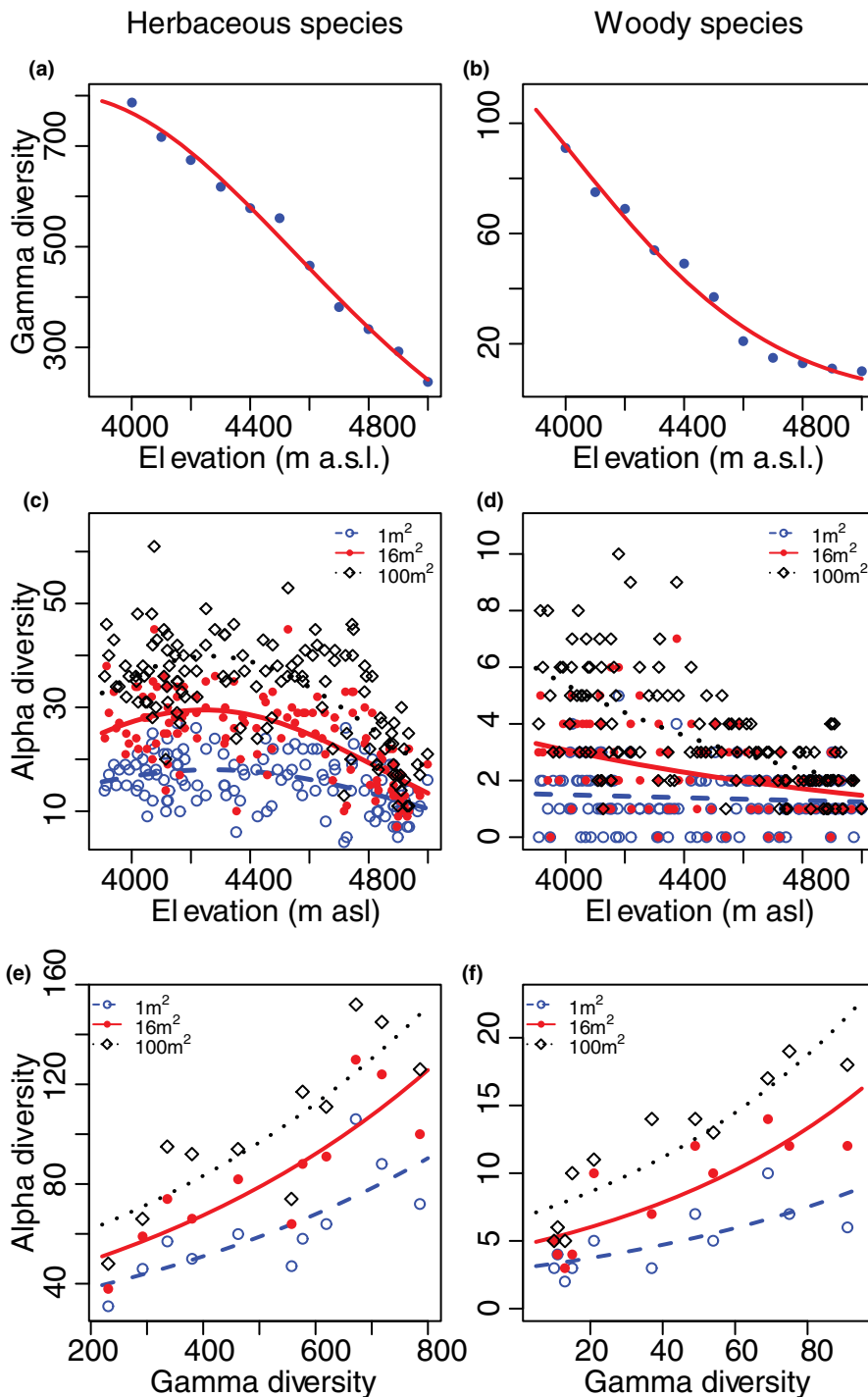
Overall, we found significant correlation between elevational patterns of alpha diversity and gamma diversity, at all grain sizes and for both plant life-forms (Table 1, Figure 2). The effect of grain size and plant life-form on the relationship between elevational gamma and alpha diversity was statistically insignificant (Table S1 in Appendix S2).

Within this overall scale-invariant pattern, minor but systematic variation in the degree of concordance between elevational alpha and gamma diversity patterns was observed. As indicated by the explained deviances of the regression models, the correspondence between alpha and gamma diversity mostly increased with increasing grain size (Table 1, Figure 2e,f). For both life-forms, the finest grain size explained less deviance than did the coarser grain sizes, particularly for woody species, for which the explained deviance was only marginally significant at the fine grain size (Expl. dev. = 55.31%,  $p = 0.01$ ), but increased linearly with increasing grain size (Expl. dev. = 66.08%,  $p = 2.00\text{e-}04$  and Expl. dev. = 76.67%,  $p = 2.37\text{e-}05$  for 16 m<sup>2</sup> and 100 m<sup>2</sup> grain size respectively). However, for the herbaceous species, the explained deviance increased only up to the

**TABLE 1** Relationship between plot-based plant species richness and gamma diversity at different grain sizes along an alpine elevation gradient in Nepal Himalaya. Plot richness is the response variable and gamma diversity is the predictor variable in the generalized linear models

Predictor	Response	Gr. (m <sup>2</sup> )	df	Null dev.	Resid. dev.	Z-value	p-value	Expl. dev.
(a) Regional gamma diversity (RGD) vs. empirical richness of different grain sizes								
RGD	Herb spp.	1	9	67.67	26.32	6.34	2.10e-10	61.11
RGD	Herb spp.	16	9	92.37	26.58	7.98	1.50e-15	71.22
RGD	Herb spp.	100	9	106.23	32.26	8.47	<2e-16	69.63
RGD	Woody spp.	1	9	10.83	4.84	2.45	0.01	55.31
RGD	Woody spp.	16	9	19.96	6.77	3.64	2.00e-04	66.08
RGD	Woody spp.	100	9	23.23	5.42	4.22	2.37e-05	76.67
(b) Local gamma diversity of the 100 m <sup>2</sup> grains (LGD) vs. empirical richness of smaller grains								
LGD	Herb spp.	1	9	67.67	4.53	7.87	3.80e-15	93.31
LGD	Herb spp.	16	9	92.36	3.95	9.29	<2e-16	95.72
LGD	Woody spp.	1	9	10.83	4.34	2.47	0.01	59.93
LGD	Woody spp.	16	9	19.96	5.18	3.7	2.14e-04	74.05

Gr., grain size; df, degrees of freedom; Null dev., null deviance; Resid. dev., residual deviance; Expl. dev., explained deviance.



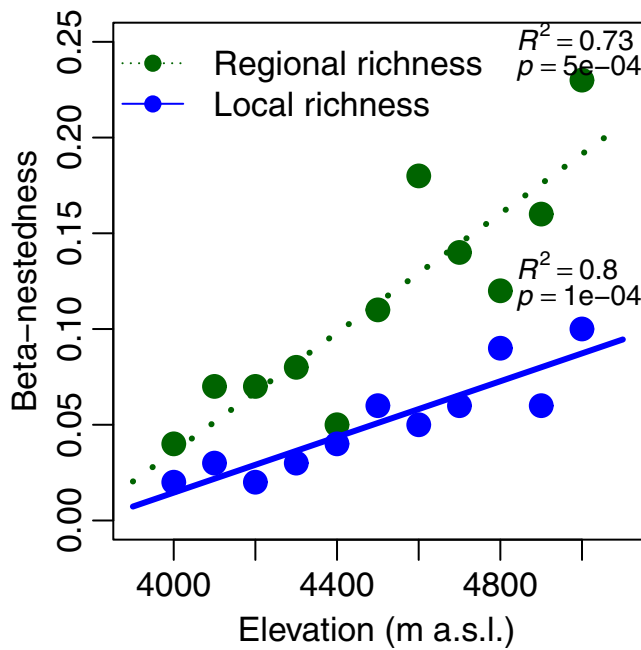
**FIGURE 2** Elevational gradients in plant gamma (regional richness) and alpha diversity (plot richness) in the alpine Nepal Himalaya. Gamma diversity pattern for (a) herbs and (b) woody species; empirical alpha diversity pattern for (c) herbs and (d) woody species at different grain sizes; concordance between gamma and alpha diversity for (e) herbs and (f) woody species at different grain sizes, with plot richness as the response variable and regional gamma diversity as the predictor variable in a generalized linear model

intermediate grain size (16 m<sup>2</sup>) (Expl. dev. = 61.11%, 71.22% and 69.63% for 1 m<sup>2</sup>, 16 m<sup>2</sup> and 100 m<sup>2</sup> grain size respectively (Figure 2e). The elevational pattern of site-to-site species loss was similar for the local (alpha) and regional (gamma) species richness, where the beta-nestedness for both alpha and gamma diversity increased linearly with elevation (Figure 3).

When we reduced the area for the gamma estimation from the regional to local scale (100 m<sup>2</sup> grain size), differences were apparent between the life-forms in their responses to gamma diversity. The

explained deviance for the herbaceous species increased significantly at all grain sizes (Expl. dev. = 93.31% and 95.72% for 1 m<sup>2</sup> and 16 m<sup>2</sup> grain size respectively), whereas increases in the explained deviance for the woody species were minor (Expl. dev. = 59.93% and 74.05% for 1 m<sup>2</sup> and 16 m<sup>2</sup> grain size respectively) (Appendix S3). In this case, for both life-forms, fine grain size explained less deviance than did coarse grain size. Notably, for the woody species, the explained deviance was only marginally significant at the fine grain size ( $p = 0.01$ ; Table 1b).





**FIGURE 3** Elevational trend of beta-nestedness (species loss) for regional and local plant species richness in the alpine Nepal Himalaya. Beta-nestedness was calculated for each 100-m elevation band

### 3.2 | Alpha diversity along the alpine elevation gradient

The empirical species richness (merged data of herbaceous and woody species) of both study sites revealed a prominent hump-shaped elevational pattern for all grain sizes, which reached a maximum between 4,000 and 4,400 m a.s.l. (Appendix S4). A similar pattern was revealed by the combined data set in which the maximum species richness was at ca. 4,200 m. The random effect of sampling site was not significant, and that of transect locality was only marginally significant (Table S2a in Appendix S2). However, there was a significant interaction ( $p = 0.01$ ) between grain size, life-form and elevation (Table S2a in Appendix S2). Accordingly, when we analysed the patterns of the different life-forms separately, differences were apparent. The pattern of herbaceous species richness with elevation was hump-shaped, whereas woody species richness showed a linear decline with

elevation; notably, there was no pattern of woody species richness observed at the finest grain size (Table 2, Figure 2c,d).

### 3.3 | Cross-grain variation of elevational alpha diversity patterns

We found a broad consistency in the cross-grain alpha diversity patterns of the two plant life-forms (herbs and woody species) largely irrespective of grain size, and the observed variations were minor and mostly not significant (Figure 2c,d, Table S2a in Appendix S2). However, the variations within the overall pattern were systematic. The hump-shaped pattern for herbaceous species and the linear pattern for woody species became more pronounced at coarse grain sizes (for herbs: Expl. dev. = 18.60%, 39.56% and 44.11% at 1 m<sup>2</sup>, 16 m<sup>2</sup> and 100 m<sup>2</sup> respectively; for woody species: Expl. dev. = 0.91%, 15.71% and 39.63% at 1 m<sup>2</sup>, 16 m<sup>2</sup> and 100 m<sup>2</sup> respectively) (Table 2). The separate analyses for each life-form revealed only a slightly significant ( $p = 0.05$ ) interaction between grain size and elevation (only at the first order) for herbaceous species richness (Table S2b in Appendix S2). However, woody species richness at the fine grain size did not reveal any pattern (Fig. 2d, Table 2), and a significant ( $p = 9.34e-04$ ) interaction between grain size and elevation was observed for woody species richness (Table S2c in Appendix S2).

## 4 | DISCUSSION

### 4.1 | Alpha–gamma diversity relationship

We hypothesized a significant concordance between elevational alpha and gamma diversity, which, if upheld, would verify the successful prediction of plot-based alpha diversity patterns by gamma diversity. Consistent with the hypothesis, we found that all the patterns produced by gamma diversity were reproduced at the alpha diversity scale; this finding was consistent for all grain sizes used to estimate alpha diversity and for both response variables (herbaceous and woody species). Similar results have been demonstrated, in part, by previous studies (e.g. Karger et al., 2011; Kessler et al., 2009). The underlying reason for this relation might be that in high mountain regions, the regional gamma diversity declines with increasing

**TABLE 2** Elevational pattern of plant species richness across grain sizes. Plot richness is the response variable and elevation of the sample plots is the predictor variable in the generalized linear models

Data set	Gr. (m <sup>2</sup> )	Model test	Null dev.	Resid. dev.	Expl. dev.	Z-value	df	p-value	Opt. (m a.s.l.)
Herb spp.	1	1st vs. 2nd order	215.13	175.10	18.60	−3.64	120	2.7e-04	4271
Herb spp.	16	1st vs. 2nd order	333.91	201.79	39.56	−6.10	120	1.0e-09	4245
Herb spp.	100	1st vs. 2nd order	389.68	217.78	44.11	−7.51	120	5.7e-14	4267
Woody spp.	1	Null vs. 1st order	106.11	105.14	0.91	−0.78	122	0.43	NA
Woody spp.	16	Null vs. 1st order	107.38	90.51	15.71	−3.99	122	6.5e-05	NA
Woody spp.	100	1st vs. 2nd order	126.97	76.65	39.63	−6.75	122	1.4e-11	NA

Gr., grain size; Null dev., null deviance; Resid. dev., residual deviance; Expl. dev., explained deviance; Opt., optimum of the richness curve; m a.s.l., metre above sea level; NA, not available.



elevation due to the decreases in land surface area (spatial extent) and length of growing season (temporal extent) (Körner, 2000, 2007). Therefore, the patterns of decrease in site-to-site compositional dissimilarity and the simultaneous increase in species loss with increasing elevation (indicating that more species were lost than new species were added into the locations) became similar for gamma and alpha diversity. Thus, in general, with respect to the type of existing species (regarding their gross adaptive features), habitats colonized by these species and the seasonality (Körner, 1997), the species diversity likely became more similar at both scales. Under such conditions, the species diversity at both scales was likely governed by similar types of drivers (primarily temperature and liquid soil water) in similar ways, resulting in similar elevational patterns (O'Brien, 2006).

Despite this general scale-invariant pattern, minor but systematic variation in the degree of concordance between alpha and gamma richness was detected. Thus, our results also support the assumption that the degree of concordance between gamma and alpha richness is higher at coarser grain sizes, which has been documented, in part, for other mountain areas (e.g. Romdal & Grytnes, 2007). At a coarser grain size, the regional gamma diversity can be more completely sampled and better represents the species diversity and abiotic environmental heterogeneity in a region (Connor & McCoy, 1979; Romdal & Grytnes, 2007; Rosenzweig & Ziv, 1999; Scheiner et al., 2011). In contrast, at a fine grain size, the number of species is constrained to a greater extent by the number of individuals that can occupy the small area (1 m<sup>2</sup>) than by the number of species in the regional gamma diversity (Connor & McCoy, 1979; Crawley & Harral, 2001; Oksanen, 1996; Rosenzweig, 1995). Furthermore, the heterogeneity of different environmental variables is expressed with different grain sizes, and hence, different factors regulate species richness at different grain size (Tuomisto et al., 2016). Therefore, as the grain size becomes finer, the environment becomes more unique, causing the filtering of the species that colonize in such small areas. These factors collectively lead to weaker concordance between alpha diversity and regional gamma diversity and regional environmental factors. This pattern was particularly apparent for the woody species. In contrast, many individuals (hence, many species) of the low-statured alpine herbs can occupy a small area (of 1–16 m<sup>2</sup>) and represent a good proportion of the overall species composition at that site. However, at such a fine scale, species diversity is structured more by local non-climatic factors, such as fine-scale habitat heterogeneity, soil chemistry, and disturbances, than by regional factors (Grytnes, 2003; Palmer, 2006; Wang et al., 2009). Consequently, herbaceous species richness and its correspondence to the regional gamma diversity did not increase proportionately with increasing grain size. Therefore, the causal factors of the richness patterns and their relative influences are particularly sensitive to spatial scale and thereby affect species–environment relationships in addition to those of gamma–alpha diversity (Belmaker & Jetz, 2011; Rowe et al., 2015).

Similarly, an increase in area for the gamma estimation from the local to regional scale provides a more complete and representative share of species, habitat diversity and environmental conditions that

increase the match with the pattern of local species composition (Drakare, Lennon, & Hillebrand, 2006; MacArthur & Wilson, 1967). Environmental heterogeneity is a universal driver of species richness and is sensitive to spatial scale (Stein, Gerstner, & Kreft, 2014). Incorporating more habitat diversity and abiotic environmental heterogeneity (*sensu* Stein & Kreft, 2015) such as different microtopography, soil conditions, slope expositions, physical disturbances such as snow and frost conditions, and regional climate (elevation gradient) is particularly important for capturing a representative woody species composition. This is because woody species richness along a high-elevation gradient remains low but in good concordance with the regional climate (primarily temperature) due to the high temperature sensitivity of the woody species (Bhattarai & Vetaas, 2003; D'Odorico et al., 2013; Qian, 2013; Wang et al., 2009). Hence, the regional gamma diversity can adequately represent the association of regional woody species diversity and climate, whereby species are filtered into local habitats. This indirect influence of the regional gamma diversity on plot richness is termed the “echo-effect” (*sensu* Rosenzweig & Ziv, 1999). However, the plot richness of woody species (of the smaller grain sizes) also revealed slightly higher concordance to local gamma diversity than to regional gamma diversity, which was most likely due to spatial effects rather than to the effects of gamma diversity and its environmental factors. Because the grains were nested in the present study, the distance between the centres of the smallest and the largest plot was only 4.5 m. Under such conditions, similarity in the species composition and the habitat conditions of such closely spaced grains is expected. Nevertheless, the response of herbaceous species richness to the local gamma diversity was clearly greater than was the response of woody species richness (see the above explanations).

## 4.2 | Alpha diversity along an alpine elevation gradient

We found a hump-shaped pattern of empirical species richness along an alpine elevation gradient, which is in contrast to the argument that the humped pattern of species richness might not be prominent, particularly for small grain sizes and along incomplete gradients (e.g. Nogués-Bravo et al., 2008; Rahbek, 2005). The broad consistency of the overall pattern not only across different grain sizes but also irrespective of sampling location and analytical technique suggests that the pattern was robust and real, at least at the regional scale. However, clear differences were observed in the patterns between the different life-forms, which are consistent with our second hypothesis. Herbaceous species richness exhibited a prominent hump-shaped pattern, whereas the pattern of woody species richness was a linear decline. These patterns are broadly consistent with elevational gamma richness patterns for Nepal, i.e. a hump-shaped pattern for herbaceous species with a richness maximum between 4,000 and 4,100 m a.s.l. (results not presented here) and a pattern of linear decline for woody species (Bhattarai & Vetaas, 2006).

The most plausible explanation for the humped pattern is that the lower alpine belt of Nepal Himalaya (i.e. above the forest limit at



~3,800 m [Miehe et al., 2015]) is dominated by shrub species from the genera *Cotoneaster*, *Juniperus* and *Rhododendron*. Herbaceous vegetation in this belt remains sparse under the dense cover of these shrubs. Herbs dominate the belt of alpine meadows above ca. 4,200 m; however, the upper elevation distribution of most of the alpine species is limited by extreme low temperature, frost and a scarcity of soil water. Herbaceous species, which constitute most of the alpine flora, find optimal environmental conditions in the areas between these extreme habitat conditions. A linear decline in the woody species richness along an alpine elevation gradient is most likely due to climatic factors, primarily temperature, that vary strongly with elevation and seasonal gradients in high mountain regions (Bhattarai & Vetaas, 2003; Qian, 2013; Wang et al., 2009). These climatic factors control the availability of liquid water and therefore the length of the growing season (O'Brien, 2006; Vetaas, 2006), which is particularly important for woody species because they generally have lower cold tolerances than do herbaceous species (D'Odorico et al., 2013; Körner, 1997).

### 4.3 | Cross-grain variation in alpha diversity

Partly verifying our third hypothesis, the elevational alpha diversity patterns for herbaceous species was largely independent of grain size in our study, as has been found in previous studies (e.g. Grytnes, 2003; Nogués-Bravo et al., 2008; Rowe et al., 2015). However, within the general scale-invariance, we observed some systematic differences in the patterns across grain sizes. As indicated by the increase in explained deviance of the regressions at the larger grain sizes, all the patterns became slightly more apparent with larger grain size. Because the sampling area (per 100-m elevation band), sampling technique, and the proportion of the elevation gradient were constant for each grain size, the minor but systematic variation in the elevational richness patterns can be attributed to the difference in the spatial scale of the grains. Such grain size dependency of alpha diversity richness was also revealed in several coarse-scale studies (Belmaker & Jetz, 2011; Crawley & Haral, 2001; Rahbek & Graves, 2001). The underlying cause might be that the coarse-scale driving factors of species diversity are scale-sensitive and their ability to explain the richness patterns declines significantly towards the finer grains (Belmaker & Jetz, 2011; Rowe et al., 2015). Therefore, although our analysis was somewhat crude (as we did not account for other community assembly processes such as dispersal or biotic interactions), perceived grain size sensitivity is a classic indication of environmental filtering, wherein the environment becomes more unique as the grain size decreases, causing deviation of local patterns from those at coarser scales. The patterns at the very fine grain size (e.g. 1 m<sup>2</sup>) are also restricted by the number of individuals that can occupy such small areas and by local factors such as disturbance and stochastic processes, which dampen the strength of the richness–environment relationship at fine grain sizes (Belmaker & Jetz, 2011; Gotelli & Colwell, 2001; Oksanen, 1996; Whittaker, Willis, & Field, 2001).

Woody species richness showed higher grain size sensitivity than did herbaceous species richness, as indicated by the trend of explained

deviance of the regression models across grain sizes. This higher sensitivity was most likely related to the scale sensitivity of the primary causal factor (temperature) of woody plant distribution along the elevation gradient and the life-form characteristics of the woody species. The likelihood of recording the woody species within a finer grain size is consistently low because of their large sizes and low densities compared with those of herbs in an alpine region (Oksanen, 1996), which could cause deviation from broad-scale patterns. However, at a coarser grain size, the gradient of woody species composition and its driving factor, i.e. elevation (regional temperature), are sampled more completely, resulting in stronger concordance than observed for woody species at smaller grain sizes (Belmaker & Jetz, 2011).

In conclusion, the correspondence of elevational gamma and alpha diversity was largely scale invariant in this study, which implies that elevational and possibly other geographical diversity patterns can reliably be studied at different spatial scales and that scale difference does not significantly distort the basic spatial pattern. Nonetheless, the least pronounced alpha diversity pattern was observed at the fine grain size, particularly for woody life-forms, which is most likely a consequence of small area and environmental filtering. This finding suggests that for large-scale patterns such as elevational gradients at regional or continental scales, coarse grain sizes and large areas for gamma estimation are desirable.

### ACKNOWLEDGEMENTS

The first author thanks the Meltzer Research Grant Commission for providing partial financial support for the research. We thank the Department of National Parks and Wildlife Conservation, Nepal, for granting permission to conduct research in the area under their administration. We also thank Joaquín Hortal and Marti Anderson for their valuable suggestions during data analyses, and Madan K. Suwal, Prakash Bhattarai, and Raghunath Chaudhary for their help during fieldwork.

### ORCID

Kuber Prasad Bhatta  <http://orcid.org/0000-0001-7837-1395>

Ole Reidar Vetaas  <http://orcid.org/0000-0002-0185-1128>

### REFERENCES

- Baselga, A., & Orme, C. D. L. (2012). betapart: An R package for the study of beta diversity. *Methods in Ecology and Evolution*, 3, 808–812. <https://doi.org/10.1111/j.2041-210X.2012.00224.x>
- Belmaker, J., & Jetz, W. (2011). Cross-scale variation in species richness–environment associations. *Global Ecology and Biogeography*, 20, 464–474. <https://doi.org/10.1111/j.1466-8238.2010.00615.x>
- Bhatta, K. P., Chaudhary, R. P., & Vetaas, O. R. (2012). A comparison of systematic versus stratified-random sampling design for gradient analyses: A case study in subalpine Himalaya, Nepal. *Phytocoenologia*, 42, 191–202. <https://doi.org/10.1127/0340-269X/2012/0042-0519>
- Bhatta, K. P., Grytnes, J.-A., & Vetaas, O. R. (2018). Downhill shift of alpine plant assemblages under contemporary climate and land-use changes. *Ecosphere*, 9, e02084. <https://doi.org/10.1002/ecs2.2084>

- Bhatta, K. P., Rokaya, M. B., & Münzbergová, Z. (2015). Environmental feedbacks of the subalpine ecotone species in the Langtang National Park, central Nepal Himalaya. *Pakistan Journal of Botany*, 47, 2115–2125.
- Bhattarai, K. R., & Vetaas, O. R. (2003). Variation in plant species richness of different life forms along a subtropical elevation gradient in the Himalayas, east Nepal. *Global Ecology and Biogeography*, 12, 327–340. <https://doi.org/10.1046/j.1466-822X.2003.00044.x>
- Bhattarai, K. R., & Vetaas, O. R. (2006). Can Rapoport's rule explain tree species richness along the Himalayan elevation gradient, Nepal? *Diversity and Distributions*, 12, 373–378. <https://doi.org/10.1111/j.1366-9516.2006.00244.x>
- Connor, E. F., & McCoy, E. D. (1979). The statistics and biology of the species-area relationship. *The American Naturalist*, 113, 791–833. <https://doi.org/10.1086/283438>
- Cornell, H. V., & Harrison, S. P. (2014). What are species pools and when are they important? *Annual Review of Ecology, Evolution, and Systematics*, 45, 45–67. <https://doi.org/10.1146/annurev-ecolsys-120213-091759>
- Crawley, M. J., & Harral, J. E. (2001). Scale dependence in plant biodiversity. *Science*, 291, 864–868. <https://doi.org/10.1126/science.291.5505.864>
- D'Odorico, P., He, Y., Collins, S., De Wekker, S. F. J., Engel, V., & Fuentes, J. D. (2013). Vegetation–microclimate feedbacks in woodland–grassland ecotones. *Global Ecology and Biogeography*, 22, 364–379. <https://doi.org/10.1111/geb.12000>
- Drakare, S., Lennon, J. J., & Hillebrand, H. (2006). The imprint of the geographical, evolutionary and ecological context on species–area relationships. *Ecology Letters*, 9, 215–227. <https://doi.org/10.1111/j.1461-0248.2005.00848.x>
- Gering, J. C., & Crist, T. O. (2002). The alpha–beta–regional relationship: Providing new insights into local–regional patterns of species richness and scale dependence of diversity components. *Ecology Letters*, 5, 433–444. <https://doi.org/10.1046/j.1461-0248.2002.00335.x>
- Gotelli, N. J., & Colwell, R. K. (2001). Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, 4, 379–391. <https://doi.org/10.1046/j.1461-0248.2001.00230.x>
- Grytnes, J. A. (2003). Species-richness patterns of vascular plants along seven altitudinal transects in Norway. *Ecography*, 26, 291–300. <https://doi.org/10.1034/j.1600-0587.2003.03358.x>
- Grytnes, J. A., & Birks, H. J. B. (2003). The influence of scale and species pool on the relationship between vascular plant species richness and cover in an alpine area in Norway. *Plant Ecology*, 169, 273–284. <https://doi.org/10.1023/A:1026099705238>
- Grytnes, J.-A., & McCain, C. M. (2007). Elevational trends in biodiversity. In S. A. Levin (Ed.), *Encyclopedia of biodiversity*, (pp. 1–8). New York: Elsevier.
- Karger, D. N., Kluge, J., Krömer, T., Hemp, A., Lehnert, M., & Kessler, M. (2011). The effect of area on local and regional elevational patterns of species richness. *Journal of Biogeography*, 38, 1177–1185. <https://doi.org/10.1111/j.1365-2699.2010.02468.x>
- Kessler, M., Kluge, J., Hemp, A., & Ohlemüller, R. (2011). A global comparative analysis of elevational species richness patterns of ferns. *Global Ecology and Biogeography*, 20, 868–880. <https://doi.org/10.1111/j.1466-8238.2011.00653.x>
- Kessler, M., Krömer, T., Kluge, J., Karger, D. N., Acebey, A., Hemp, A., & Lehnert, M. (2009). Elevational gradients of species richness derived from local field surveys versus 'mining' of archive data. In E. M. Spehn, & C. Körner (Eds), *Data mining for global trends in mountain biodiversity* (pp. 57–63). Boca Raton, FL: CRC Press/Taylor & Francis. <https://doi.org/10.1201/9781420083705>
- Knudson, C. (2017). *glmm: Generalized Linear Mixed Models via Monte Carlo Likelihood Approximation*, R package version 1.2.1. Retrieved from <https://cran.r-project.org/web/packages/glmm/index.html>
- Körner, C. (1997). *Alpine plant life*. Berlin: Springer Verlag.
- Körner, C. (2000). Why are there global gradients in species richness? mountains might hold the answer. *Trends in Ecology & Evolution*, 15, 513–514. [https://doi.org/10.1016/S0169-5347\(00\)02004-8](https://doi.org/10.1016/S0169-5347(00)02004-8)
- Körner, C. (2007). The use of 'altitude' in ecological research. *Trends in Ecology & Evolution*, 22, 569–574. <https://doi.org/10.1016/j.tree.2007.09.006>
- Lomolino, M. V. (2000). Ecology's most general, yet protean<sup>1</sup> pattern: The species-area relationship. *Journal of Biogeography*, 27, 17–26. <https://doi.org/10.1046/j.1365-2699.2000.00377.x>
- Lomolino, M. V. (2001). Elevation gradients of species-density: Historical and prospective views. *Global Ecology and Biogeography*, 10, 3–13. <https://doi.org/10.1046/j.1466-822X.2001.00229.x>
- Lomolino, M. V., Riddle, B. R., Whittaker, R. J., & Brown, J. H. (2010). *Biogeography*, 4th ed. Sunderland, MA: Sinauer Associates, Inc.
- MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton, NJ: Princeton University Press.
- Michalet, R., Maalouf, J.-P., Choler, P., Clément, B., Rosebery, D., Royer, J.-M., & Lortie, C. J. (2015). Competition, facilitation and environmental severity shape the relationship between local and regional species richness in plant communities. *Ecography*, 38, 335–345. <https://doi.org/10.1111/ecog.01106>
- Miehe, G., Miehe, S., Böhner, J., Bäumler, R., Ghimire, S. K., Bhattarai, K., ... Pendry, C. (2015). Vegetation Ecology. In G. Miehe, C. Pendry & R. Chaudhary (Eds), *Nepal: An Introduction to the natural history, ecology and human environment of the Himalayas* (pp. 385–472). Edinburgh: Royal Botanic Garden Edinburgh.
- Nogués-Bravo, D., Araújo, M. B., Romdal, T., & Rahbek, C. (2008). Scale effects and human impact on the elevational species richness gradients. *Nature*, 453, 216–219. <https://doi.org/10.1038/nature06812>
- O'Brien, E. M. (2006). Biological relativity to water–energy dynamics. *Journal of Biogeography*, 33, 1868–1888. <https://doi.org/10.1111/j.1365-2699.2006.01534.x>
- Oksanen, J. (1996). Is the humped relationship between species richness and biomass an artefact due to plot size? *Journal of Ecology*, 84, 293–295. <https://doi.org/10.2307/2261364>
- Palmer, M. W. (2006). Scale dependence of native and alien species richness in North American floras. *Preslia*, 78, 427–436.
- Press, J. R., Shrestha, K. K., & Sutton, D. A. (2000). *Annotated checklist of the flowering plants of Nepal*. London: The Natural History Museum.
- Qian, H. (2013). Environmental determinants of woody plant diversity at a regional scale in China. *PLoS ONE*, 8, e75832. <https://doi.org/10.1371/journal.pone.0075832>
- R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing Retrieved from <https://www.R-project.org/>
- Rahbek, C. (2005). The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, 8, 224–239. <https://doi.org/10.1111/j.1461-0248.2004.00701.x>
- Rahbek, C., & Graves, G. R. (2001). Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences of the United States of America*, 98, 4534–4539. <https://doi.org/10.1073/pnas.071034898>
- Romdal, T. S., & Grytnes, J.-A. (2007). An indirect area effect on elevational species richness patterns. *Ecography*, 30, 440–448. <https://doi.org/10.1111/j.0906-7590.2007.04954.x>
- Rosenzweig, M. L. (1995). *Species diversity in space and time*. Cambridge: Cambridge University Press. <https://doi.org/10.1017/CBO9780511623387>
- Rosenzweig, M. L., & Ziv, Y. (1999). The echo pattern of species diversity: Pattern and processes. *Ecography*, 22, 614–628. <https://doi.org/10.1111/j.1600-0587.1999.tb00510.x>
- Rowe, R. J., Heaney, L. R., & Rickart, E. A. (2015). Scale effects on the pattern and predictors of small mammal diversity along a local elevational gradient in the Great Basin. *Journal of Biogeography*, 42, 1964–1974. <https://doi.org/10.1111/jbi.12554>



- Scheiner, S. M., Chiarucci, A., Fox, G. A., Helmus, M. R., McGlinn, D. J., & Willig, M. R. (2011). The underpinnings of the relationship of species richness with space and time. *Ecological Monographs*, 81, 195–213. <https://doi.org/10.1890/10-1426.1>
- Stein, A., Gerstner, K., & Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, 17, 866–880. <https://doi.org/10.1111/ele.12277>
- Stein, A., & Kreft, H. (2015). Terminology and quantification of environmental heterogeneity in species-richness research. *Biological Reviews*, 90, 815–836. <https://doi.org/10.1111/brev.12135>
- Szava-Kovats, R. C., Ronk, A., & Pärtel, M. (2013). Pattern without bias: Local–regional richness relationship revisited. *Ecology*, 94, 1986–1992. <https://doi.org/10.1890/13-0244.1>
- Tuomisto, H., Ruokolainen, K., Vormisto, J., Duque, A., Sánchez, M., Paredes, V. V., & Lähteenoja, O. (2016). Effect of sampling grain on patterns of species richness and turnover in Amazonian forests. *Ecography*, 40, 840–852. <https://doi.org/10.1111/ecog.02453>
- Vetaas, O. R. (2006). Biological relativity to water–energy dynamics: A potential unifying theory? *Journal of Biogeography*, 33, 1866–1867. <https://doi.org/10.1111/j.1365-2699.2006.01618.x>
- Wang, X., Fang, J., Sanders, N. J., White, P. S., & Tang, Z. (2009). Relative importance of climate vs local factors in shaping the regional patterns of forest plant richness across northeast China. *Ecography*, 32, 133–142. <https://doi.org/10.1111/j.1600-0587.2008.05507.x>
- Whittaker, R. J., Willis, K. J., & Field, R. (2001). Scale and species richness: Towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, 28, 453–470. <https://doi.org/10.1046/j.1365-2699.2001.00563.x>

## BIOSKETCH

**Kuber P. Bhatta** is a PhD student in the Environment and Landscape Geography Unit in the Department of Geography, University of Bergen, Norway. His research interests are phytogeography, plant systematics and vegetation dynamics on temporal and spatial scales.

**Ole R. Vetaas** is a Professor in the Environment and Landscape Geography Unit in the Department of Geography, University of Bergen, Norway. He is a vegetation ecologist and biogeographer with research interests in diversity, succession and spatial dynamics. His theoretical interests include macroecology, gradients and the niche concept.

**John-Arvid Grytnes** is a Professor in the Ecological and Environmental Change Research Group at the University of Bergen, Norway. His primary focus is on patterns of biodiversity and on observed changes of biodiversity as a result of climate and environmental changes. To achieve his research goals, his primary study system is vascular plants along elevational gradients.

Author contributions: K.P.B., J.A.G. and O.R.V. conceived the ideas; K.P.B. collected, prepared and analysed the data and led the writing; all authors contributed to revising the text.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

**How to cite this article:** Bhatta KP, Grytnes J-A, Vetaas OR. Scale sensitivity of the relationship between alpha and gamma diversity along an alpine elevation gradient in central Nepal. *J Biogeogr*. 2018;00:1–11. <https://doi.org/10.1111/jbi.13188>