

UC Merced

Frontiers of Biogeography

Title

Investigating elevational gradients of species richness in a Mediterranean plant hotspot using a published flora

Permalink

<https://escholarship.org/uc/item/21r2804z>

Journal

Frontiers of Biogeography, 0(0)

Authors

Di Musciano, Michele
Zannini, Piero
Ferrara, Chiara
[et al.](#)

Publication Date

2021

DOI

10.21425/F5FBG50007

Supplemental Material

<https://escholarship.org/uc/item/21r2804z#supplemental>









License

<https://creativecommons.org/licenses/by/4.0/> 4.0

Peer reviewed



Investigating elevational gradients of species richness in a Mediterranean plant hotspot using a published flora

Michele Di Musciano^{1,2} , Piero Zannini² , Chiara Ferrara²,
Lorenzo Spina², Juri Nascimbene² , Ole R. Vetaas³ ,
Kuber P. Bhatta⁴ , Marco d'Agostino², Lorenzo Peruzzi⁵ ,
Angelino Carta⁵  and Alessandro Chiarucci² 

¹ Department of Life Health and Environmental Science (MESVA), University of L'Aquila, 67100, Italy; ² BIOME Lab, Department of Biological, Geological and Environmental Sciences (BiGeA), Alma Mater Studiorum University of Bologna, Via Irnerio 42, 40126, Bologna, Italy; ³ Department of Geography, University of Bergen, Bergen, N-5020, Norway; ⁴ Department of Biological Sciences, University of Bergen, Bergen, N-5020, Norway; ⁵ Department of Biology, University of Pisa, Italy. Corresponding author: Piero Zannini, piero.zannini2@unibo.it

This paper is part of an Elevational Gradients and Mountain Biodiversity Special Issue.

Abstract

The Apuan Alps are one of the most peculiar mountain chains in the Mediterranean, being very close to the coastline and reaching an elevation of almost 2000 m. Based on published flora, we investigated the distribution of plant species richness along the whole elevational gradient of this chain considering: (i) native species, (ii) endemic versus alien species; and (iii) functional groups of species based on Raunkiær life forms (RLF). Generalized Linear Models (GLMs) were used to analyse richness patterns along the elevational gradient, and elevational richness models versus the area of the elevational belts were fitted to test the effect of surface area. Our results showed decreasing species richness with increasing elevation. In contrast, endemic species richness increased along the elevational gradient. Alien species were mainly distributed at low elevations, but this result should be taken with caution since we used historical data. Species life forms were not equally distributed along the elevation gradient: chamaephytes and hemicryptophytes were the richest groups at high elevations, while therophytes showed highest species richness at low elevations. Our findings suggest that in the Apuan Alps there is a major elevational gradient in species composition that could reflect plant evolutionary history. Furthermore, we highlight the key role of published floras as a relevant source of biodiversity data.

Highlights

- The published flora of the Apuan Alps was explored to detect biogeographical patterns.
- Native and alien plant species richness decreased with elevation, while endemics increased, pointing at the conservation relevance of the Apuan Alps.
- Functional groups based on Raunkiær Life Forms show differentiated responses to the elevational gradient.
- Area size of elevational belts have only marginal effects on patterns of species richness: the observed trends are likely due to environmental constraints.
- Current climate change is likely to affect observed patterns, high-elevation rare species are likely to be threatened by competition from species moving upwards from lower elevations.

Keywords: alien species, Apuan Alps, elevational gradient, endemics, plant diversity, Raunkiær lifeforms, species richness.

Introduction

Patterns of plant species richness have always been a topic of interest in biogeography and ecology (Pianka 1966, Huston and Huston 1994, Lomolino 2001, Whittaker et al. 2001). Historically, species richness

trends have been associated with available area and environmental gradients. An increase in species richness with increasing area is one of the most robust ecological generalizations (Rosenzweig 1995, Lomolino 2000), and a vast literature has been published on species–area relationships (e.g., Karger et al. 2011,

Dengler et al. 2019, Moradi et al. 2020, Matthews et al. 2021). Species richness patterns have also been evaluated along several environmental gradients (Gaston 2000), such as temperature, productivity, potential evapotranspiration, etc. However, the two most investigated environmental gradients related to species richness patterns are latitude and elevation.

In particular, the variation of species richness along elevational gradients has been documented for a variety of taxa and geographical areas (see e.g., Terborgh 1977, Stevens 1992, Rahbek 1995, Bhattarai and Vetaas 2003, Grytnes 2003, Bhattarai et al. 2004, Bhattarai and Vetaas 2005, Carpenter 2005, McCain and Grytnes 2010, Bhatta et al. 2018). The two most frequent patterns that have emerged: a monotonic decrease in species richness as a function of elevation (Yoda 1968, MacArthur 1972, Stevens 1992, Liang et al. 2020, Subedi et al. 2020) and a hump-shaped relationship, with a peak in species richness at intermediate elevations (Grytnes and Vetaas 2002, Rahbek 2005, Bhattarai and Vetaas 2006, Ibanez et al. 2016).

The elevation gradient of species richness has been commonly explained by the same factors driving the latitudinal gradient of species richness, such as climate, productivity, and other energy-related processes (Richerson and Lum 1980, Turner et al. 1987, Currie 1991, Wright et al. 1993, Panda et al. 2017, Vetaas et al. 2019). Indeed, increase in elevation leads to changes in several environmental factors, such as temperature, precipitation, evapotranspiration, soil nutrient availability, and solar radiation, potentially driving species richness. For this reason, since the pioneering studies of Alexander von Humboldt, analyses of elevational gradients have been pivotal to disentangling the causes behind broad-scale patterns of biodiversity (Fattorini et al. 2019). However, despite the large number of studies investigating elevational patterns of species richness, many questions still remain unresolved (Wang et al. 2017), and the factors determining the elevation–richness relationship and its variations across spatial scales, clades, and biomes still require clarifications. Understanding how elevational gradients affect species richness is both of theoretical and practical concern, especially in a climate change scenario, since it links biodiversity patterns to conservation (Rahbek 1995, Lomolino 2001, Thuiller et al. 2005, Loarie et al. 2009).

Within this theoretical and analytical framework, published Floras represent a highly valuable source of data for ecological and biogeographical analyses (König et al. 2019). This view is corroborated by several papers focused on island biogeography theory (Wilson 1988, Chiarucci et al. 2017), land-use changes (Aggemyr and Cousins 2012, Finderup Nielsen et al. 2019), biogeographical networks (Kougioumoutzis et al. 2014, 2017, Torre et al. 2019), large-scale drivers of species richness (Weigelt et al. 2020), and patterns of species richness along elevational gradients (Kluge et al. 2017).

In the present study, we used the detailed data on the local elevational distribution of more than 2,000 plant taxa included in a published Flora of

the Apuan Alps (Central Italy) to model patterns of species richness for: (i) native species, (ii) endemic and alien species separately, and (iii) functional groups of species based on Raunkiaer life forms (RLF; Raunkiaer 1934). Specifically, we investigated how species richness varies along the elevational gradient, both for the whole flora and for endemic and alien species, as well as for different Raunkiaer's life forms. Additionally, we assessed whether or not the species richness–elevation relationship may be influenced by differences in available surface area among elevational belts. Finally, we explored the elevational ranges of endemics, aliens, and different Raunkiaer's life forms.

Materials and Methods

Study Area

The Apuan Alps are a mountain chain located in north-western Tuscany (Italy, Fig. 1), belonging to the Mediterranean biogeographical region (Cervellini et al. 2020). This mountain chain is characterized by steep slopes, especially on the south-west facing side, and broad rocky outcrops reaching up to 1946 m. a.s.l. at Monte Pisanino. The harsh morphology and the substrate variability of these mountains, made up of metamorphic and sedimentary rocks, shape local habitat heterogeneity (Tomaselli and Agostini 1994) that combined with recent geomorphologic and neotectonic events likely drive current plant biodiversity (Bedini et al. 2011).

The lowlands of the southern mountain side are dominated by evergreen sclerophyllous plants, which are replaced by *Carpinus* and *Quercus* forests at mid-elevations (Tomaselli et al. 2019). On the

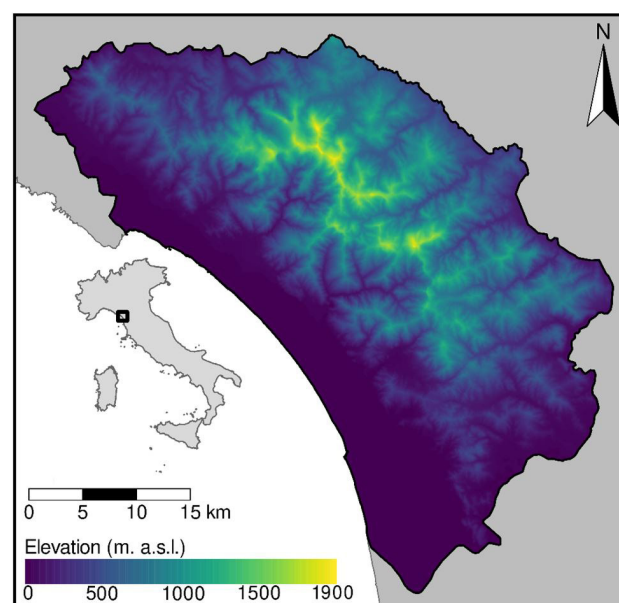


Fig. 1. Study area. The coloured area corresponds to the Apuan Alps according to Ferrarini and Marchetti 1994. Dark blue to light yellow represents the elevation gradient. In the bottom-left corner, we show the position of the study area within a map of Italy.

summit areas, vegetation includes a mosaic of natural grasslands dominated by *Sesleria apennina* and *Carex sempervirens* and of secondary grasslands dominated by *Brachypodium genuense* (Tomaselli and Agostini 1994). These areas host moorlands on the siliceous peaks, while the calcareous peaks are typically dominated by casmophytic (cliff dwelling) plant communities.

Dataset building

The floristic dataset used for the analyses was built by recording each taxon ("species" hereafter) listed in the three volumes of *Prodromo alla Flora della Regione Apuana* (Ferrarini and Marchetti 1994, Ferrarini et al. 1997, Ferrarini 2000), and its elevational distribution (minimum and maximum elevation at which each species is recorded for the area) and chorotype (native, endemic or alien, in all cases relatively to Apuan Alps). Taxonomical nomenclature was standardised according to Pignatti et al. (2017) and RLF were assigned to each species. When more than one RLF was listed for a species we retained the more durable RLF (e.g., between phanerophyte and chamaephyte we retained the former, and between therophyte and hemicryptophyte we retained the latter). Finally, we excluded all the species whose elevation distribution was uncertain ($n=116$), as well as all those species reported as extinct or cultivated ($n=3$ and $n=32$, respectively). Thus, 1,952 species were retained in the final dataset. Lastly, since hydrophytes and helophytes were missing from most of the elevational belts, occurring only below 500 m, we did not account for these RLFs in the models.

Data analysis

We used species richness estimated in each 50-m elevation belt to model the elevational patterns of plant richness in the study area. A total of 39 belts were obtained, ranging from 0 to 1950 m. In the text and plots, the upper elevation limit was used to indicate the corresponding belt, both in the text and in the plots. For each belt, we calculated the planar area and the overall species richness, the richness of endemic and alien species, and that of the seven RLF categories.

In order to graphically explore the elevational patterns of species richness, we plotted overall species richness and species richness for each category against the elevational belts, both as absolute values (i.e., counts of species) and as relative species richness (% of total richness).

We applied polynomial linear regression using Generalized Linear Models (GLMs) with a Poisson or Quasipoisson (in case of overdispersion) distribution of error to investigate the variation of species richness along the elevational gradient. In case of overdispersion, we used negative binomial regression models. In the same way, the relative richness of different chorotypes and RLF was modelled using GLMs with quasibinomial distribution of error. The best model among linear, quadratic and cubic was assessed based on Akaike Information Criterion (AIC) and parsimony criterion. The most parsimonious model

was chosen if the decrease in AIC when adding the next order term was small. In particular, we assumed that models in which the difference in AIC is < 2 can be considered as equally supported (Burnham 1998, Burnham et al. 2011).

It has been widely reported that species richness increases as a function of area (Romdal and Grytnes 2007, Lee et al. 2013). Therefore, to assess the species–area relationship we fitted linear models between the residuals of each GLM model as the response variable and the area of each belt as the predictor variable.

To investigate the elevational distribution of endemic and alien species as well as of RLF, we compared the lower and upper limits of elevational distribution and elevational ranges of the species. As the distributions of lower and upper limits, as well those of elevational ranges, were highly skewed, we used non-parametric tests. We compared the elevational distributions of alien and endemic species by means of Wilcoxon rank sum test. For the RLF, we first tested the differences among all groups by means of Kruskal-Wallis test. As we found significant differences, we applied pairwise Wilcoxon rank sum as a post-hoc test, by adjusting the p-values with a Holm correction to prevent Type I error. All the analyses were performed using in R v. 3.6.3 (R Core Team 2020) and the following R packages: sars (Matthews et al. 2019), reshape (Wickham 2007), ggplot2 (Wickham 2016), sf (Pebesma 2018), raster (Hijmans 2020) and tmap (Tennekes 2018), and MASS (Venables and Ripley 2002).

Results

Among the 1,952 species, 14 endemic or nearly endemic species and 22 alien species were included. Thus, endemics represented 0.72% and aliens 1.13% of the total flora.

Total species richness decreased along the elevational gradient (Fig. 2a), with about 58.35% of the total flora being found at the lowest elevational belt and 2.77% at the highest elevational belt (Fig. 3a). The model accounting for native species showed a decrease ($D^2=0.94$) of species richness. In the lowest elevational belts more than 1,000 species were found, while at the highest belts less than 150 species occurred (Table 1).

Endemic and alien species

The endemic and alien species showed contrasting trends. The former had a unimodal positive pattern along the elevational gradient (Fig. 2b), peaking around 1200 m a.s.l. ($D^2=0.74$), whereas alien species displayed a less definite trend, with a drastic decrease of species richness starting from 200 m a.s.l. and a complete lack of recorded alien species from the 1,050 m belt up to the 1,400 m belt ($D^2=0.75$; Table 1).

The relative species richness along the elevational gradient for endemic species showed a positive relationship, with an increase of 5% along the gradient ($D^2=0.92$). In contrast, alien species did not reveal a clear trend and the relative richness never exceeded 1.2% (Table 2). Both groups fitted to a quadratic model, but alien species showed a downward convexity ($D^2=0.37$; Fig. 3b).

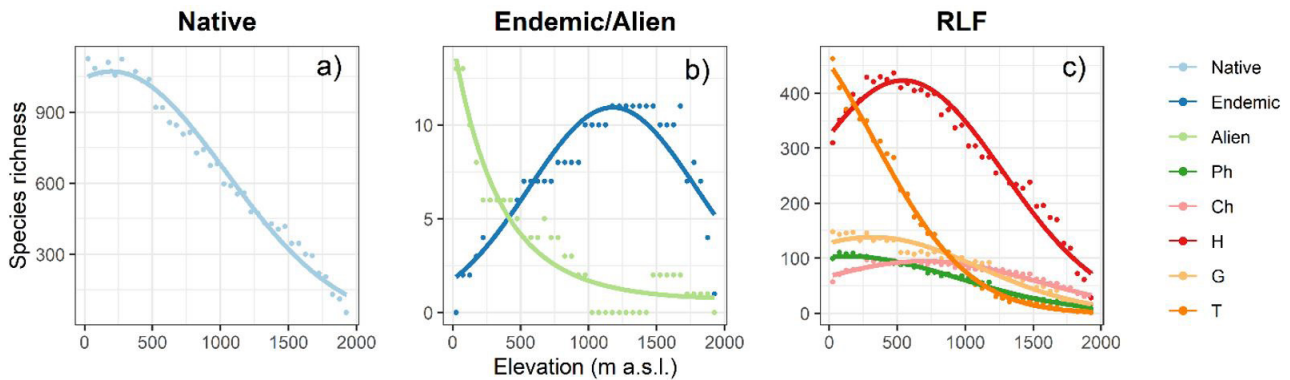


Fig. 2. Scatter plots of plant species richness in the Apuan Alps as a function of 50-metres elevational belts: (a) native species; (b) endemic and alien species; (c) all species classified into different Raunkiaer life forms (helophytes and hydrophytes are not shown as they are limited to basal elevational belts in the study area). Lines are predictions of fitted second-order polynomial Poisson GLMs, except for native species where we employed a negative binomial GLM in order to avoid overdispersion (all models were significant at $p < 0.05$).

Table 1. Summary statistics of fitted polynomial GLMs with vascular plant species richness as a function of 50-metres elevational belts in the Apuan Alps. For all models we employed a Poisson distribution of error, except for native species where we used a negative binomial distribution of error. “Int” is the intercept, “Elev” and “Elev²” are first- and second-order angular coefficients. D² is the percentage of deviance explained by the models.

	Int	Elev	Elev ²	D ²
Native	6.32	-3.87	-1.26	0.94
Endemic	1.92	1.86	-2.33	0.71
Alien	0.79	-5.22	1.22	0.75
Phanerophyte	3.90	-4.23	-1.23	0.99
Chamaephyte	4.27	-1.39	-1.26	0.88
Hemicryptophyte	5.59	-2.80	-1.63	0.92
Geophyte	4.32	-3.72	-1.33	0.93

Table 2. Summary statistics of fitted polynomial quasi-binomial GLMs with proportional species richness as a function of 50-metres elevational belts. “Int” is the intercept, “Elev” and “Elev²” are first- and second-order angular coefficients. D² is the percentage of deviance explained by the models. Proportions are calculated on overall species richness per belt.

	Int	Elev	Elev ²	D ²
Endemic	-4.30	5.60	-1.26	0.93
Alien	-5.55	-1.24	2.60	0.37
Phanerophyte	-2.31	-0.26	/	0.06
Chamaephyte	-1.89	2.91	0.21	0.96
Hemicryptophyte	-0.07	1.87	-0.73	0.97
Geophyte	-1.91	-0.43	-1.03	0.44

Raunkiaer life forms

The sharpest trends were observed for hemicryptophytes and therophytes as the majority of the species belong to these two categories (Fig. 2c). Hemicryptophyte species richness showed a bell-shaped trend, with a peak at about 500 m a.s.l. ($D^2 = 0.92$), while therophyte species richness had a negative exponential pattern, with a rapid decrease from the sea level up to 1,200 m a.s.l., and a less steep decline at higher elevations ($D^2 = 0.99$).

Phanerophytes, geophytes, and chamaephytes displayed weaker trends. Phanerophyte and geophyte species richness showed an approximately linear decrease with elevation ($D^2_{\text{phanerophyte}} = 0.99$, $D^2_{\text{geophyte}} = 0.91$), while chamaephytes showed a weak increase in species richness with a plateau between the 500 m and the 1,000 m belts and decreased up to the summit ($D^2 = 0.88$; Table 1 and supplementary Table S1). The proportional values of RLF along the elevational gradient showed positive trends for hemicryptophyte and chamaephyte species richness with an increase of about 20% ($D^2_{\text{hemicryptophyte}} = 0.97$, $D^2_{\text{chamaephyte}} = 0.96$). Therophytes and geophytes decreased along the elevational gradient ($D^2_{\text{therophyte}} = 0.99$, $D^2_{\text{geophyte}} = 0.44$; Fig. 3c). Phanerophytes had only a slight decrease with elevation and showed the lowest D^2 ($D^2_{\text{phanerophyte}} = 0.06$; Table 2).

Effect of area

A strong negative correlation ($R^2 0.7$) between elevation and area of the belts was found. The linear model between the residuals of each elevational model versus belt areas showed no significant effect of the area in almost all cases. Significant effect of the area was found only for endemic species even if the linear model had an adjusted R^2 of 0.19. This result is due to the effect of the lowest elevational belt (see supplementary Figure S1), which has the largest area and, in this case, the highest residual value. All the other models had a p-value higher than 0.2 and

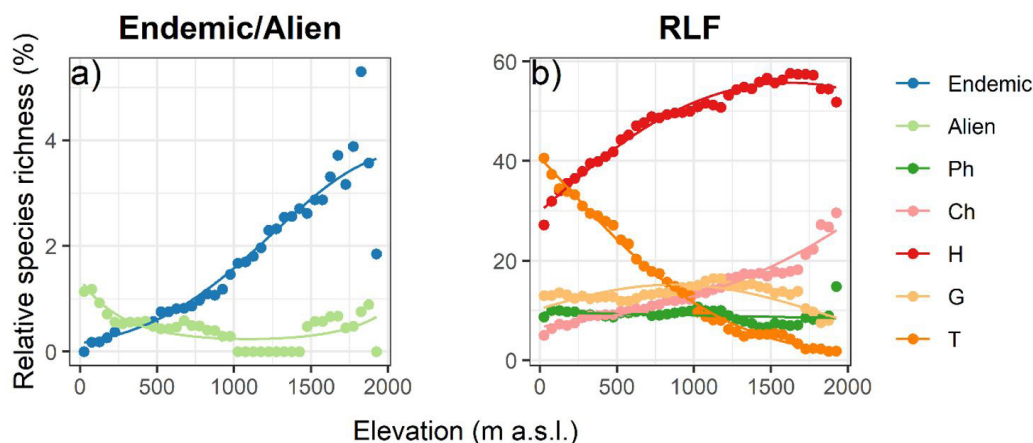


Fig. 3. Scatter plots of proportional species richness in the Apuan Alps as a function of 50-metres elevational belts. In a) endemic and alien species; b) all species classified into different Raunkiaer life forms, helophytes and hydrophytes are not shown as they are limited to basal elevational belts in the study area. Lines are predictions of fitted second-order polynomial quasi-binomial GLMs (all models were significant at $p < 0.05$). Proportions are calculated on overall species richness per belt.

an adjusted R^2 lower than 0.1 (see supplementary Figure S1).

Elevational range

Endemic species showed heterogeneous elevational ranges. Indeed, some species were distributed along the entire gradient, while others had a narrow range, being centered at about 1,800 m a.s.l. On the other hand, alien species showed similar range sizes (ca. 700 m width) and almost all the species had their minimum height of occurrence near the sea level. All the comparisons between endemic and alien species showed significant differences (Fig. 4A; $p < .001$). Therefore, endemic species had wider elevational ranges and higher minimum and maximum elevation of occurrence compared to alien species.

The RLF range sizes showed a strong variability among groups (Fig. 4b), which differed significantly in all comparisons ($p < .001$). The most common pattern was the minimum height of occurrence, indeed all the RLF included a large number of species that had their lowest limit near the sea level. As mentioned before, hydrophyte and helophyte species had very narrow elevational ranges. Within the remaining categories species were distributed very differently. Therophytes and geophytes, on average, had smaller elevational ranges, with therophytes showing the lowest elevational occurrences both for minimum and maximum limits. Chamaephytes showed the widest elevational ranges while most of the hemicryptophytes and phanerophytes had their elevational ranges varying from 500 m to 1,250 m. On the other hand, hemicryptophytes and chamaephytes showed the highest minimum limits with median maximum limits above 1,000 m a.s.l.

Discussion

Our study area hosts over 25% of the Italian flora (Bartolucci et al. 2018), supporting the view that

this mountain chain can be regarded as a hotspot of plant diversity (Gentili et al. 2015, Carta et al. 2018, Carta et al. 2019). The large number of species is supported by the great habitat heterogeneity of the Apuan Alps (Tomaselli and Agostini 1994). Indeed, high environmental heterogeneity provides great niche diversity and facilitates species coexistence, resulting in greater species richness (López-González et al. 2015). The high number of endemics may be associated with the role of Apuan Alps as a refuge during the last glacial maximum (Médail and Diadema 2009, Gentili et al. 2015), indeed these data highlight the great biogeographical importance of the Apuan Alps for generating and preserving plant evolutionary history (Carta et al. 2019).

The observed pattern along the elevational gradient confirms the hypothesis of a linear decrease in species richness. It is currently considered that the most common pattern of plant species richness along an elevational gradient is a hump at middle heights (Colwell et al. 2004, Grytnes and McCain 2007). However, our gradient spans less than 2,000 metres in elevation and it is not uncommon to find linear trends along relatively short gradients (Nogués-Bravo et al. 2008). Moreover, elevational gradients of species richness were usually investigated using standardised plots with equal area (Bhattarai and Vetaas 2003, Lee et al. 2013). In contrast, we used data from a published flora listing all the recorded species for each elevational belt and the effect of area could have potentially emerged. However, we note that, with the exception of the lowest one, there was only slight variation in area size across the elevational belts. Moreover, the results of linear models carried out to investigate the effect of area suggest, as in this case, that area has a secondary and not significant effect on species richness.

The decrease of species richness along the gradient suggests that environmental constraints related to

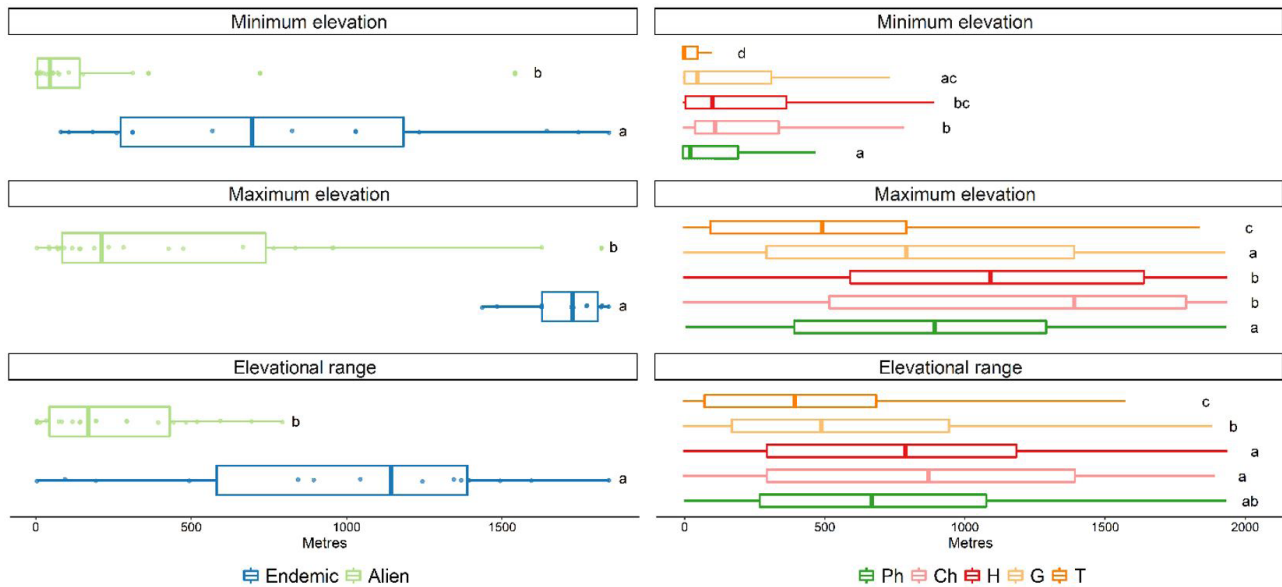


Fig. 4. Box-and-whiskers plots comparing minimum and maximum elevational distribution and elevational ranges (minimum and maximum elevational distribution are in metres above sea level, whereas elevational ranges are in metres) of different plant groups in the Apuan Alps: (a) endemic vs alien species; (b) different Raunkiær life forms. Different letters indicate differences among groups ($p < 0.05$): endemic vs alien species distributions were compared by means of two-sample Wilcoxon Rank Sum tests, in the case of Raunkiær life forms we first used Kruskal-Wallis test and then, as we found significant differences, pairwise Wilcoxon Rank Sum tests with Bonferroni correction.

mountain ecosystems may act as filters for species distributions (Körner 2003). Nevertheless, we found that the percentage of endemic species increases along the elevational gradient and their elevational ranges showed higher median values than other groups, confirming the hypothesis that endemics are more commonly found at higher elevations (Vetaas and Grytnes 2002, Steinbauer et al., 2016). These results can be explained by the biogeographical effect of the mountain region, which can be considered as an ecological archipelago for evolutionary processes (Körner 2003, Ægisdóttir et al. 2009, Sklenář et al. 2014, Rahbek et al. 2019). However, these crucial areas for biodiversity conservation have been threatened by direct and indirect effects of human activities in the last decades (IPCC 2019). Moreover, high-mountain areas have been experiencing some of the greatest increases in temperature in the last half century (Pepin et al. 2020). Thus, these habitats, extremely important for species conservation, are among the most vulnerable to current climate and land use changes (Walther et al. 2005). The endemic or rare species that are found at high elevations are more likely to be threatened by local extinctions in the near future (Thuiller et al. 2005, Pauli et al. 2007, Bellard et al. 2014). Thus, it is important to improve conservation strategies, particularly for endemic and threatened species growing in the Apuan Alps (IUCN 2020). Phylogeographic studies on endemics should be implemented to assess the genetic diversity of these species and the refuge role of the Apuan Alps in the last glacial maximum (Bedini et al. 2011).

Alien species richness peaked at the lowest elevations, where human impact is stronger and human

population density is higher. Currently, the greatest number of alien species in the world and the greatest knowledge about the extent of invasions are reported in economically developed countries (Pyšek et al. 2008, McGeoch et al. 2010, Early et al. 2016, Corcos et al. 2020). Due to an interplay between climate warming and direct human impact, an upward shift of the alien species is expected in the near future (Walther et al. 2009, Alexander and Edwards 2010). This shift could threaten vulnerable habitats that host endemic species, potentially leading these taxa to local extinctions (Bellard et al. 2016, Blackburn et al. 2019).

The elevational patterns of species richness for different RLF show how the plant life strategies shape their elevational distribution. As demonstrated by previous studies on the dominant role of hemicryptophytes and chamaephytes in high mountain ecosystems (Körner 2003, Matteodo et al. 2013, Irl et al. 2020), we observed a positive relationship between the percentages of hemicryptophytes and of chamaephytes and elevation. This is most likely due to the climatic and topographic features of the Apuan Alps. Indeed, the highest peaks of these mountains are characterized by steep slopes and calcareous plateaus with thin soils colonised by stress tolerant communities. On the other hand, the proportion of therophytes showed that this group is dominant in lowland habitats, probably due to the high human impact occurring therein. Annuals (sometimes biannual), which become quite rare at high elevations (Körner 2003), commonly do not represent more than 2% of the total mountain flora, and become increasingly rare with increasing elevation (Bliss 1971, Billings 1974).

Phanerophytes had relatively wider elevational ranges, but their distribution was limited by low seasonal mean ground temperature: a value of 6.7 °C mean temperature during the growing season is usually considered as the thermal threshold for forest growth at high elevation (Körner and Paulsen 2004). A linear decrease of phanerophyte species richness with increasing elevation has been recorded at the plot scale for the forest plant communities of Tuscany (Chiarucci and Bonini 2005), confirming the marked dependence of this RLF type on elevation.

Finally, although the use of published floras has been shown potentially to help disentangle ecological and biogeographical patterns and processes, it is not free of bias. One major limitation could be the underestimation of elevational gradient for rare species. Indeed, these species could actually show distributional gaps, both for their real absence or due to the sampling effort. Even if these limitations could affect the results, the great number of species with a lower elevational limit near the sea level and the relatively small areas of the higher belts ensure the reliability of the sampling effort. Moreover, we note that the Apuan Alps flora comes from a life's work with a great sampling effort distributed over more than 20 years (see Ferrarini and Marchetti 1994).

Conclusions

We highlighted a general decrease of plant species richness along the elevational gradient of the Apuan Alps. The observed trends are likely due to the increase of environmental constraints along the elevational gradient (Körner 2003). On the other hand, the increase in percentage of endemics at high elevations highlighted the key role of mountain ecosystems in shaping evolutionary processes (Vetaas and Grytnes 2002, Steinbauer et al. 2016). Moreover, our results confirmed that published floras provide useful information to investigate species diversity as well as biogeographical patterns and their ecological drivers (Aggemyr and Cousins 2012; Chiarucci et al. 2017; Funderup Nielsen et al. 2019).

Acknowledgments

We would like to thank Ilaria Bonini from University of Siena, who provided us the Flora used in this study and all the members of the Biodiversity and Macroecology Group (BIOME) for the continuous support during the project. We would also like to thank Prof. Robert J. Whittaker, Dr. Patrick Weigelt and an anonymous reviewer for commenting on previous versions of the manuscript.

Author Contributions

A.Ch. conceived the idea and coordinated the study; the database was designed and compiled by C.F., later expanded by L.S.; P.Z. and M.D.M. performed the analyses and produced the outputs; M.D.M. lead the writing of the manuscript with substantial

contributions from P.Z.; all authors discussed the results and contributed to drafting the final manuscript.

Data Accessibility

Data are deposited on Zenodo and are available upon motivated request (doi:10.5281/zenodo.4419941).

Supplementary Material

The following materials are available as part of the online article at <https://escholarship.org/uc/fb>

Table S1. Vascular plant species richness per 50-metres elevational belt in the Apuan Alps.

Figure S1. Scatterplots of poisson GLMs residuals (species richness as function of elevation) vs. 50-metres elevational belts' areas.

References

- Ægisdóttir, H.H., Kuss, P. & Stöcklin, J. (2009) Isolated populations of a rare alpine plant show high genetic diversity and considerable population differentiation. *Annals of Botany*, 104, 1313-1322.
- Aggemyr, E. & Cousins, S.A.O. (2012) Landscape structure and land use history influence changes in island plant composition after 100 years. *Journal of Biogeography*, 39, 1645-1656.
- Alexander, J.M. & Edwards, P.J. (2010) Limits to the niche and range margins of alien species. *Oikos*, 119, 1377-1386.
- Bedini, G., Carta, A., Zecca, G., Grassi, F., Casazza, G. & Minuto, L. (2011) Genetic structure of *Rhamnus glaucophylla* Sommier endemic to Tuscany. *Plant Systematics and Evolution*, 294, 273-280.
- Bartolucci, F., Peruzzi, L., Galasso, G., et al. (2018) An updated checklist of the vascular flora native to Italy. *Plant Biosystems*, 152, 179-303.
- Bellard, C., Cassey, P. & Blackburn, T.M. (2016) Alien species as a driver of recent extinctions. *Biology Letters*, 12, doi.org/10.1098/rsbl.2015.0623.
- Bellard, C., Leclerc, C., Leroy, B., Bakkenes, M., Veloz, S., Thuiller, W. & Courchamp, F. (2014) Vulnerability of biodiversity hotspots to global change. *Global Ecology and Biogeography*, 23, 1376-1386.
- Bhatta, K.P., Grytnes, J. & Vetaas, O.R. (2018) Scale sensitivity of the relationship between alpha and gamma diversity along an alpine elevation gradient in central Nepal. *Journal of Biogeography*, 45, 804-814.

- Bhattacharai, 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.
- Bhattacharai, K.R. & Vetaas, O.R. (2005) Do fern and fern-allies show a similar response along the ecological gradient in the Himalayas. *Bulletin Department of Plant Resources*, 26, 24–29.
- Bhattacharai, 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.
- Bhattacharai, K.R., Vetaas, O.R. & Grytnes, J.A. (2004) Fern species richness along a central Himalayan elevational gradient, Nepal. *Journal of Biogeography*, 31, 389–400.
- Billings, W.D. (1974) Arctic and alpine vegetation: plant adaptations to cold summer climates (ed. by J.D. Ives and R.G. Barry), pp. 403–444. Methuen, London.
- Blackburn, T.M., Bellard, C. & Ricciardi, A. (2019) Alien versus native species as drivers of recent extinctions. *Frontiers in Ecology and the Environment*, 17, 203–207.
- Bliss, L.C. (1971) Arctic and alpine plant life cycles. *Annual Review of Ecology and Systematics*, 2, 405–438.
- Burnham, K.P. (1998) Model selection and multimodel inference. A practical information-theoretic approach. Springer-Verlag, Heidelberg.
- Burnham, K.P., Anderson, D.R. & Huyvaert, K.P. (2011) AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, 65, 23–35.
- Carpenter, C. (2005) The environmental control of plant species density on a Himalayan elevation gradient. *Journal of Biogeography*, 32, 999–1018.
- Carta, A., Bedini, G. & Peruzzi, L. (2018) Unscrambling phylogenetic effects and ecological determinants of chromosome number in major angiosperm clades. *Scientific Reports*, 8, 1–14.
- Carta, A., Pierini, B., Roma-Marzio, F., Bedini, G. & Peruzzi, L. (2018) Phylogenetic measures of biodiversity uncover pteridophyte centres of diversity and hotspots in Tuscany. *Plant Biosystems*, 152, 831–839.
- Carta, A., Gargano, D., Rossi, G., Bacchetta, G., Fenu, G., Montagnani, C., Abeli, T., Peruzzi, L. & Orsenigo, S. (2019) Phylogenetically informed spatial planning as a tool to prioritise areas for threatened plant conservation within a Mediterranean biodiversity hotspot. *Science of The Total Environment*, 665, 1046–1052.
- Cervellini, M., Zannini, P., Di Musciano, M. et al. (2020) A grid-based map for the biogeographical regions of Europe. *Biodiversity Data Journal*, 8, e53720.
- Chiarucci, A. & Bonini, I. (2005) Quantitative floristics as a tool for the assessment of plant diversity in Tuscan forests. *Forest Ecology and Management*, 212, 160–170.
- Chiarucci, A., Fattorini, S., Foggi, B., Landi, S., Lazzaro, L., Podani, J. & Simberloff, D. (2017) Plant recording across two centuries reveals dramatic changes in species diversity of a Mediterranean archipelago. *Scientific Reports*, 7, 5415. doi.org/10.1038/s41598-017-05114-5 after 5415
- Colwell, R.K., Rahbek, C. & Gotelli, N.J. (2004) The mid-domain effect and species richness patterns: what have we learned so far? *The American Naturalist*, 163, E1–E23.
- Corcos, D., Nascimbene, J., Campesan, M., Donadello, D., Segat, V. & Marini, L. (2020) Establishment dynamics of native and exotic plants after disturbance along roadsides. *Applied Vegetation Science*, 23, 277–284.
- Currie, D.J. (1991) Energy and large-scale patterns of animal-and plant-species richness. *The American Naturalist*, 137, 27–49.
- Dengler, J., Matthews, T.J., Steinbauer, M., et al. (2019) Species–area relationships in continuous vegetation: evidence from Palaearctic grasslands. *Journal of Biogeography*, 47, 72–86.
- Early, R., Bradley, B.A., Dukes, J.S., Lawler, J.J., Olden, J.D., Blumenthal, D.M., Gonzalez, P., Grosholz, E.D., Ibañez, I. & Miller, L.P. (2016) Global threats from invasive alien species in the twenty-first century and national response capacities. *Nature Communications*, 7, 1–9.
- Fattorini, S., Di Biase, L. & Chiarucci, A. (2019) Recognizing and interpreting vegetational belts: new wine in the old bottles of a von Humboldt's legacy. *Journal of Biogeography*, 46, 1643–1651.

- Ferrarini, E. (2000) Prodrómo alla flora della regione Apuana. Parte terza. (Compositae-Orchidaceae). Accademia Lunigianese di Scienze Giovanni Capellini, La Spezia.
- Ferrarini, E. & Marchetti, D. (1994) Prodrómo alla flora della Regione Apuana. Parte prima. (Lycopodiaceae-Leguminosae). Accademia Lunigianese di Scienze Giovanni Capellini, La Spezia.
- Ferrarini, E., Pichi Sermolli, R., Bizzarri, M. & Ronchieri, I. (1997) Prodrómo alla flora della regione Apuana. Parte seconda. Accademia Lunigianese di Scienze Giovanni Cappellini, La Spezia.
- Finderup Nielsen, T., Sand-Jensen, K., Dornelas, M. & Bruun, H.H. (2019) More is less: net gain in species richness, but biotic homogenization over 140 years. *Ecology Letters*, 22, 1650–1657.
- Gaston, K. (2000) Global patterns in biodiversity. *Nature*, 405, 220–227.
- Gentili, R., Bacchetta, G., Fenu, G., Cogoni, D., Abeli, T., Rossi, G., Salvatore, M.C., Baroni, C. & Citterio, S. (2015) From cold to warm-stage refugia for boreo-alpine plants in southern European and Mediterranean mountains: the last chance to survive or an opportunity for speciation? *Biodiversity*, 16, 247–261.
- Grytnes, J.A. (2003) Species-richness patterns of vascular plants along seven altitudinal transects in Norway. *Ecography*, 26, 291–300.
- Grytnes, J.A. & McCain, C.M. (2007) Elevational trends in biodiversity. *Encyclopedia of Biodiversity*, 2, 1–8.
- Grytnes, J.A. & Vetaas, O.R. (2002) Species richness and altitude: a comparison between null models and interpolated plant species richness along the Himalayan altitudinal gradient, Nepal. *The American Naturalist*, 159, 294–304.
- Hijmans, R.J. (2020) raster: geographic data analysis and modeling, R package version 3.4-5. <https://CRAN.R-project.org/package=raster>
- Huston, M.A. (1994) Biological diversity: the coexistence of species. Cambridge University Press, Cambridge.
- Ibanez, T., Grytnes, J.A. & Birnbaum, P. (2016) Rarefaction and elevational richness pattern: a case study in a high tropical island (New Caledonia, SW Pacific). *Journal of Vegetation Science*, 27, 441–451.
- Irl, S.D., Obermeier, A., Beierkuhnlein, C. & Steinbauer, M.J. (2020) Climate controls plant life-form patterns on a high-elevation oceanic island. *Journal of Biogeography*, 47, 2261–2273.
- IPCC (2019) Global Warming of 1.5 C. An IPCC special report on the impacts of global warming of 1.5 C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. Digital resource available at <https://www.ipcc.ch/sr15/>
- IUCN (2020) The IUCN Red List of Threatened Species, Version 2020-2. <https://www.iucnredlist.org>. Downloaded on 10 August 2020.
- Kluge, J., Worm, S., Lange, S., Long, D., Böhrner, J., Yangzom, R. & Miehe, G. (2017) Elevational seed plants richness patterns in Bhutan, Eastern Himalaya. *Journal of Biogeography*, 44, 1711–1722.
- 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.
- König, C., Weigelt, P., Schrader, J., Taylor, A., Kattge, J. & Kreft, H. (2019) Biodiversity data integration - the significance of data resolution and domain. *PLOS Biology*, 17, e3000183.
- Körner, C. (2003) Alpine plant life: functional plant ecology of high mountain ecosystems; with 47 tables. Springer Science & Business Media, Heidelberg.
- Körner, C. & Paulsen, J. (2004) A world-wide study of high altitude treeline temperatures. *Journal of Biogeography*, 31, 713–732.
- Kougioumoutzis, K., Simaiakis, S.M. & Tiniakou, A. (2014) Network biogeographical analysis of the central Aegean archipelago. *Journal of Biogeography*, 41, 1848–1858.
- Kougioumoutzis, K., Valli, A.T., Georgopoulou, E., Simaiakis, S.M., Triantis, K.A. & Trigas, P. (2017) Network biogeography of a complex island system: the Aegean Archipelago revisited. *Journal of Biogeography*, 44, 651–660.
- Lee, C., Chun, J., Song, H. & Cho, H. (2013) Altitudinal patterns of plant species richness on the Baekdudaegan Mountains, South Korea: mid-

- domain effect, area, climate, and Rapoport's rule. *Ecological Research*, 28, 67–79.
- Liang J., Ding Z., Lie G., Zhou Z., Singh P.B., Zhang Z. & Hu H. (2020) Species richness patterns of vascular plants and their drivers along an elevational gradient in the central Himalayas. *Global Ecology and Conservation*, 24, e01279.
- Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009) The velocity of climate change. *Nature*, 462, 1052–1055.
- Lomolino, M.V. (2000) Ecology's most general, yet protean pattern: the species-area relationship. *Journal of Biogeography*, 27, 17–26.
- Lomolino, M.V. (2001) Elevation gradients of species-density: historical and prospective views. *Global Ecology and Biogeography*, 10, 3–13.
- López-González, C., Presley, S.J., Lozano, A., Stevens, R.D. & Higgins, C.L. (2015) Ecological biogeography of Mexican bats: the relative contributions of habitat heterogeneity, beta diversity, and environmental gradients to species richness and composition patterns. *Ecography*, 38, 261–272.
- MacArthur, R.H. (1972) *Geographical ecology: patterns in the distribution of species*. Harper & Row, New York.
- Marini, L., Gaston, K.J., Prosser, F. & Hulme, P.E. (2009) Contrasting response of native and alien plant species richness to environmental energy and human impact along alpine elevation gradients. *Global Ecology and Biogeography*, 18, 652–661.
- Matteodo, M., Wipf, S., Rixen, C. & Vittoz, P. (2013) Elevation gradient of successful plant traits for colonizing alpine summits under climate change. *Environmental Research Letters*, 8, 024043.
- Matthews, T.J., Triantis, K., Whittaker, R.J. & Guilhaumon, F. (2019) sars: an R package for fitting, evaluating and comparing species-area relationship models. *Ecography*, 42, 1446–1455.
- McCain, C.M. & Grytnes, J.A. (2010) Elevational gradients in species richness. *eLS*, doi: 10.1002/9780470015902.a0022548.
- McGeoch, M.A., Butchart, S.H., Spear, D., Marais, E., Kleyhans, E.J., Symes, A., Chanson, J. & Hoffmann, M. (2010) Global indicators of biological invasion: species numbers, biodiversity impact and policy responses. *Diversity and Distributions*, 16, 95–108.
- Médail, F., & Diadema, K. (2009) Glacial refugia influence plant diversity patterns in the Mediterranean Basin. *Journal of Biogeography*, 36, 1333–1345.
- Matthews, T.J., Triantis, K.A. & Whittaker, R.J. (2020) *The species-area relationship: theory and Application*. Cambridge University Press, Cambridge.
- Moradi H., Fattorini S. & Oldeland J. (2020) Influence of elevation on the species–area relationship. *Journal of Biogeography*, 47, 2029–2041.
- Nogués-Bravo, D., Araújo, M., Romdal, T. & Rahbek, C. (2008) Scale effects and human impact on the elevational species richness gradients. *Nature*, 453, 216.
- Panda, R.M., Behera, M.D., Roy, P.S. & Biradar, C. (2017) Energy determines broad pattern of plant distribution in Western Himalaya. *Ecology and Evolution*, 7, 10850–10860.
- Pauli, H., Gottfried, M., Reiter, K., Klettner, C. & Grabherr, G. (2007) Signals of range expansions and contractions of vascular plants in the high Alps: observations (1994–2004) at the GLORIA master site Schrankogel, Tyrol, Austria. *Global Change Biology*, 13, 147–156.
- Pebesma, E. (2018) Simple features for R: standardized support for spatial vector data. *The R Journal*, 10, 439–446.
- Pepin N., Bradley R.S., Diaz H.F., et al. (2015) Elevation-dependent warming in mountain regions of the world. *Nature Climate Change*, 5, 424–430.
- Pianka, E.R. (1966) Latitudinal gradients in species diversity: a review of concepts. *The American Naturalist*, 100, 33–46.
- Pignatti, S., Guarino, R. & La Rosa, M. (2017) *Flora d'Italia*, 2ª edizione. Edagricole, New Business Media, Bologna.
- Pyšek, P., Richardson, D.M., Pergl, J., Jarošík, V., Sixtova, Z. & Weber, E. (2008) Geographical and taxonomic biases in invasion ecology. *Trends in Ecology and Evolution*, 23, 237–244.
- R Core Team (2020) *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>
- Rahbek, C. (1995) The elevational gradient of species richness: a uniform pattern? *Ecography*, 18, 200–205.

- Rahbek, C. (2005) The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, 8, 224–239.
- Rahbek, C., Borregaard, M.K., Colwell, R.K., Dalsgaard, B., Holt, B.G., Morueta-Holme, N., Nogues-Bravo, D., Whittaker, R.J. & Fjeldsø, J. (2019) Humboldt's enigma: what causes global patterns of mountain biodiversity? *Science*, 365, 1108–1113.
- Raunkjær, C. (1934) *The life forms of plants and statistical plant geography; being the collected papers of C. Raunkjær*. Clarendon Press, Oxford.
- Richerson, P.J. & Lum, K. (1980) Patterns of plant species diversity in California: relation to weather and topography. *The American Naturalist*, 116, 504–536.
- Romdal, T.S. & Grytnes, J.A. (2007) An indirect area effect on elevational species richness patterns. *Ecography*, 30, 440–448.
- Rosenzweig, M. L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Venables, W.N. & Ripley, B.D. (2002) *Modern Applied Statistics with S*, 4th edn. Springer, New York.
- Sklenář, P., Hedberg, I. & Cleef, A.M. (2014) Island biogeography of tropical alpine floras. *Journal of Biogeography*, 41, 287–297.
- Steinbauer, M. J., Field, R., Grytnes, J.A., et al. (2016) Topography-driven isolation, speciation and a global increase of endemism with elevation. *Global Ecology and Biogeography*, 25, 1097–1107.
- Stevens, G.C. (1992) The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *The American Naturalist*, 140, 893–911.
- Subedi C.K., Rokaya M.B., Münzbergová Z., Timsina B., Gurung J., Chettri N., Baniya C.B., Ghimire S.K. & Chaudhary R.P. (2020) Vascular plant diversity along an elevational gradient in the Central Himalayas, western Nepal. *Folia Geobotanica*, 55, 127–140.
- Tennekes, M. (2018) tmap: thematic maps in R. *Journal of Statistical Software*, 84, 1–39.
- Terborgh, J. (1977) Bird species diversity on an Andean elevational gradient. *Ecology*, 58, 1007–1019.
- Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, I.C. (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences USA*, 102, 8245–8250.
- Tomaselli, M. & Agostini, N. (1994) A comparative phytogeographic analysis of the summit flora of the Tuscan-Emilian Apennines and of the Apuan Alps (Northern Apennines). *Fitosociologia*, 26, 99–109.
- Tomaselli, M., Carbognani, M., Foggi, B., Petraglia, A., Rossi, G., Lombardi, L. & Gennai, M. (2019) The primary grasslands of the northern Apennine summits (N-Italy): a phytosociological and ecological survey. *TUEXENIA*, 39, 181–213.
- Torre, G., Fernández-Lugo, S., Guarino, R. & Fernández-Palacios, J.M. (2019) Network analysis by simulated annealing of taxa and islands of Macaronesia (North Atlantic Ocean). *Ecography*, 42, 768–779.
- Turner, J.R., Gatehouse, C.M. & Corey, C.A. (1987) Does solar energy control organic diversity? Butterflies, moths and the British climate. *Oikos*, 48, 195–205.
- Vetaas, O.R. (2002) Realized and potential climate niches: a comparison of four *Rhododendron* tree species. *Journal of Biogeography*, 29, 545–554.
- Vetaas, O.R. & Grytnes, J.A. (2002) Distribution of vascular plant species richness and endemic richness along the Himalayan elevation gradient in Nepal. *Global Ecology and Biogeography* 11, 291–301.
- Vetaas, O.R., Paudel, K.P. & Christensen, M. (2019) Principal factors controlling biodiversity along an elevation gradient: water, energy and their interaction. *Journal of Biogeography*, 46, 1652–1663.
- Walther, G.-R., Beißner, S. & Pott, R. (2005) Climate change and high mountain vegetation shifts. In: *Mountain ecosystems: studies in treeline ecology* (ed. by G. Broll and B. Keplin), pp. 77–96. Springer, Heidelberg.
- Walther, G.-R., Roques, A., Hulme, P.E., Sykes, M.T., Pyšek, P., Kühn, I., Zobel, M., Bacher, S., Botta-Dukat, Z. & Bugmann, H. (2009) Alien species in a warmer world: risks and opportunities. *Trends in Ecology and Evolution*, 24, 686–693.
- Wang, Q., Su, X., Shrestha, N., Liu, Y., Wang, S., Xu, X. & Wang, Z. (2017) Historical factors shaped species diversity and composition of *Salix* in eastern Asia. *Scientific Reports*, 7, doi: 10.1038/srep42038.

- Weigelt, P., König, C. & Kreft, H. (2020) GIFT – A Global Inventory of Floras and Traits for macroecology and biogeography. *Journal of Biogeography*, 47, 16-43.
- 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.
- Wickham, H. (2007) Reshaping data with the reshape package. *Journal of Statistical Software*, 21, doi: 10.18637/jss.v021.i12
- Wickham, H. (2016) *ggplot2: elegant graphics for data analysis*. Springer-Verlag, New York.
- Wilson, J.B. (1988) Community structure in the flora of islands in Lake Manapouri, New Zealand. *Journal of Ecology*, 76, 1030–1042.
- Wright, D.H., Currie, D.J., Maurer, B.A. (1993) Energy supply and patterns of species richness on local and regional scales. In: *Species diversity in ecological communities: historical and geographical perspectives* (ed. by R.E. Ricklefs and D. Schluter), pp. 66-74. The University of Chicago Press, Chicago and London.
- Yoda, K. (1968) A preliminary survey of forest vegetation of eastern Nepal. III. Plant biomass in the sample plots chosen from different vegetation zones. *Journal of the College of Arts and Sciences, Chiba Daigaku Kyōyōbu kenkyū hōkoku*, 5, 227-302.

Submitted: 12 October 2020

First decision: 5 November 2020

Accepted: 7 January 2021

Edited by Robert J. Whittaker