RESEARCH ARTICLE

Area, environmental heterogeneity, scale and the conservation of alpine diversity

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Abstract

Aim: Area and environmental heterogeneity together explain most patterns of species diversity but disentangling their relative importance has been difficult. Here, we empirically examined this relationship and parsed their relative importance, and that of the heterogeneity—effective area trade-off, at different spatial scales and in different spatial representations in simulations.

Location: Alpine grasslands of 23 mountain ranges of southern and central Europe.

Taxon: Vascular plants.

Methods: We developed metrics of climatic and edaphic heterogeneity, using principal components analyses and the shoelace algorithm, and added elevation range. We applied commonality analysis to partition the unique and shared explanation of the observed vascular plant species richness among selected metrics. A simulation was developed to separate the relative importance of area and heterogeneity at different extents and representations of spatial nestedness, and the heterogeneity—effective area trade-off was evaluated by altering spatial discreteness.

Results: The explanation of the observed regional richness was shared by area and heterogeneity. The simulation revealed that heterogeneity was consistently more important, but less so among smaller areas. This qualitative pattern was maintained regardless of whether and how nestedness was represented. The heterogeneity–effective area trade-off occurred in a few simulations of more discrete habitats.

Main Conclusions: Scale dependence may account for discrepancies among past empirical studies wherein environmental heterogeneity has usually outweighed area in the explanation of species richness; and it is not affected by nestedness. The potential heterogeneity–effective area trade-off may be limited to locations where the environmental heterogeneity is quite discrete or if the added environment is beyond the niches of any species in the potential pool. The significant importance of area per se in small territories indicates that microrefugia, even with an unlikely full range of heterogeneity, will suffer local extinctions in the face of climate change.

1 | INTRODUCTION

Explanations of diversity have been variously attributed to area and environmental heterogeneity because they are entwined (Triantis et al., 2003). Recent studies have argued that heterogeneity is the most important component of why diversity increases with area (Stein et al., 2014), but the balance of the two factors is uncertain:

> "The question is therefore not about whether species richness is correlated with area or environmental heterogeneity, respectively, but rather about the relative importance of the two in explaining species richness."
>
> Udy et al. (2021).

Area per se is important because more individuals can be divided into more species, each with a minimum population, given the basis of a fixed number of individuals per unit area (MacArthur & Wilson, 1967). Heterogeneity per se maintains diversity because more environments can support more specializations and species, each with a minimum population (e.g. Tilman, 2004). These explanations are the central elements of the neutral and niche theories of diversity (Chisolm & Pacala, 2010), and like many other ecological theories may depend on the scale of observations (McGill, 2010; Willis & Whittaker, 2002).

The importance of the area versus environmental heterogeneity (AvE) question goes beyond theoretical matters. As an example, the potential for species in alpine habitats—and other island-like environments—to survive climate change depends on the current area, heterogeneity of climate, and their effect on diversity relative to climate changes. Warming will shift alpine habitats upwards while spatially reorganizing them among microsites of current zones (e.g. Engler et al., 2011; Körner & Hiltbrunner, 2021; Malanson et al., 2019). The total area will be reduced, especially where the highest elevations are already occupied or consist of bare rock or ice. During this process, increases in local diversity may occur (Steinbauer et al., 2018), but an extinction debt will be incurred (Dullinger et al., 2012). The amount of debt, and the number of eventual extinctions, will depend on AvE: that is, whether heterogeneity is sufficient across enough area to support minimum viable populations.

Although the drivers of diversity are known to vary with extent, the role of area per se at different extents is seldom differentiated (e.g. Wang et al., 2012), The effects of extent and spatial resolution on AvE were discussed in depth by Stein et al. (2014). They highlighted the collinearity of area and heterogeneity and the entanglement of area and resolution, showing that the effects of resolution varied with area and vice versa. They concluded that heterogeneity was most important at intermediate extents—perhaps because they did not include climate, which is a factor acting at greater extents (McGill, 2010).

Scale dependence for patterns related to diversity have been proposed and observed (e.g. Belmaker & Jetz, 2011; Daru et al., 2020; Rahbek, 2005; Willis & Whittaker, 2002); thus, we expect the relationship of diversity to area and environmental heterogeneity to be scale dependent. The usual species-area curve is steeper among small areas than larger ones, which indicates greater sensitivity at the small end of the scale (except among very small islands; Triantis et al., 2006). The effect of area per se in maintaining diversity is through redundancy that provides protection from stochastic extinctions, and the value of redundancy decreases as area increases. Diversity tends to increase linearly with heterogeneity, however (see Rosenzweig, 1995 for several examples, for example, his figures 2.25, 7.8, 8.11, 8.12, 8.22). Because heterogeneity increases with area, the influence of the two on diversity will diverge as the area examined increases.

The relative importance of AvE to diversity seems to vary between continental and island systems. For greater areal extent on continents, environmental heterogeneity is relatively more important in explaining species richness in several systems, for example, Udy et al. (2021) reported contributions to explanation of 9% and 12% for area per se globally and in the Palearctic. Studies of island systems reported higher relative importance for area per se, even while emphasizing environmental heterogeneity, for example, Keppel et al. (2016) reported contributions of area at 40% and 37% for archipelagoes and individual islands, respectively, and Barajas-Barbosa et al. (2020) found that the effects for area were double those of any of the 20 heterogeneity metrics that they had calculated for oceanic islands. However, even at a larger scale, Udy et al. (2021) reported that area explained more diversity within the examined biogeographic provinces than it did for global diversity.

Kadmon and Allouche (2007) linked the spatial and niche frameworks with a complicating trade-off: a heterogeneity—effective area trade-off (HEAT); with constant area, increases in heterogeneity reduce areas of specific habitats ("effective area") and specialized species will have smaller populations and experience more stochastic extinctions. Thus, a unimodal relationship of diversity with heterogeneity can appear in a constant area (Allouche et al., 2012; Zhou et al., 2021). This relationship may be affected by the spatial resolution or grain of the observations at a given extent. Although evidence to the contrary exists (Hortal et al., 2009, 2013), it appears that HEAT has a sound theoretical basis (Allouche et al., 2012; Ben-Hur & Kadmon, 2020a). Yet, this trade-off could also be an artefact of model resolution or spatially discrete habitat patterns (Durrett & Levin, 1994) in addition to the niche characteristics of species (Sfenthourakis et al., 2021).

Here, we address extent and resolution separately for the questions of AvE and HEAT in alpine habitats, another type of island system wherein the relative importance of area and heterogeneity vary

(e.g. Bhatta et al., 2018; Meier & Hofer, 2016), probably because of the small size of the plants in relation to small-scale variation in microclimates, soil water and disturbance as well as species interactions (Körner, 2003). Most studies have examined diversity as a function of environmental variables directly, not to heterogeneity per unit area (e.g. at 10–100 m scale: Jiménez-Alfaro et al., 2014; and across mountain ranges: Engler et al., 2011, Winkler et al., 2016). Where heterogeneity has been addressed, it was at a specific scale. At fine scale (1 m^2), Rose and Malanson (2012) reported that topographic heterogeneity was an indicator of disturbance, not of microenvironmental variability, which constrained diversity. At 16 m^2, beta diversity was related to indicators of environmental difference (Malanson et al., 2020), and at 1600 m^2 both alpha and beta diversity were related to microclimatic heterogeneity (Opedal et al., 2015). At regional scale, Tordoni et al. (2020) reported the importance of geomorphic variation to diversity, and at interregional scale, Jiménez-Alfaro et al. (2021) found that topographic ruggedness, which can create heterogeneous microclimates and soils, was more important than any climatic drivers of diversity. At global scale, Testolin et al. (2021) examined the standard deviation of environmental variables within their 26 ranges and found that only the heterogeneity of soil pH was important for diversity.

To unravel the relative strengths of area versus environmental heterogeneity (AvE) and to determine whether they are scale dependent, we framed the following hypotheses for observed regional species richness in 23 alpine regions in southern and central Europe, general AvE spatial patterns, and the heterogeneity–effective area trade-off (HEAT):

> H1: The observed vascular plant species richness, or species pool size, is equally related to area and environmental heterogeneity.

> H2: The relative strengths of AvH are scale dependent, with area more important in smaller areas.

> H3: The heterogeneity–effective area trade-off (HEAT) is scale dependent and occurs more often in smaller areas.

We tested H1 at subcontinental scale with a dataset that has been used in previous empirical studies and it is relatively well known in terms of vascular plant species richness and related biogeographical drivers. We further develop a simulation model parameterized with those data but representing a full factorial array of heterogeneities and areas for three spatial patterns, to test the more general H2 and H3 hypotheses. Simulation experiments allow a full factorial separation of area and heterogeneity that can illuminate their relative effects on a gradient of areal extent, and instances of HEAT can be investigated relative to model parameterization by changing the discreteness of the environment. The simulation addresses the relative strength of explanations and does not predict actual diversity.

Connecting the AvE problem to scale dependence will provide a new perspective on the understanding of climate change effects on alpine diversity, with potential links to questions of current and future refugia.

2 | MATERIALS AND METHODS

2.1 | Observed diversity

2.1.1 | Data sources and variable selection

We used species records for the alpine habitats of 23 mountain regions in southern and central Europe (Appendix S1, Appendix 1: Figure A1.1). Jiménez-Alfaro et al. (2021) organized these data from 16,804 relevés (vegetation plots) that were above local treeline. Alpine grasslands were identified using Landsat NDVI (detailed explanation in Appendix S1 of Jiménez-Alfaro et al. (2021)). The species composition is almost entirely herbaceous and differs between calcareous and siliceous substrates, both of which occur in all regions except Corsica. For these legacy data, the sampling size in the 23 regions was not strictly even, but the vascular plant species richness, here called the regional richness, was found to represent an almost-complete sampling in all regions (Jiménez-Alfaro et al., 2021).

We examined environmental heterogeneity of climatic, edaphic, and elevation range (the latter potentially modifying the heterogeneity of climate and soils, e.g. Graae et al., 2018). We selected 8 bioclimatic variables from CHELSA V2.1 (Karger et al., 2017, 2018; see https://chelsa-climate.org/wp-admin/download-page/CHELSA_tech_specification.pdf) for the 30-arcsecond cells (c. 1 × 1 km) of the alpine grasslands (49,085 cells). Temperature variables are for 2-m above the surface. Of the 19 bioclimatic variables, we excluded: wet and dry season temperature and precipitation (4 variables) because they can use different seasons for different locations; the monthly variables (4 variables), which are highly correlated with the corresponding quarterly variables; and daily and annual ranges and isothermality (3 variables), which are correlated with temperature seasonality but do not have a corresponding precipitation variable (cf. Booth, 2022; Testolin et al., 2020).

We retained mean annual temperature and precipitation, mean temperature and precipitation of the warmest and coldest quarters, and temperature and precipitation seasonality. Mean annual temperature and precipitation capture broad differences; warm quarter temperature and precipitation emphasize the growing season; cold quarter temperature and precipitation include the effects of snow; and temperature and precipitation seasonality reflect continentality and the mid-latitude vs. Mediterranean climates. We derived two-dimensional climatic envelopes for each of the 23 ranges using principal components analysis (PCA) in PC-ORD v.7 (McCune & Mefford, 2016) with a correlation-based cross-products matrix of the eight CHELSA bioclimatic variables. We assessed the significance of the eigenvectors by using the broken-stick method. Two eigenvectors were significant and

extracted 72.9% of the variance in the climatic data (Appendix S1, Appendix 1: Table A1.1). We plotted the points for the two eigenvectors for each range, selected 5–15 points that outlined the distribution, including indentations and excursions but excluding individual points that would increase the area by > 10% as outliers, and computed the area of the polygon (labelled ClimG) using the shoelace algorithm (Meister, 1769) (Appendix S1, Appendix 1: Figure A1.2) (in preliminary analyses, we found that the standard deviations of 11 soil and 20 climate variables were not as highly correlated with diversity as the metrics used here; Appendix S1, Appendix 1: Table A1.2).

For edaphic heterogeneity, we selected 11 variables from ISRIC data (https://www.isric.org/). We used data for the uppermost layer of soil (for all 127,076 records with soil because the ISRIC coordinates could not be matched exactly to the grassland coordinates; these have a nominal spatial resolution of 250 m) for bulk density of the fine earth fraction, cation exchange capacity, volumetric fraction of coarse fragments, proportions of clay, silt, and sand, total nitrogen, pH, organic content in the fine earth fraction, organic carbon density, and organic carbon stocks. Similar to the procedure for the climate data, we ran a PCA of the soils data and computed an area in 2D PCA space (SoilsA) (Appendix S1, Appendix 1: Figure A1.3), which extracted 63.2% of the variance in the soils data, for each mountain range (Appendix S1, Appendix 1: Table A1.1).

Initially, we examined three indicators of topographic heterogeneity. Jiménez-Alfaro et al. (2021) calculated a ruggedness index (Rugged), and we added the highest elevation of the range (MaxElev) and the difference in elevation between this and the regional treeline (ElevDiff), which they had identified. After preliminary analyses, we used the latter. We also included two measures of isolation, namely the median distance to all other ranges and the distance to the 3rd nearest range (the 15th percentile, which captures the potential for exchanges with nearby ranges), in initial analyses (DistX, Dist3).

2.1.2 | Analyses of observed diversity

We used the variables as described and their log-transformed values in initial analyses. After examining correlations between regional richness, area and the PCA areas for climate and soils, topography, and isolation, we computed a commonality analysis (also referred to as "variance partitioning" in multivariate analysis) of regression (Ray-Mukherjee et al., 2014) to test our first hypothesis. We used the log of area and the climatic and edaphic heterogeneity of the grasslands and full regions, respectively (areas in PCA-space) and the untransformed topography indicator as independent variables (LogAreaG, LogClimG, LogSoilA, ElevDiff where G and A designate data from the grassland cells and the full mountain range, respectively); the isolation metrics (DistX, Dist3) were not significantly correlated with regional species richness and were not used. Commonality analysis allows for the identification of shared contributions in its explanation of variance.

2.2 | Simulations

A comparison of different combinations of area and heterogeneity configurations using virtual species adapted to an environmental gradient can elucidate how diversity responds to control by geography vs. environment. We developed a simple spatially explicit individual-based model with environmental and spatial variation represented on a grid of cells using NetLogo 6.1.1 (Wilensky, 1999). We first designed the model as a virtual microcosm of the observed areas and heterogeneities in the empirical analysis of the 23 regions and then ran the simulation in a more general experimental mode, systematically varying heterogeneity and area, still as a microcosm, to compare relative areas. After initializing the areas with heterogeneity and individuals of virtual species, those individuals reproduce, disperse among the cells, and die at each iteration, and the number of species at the end of the simulation was tallied. These steps are described here and the Overview, Design, Details Protocol recommended by Grimm et al. (2020) is reported in Appendix S1, Appendix 2, ODD.

2.2.1 | Initialization

The position of each cell on a single environmental gradient was assigned by initializing a fractal pattern across the grid. The fractal pattern resembles topography with values of the environmental gradient assigned to each cell corresponding to its relative elevation (Appendix S1, Appendix 2: Figure A2.1). The fractal pattern of topography ranged 0–1, and this value was rescaled to the range of environmental heterogeneity, either observed or experimentally defined. The range was centred on 0.5 (e.g. for a heterogeneity of 0.1, the environmental value of the cells ranged 0.45–0.55). Each grid was wrapped into a torus to eliminate edge effects, which is computationally more efficient and noting that alpine habitats are not distinct islands (obligate alpine species are only 27% of the flora of the alpine grasslands in the study area; Jiménez-Alfaro et al., 2021).

Each cell is then assigned a response value for each of 100 virtual species. Each species has a Gaussian response function over the environmental gradient (illustrated in Appendix S1, Appendix 2: Figure A2.2) from which a value is assigned to each cell based on its environment. The response of species I at position x on the environmental gradient is

$$R_{ix} = e^{-\left(\left((E_x - m_i)^2 / 2\sigma^2\right)\right)}$$

where E_x is the position of the cell on the environmental gradient; the m_i is the position of the mode of the species on the gradient, and σ^2 is the standard deviation of the Gaussian function, chosen here as 0.001, which produced distributions of regional species richness (2–100) spanning nearly the full possible range across all simulations. Thus, 100 such equations define 100 virtual species. This approach follows earlier theoretical models of species distributions

on environmental gradients (e.g. Gauch & Whittaker, 1976), but we recognize that Gaussian functions are not necessarily common (Falster et al., 2021).

The values for the distribution of modes and σ were chosen after preliminary analyses of four alternatives (see Appendix S1, Appendix 2: Simulation background, ODD Protocol). First, the modes were evenly distributed along the gradient for maximum niche differentiation and σ was constant for all species. Second, all species had an identical niche with the mode centered on the gradient; rather than demonstrating only effects of area (for which its usefulness is limited by extreme competitive exclusion), illustrates HEAT and how species parameterization can account for it in models as noted by Sfenthourakis et al. (2021). Third, modes were clustered at 10 evenly distributed points along the gradient and then minor random variation was added (limited runs with 2 and 3 clusters further illustrated HEAT in preliminary analyses). Lastly, a random distribution of modes with minor random variation in σ was included.

Projected regional richness from all versions except the single mode were nearly identical (correlations all $r > 0.93$; Appendix S1, Appendix 2: Figure A2.3 and Table A2.1), and we report the first approach because it aligns best with past theoretical representations (MacArthur & Levins, 1967), the species have the potential to fill all niches and occupy all locations, and it requires fewer replicate runs. We did not simulate specialist versus generalist species which would require further parameterization (e.g. Malanson, 1997); Sfenthourakis et al. (2021) noted that this lack can affect modelling of the HEAT phenomenon.

A Monte Carlo process was used to initialize the distributions of individuals of each species per cell, that is, a species was allotted to each active cell if a uniform random number (0–1) was less than their response value for that cell. Then, individuals were randomly selected and removed while the number per cell exceeded a carrying capacity that varied in the simulations of the regions but was constant in the general experiments.

2.2.2 | Iterated reproduction and mortality

The models cycle through two procedures at each iteration: reproduction with dispersal and mortality. In reproduction with dispersal, individuals establish an offspring on a cell in a random direction at a random distance of 0–4 cells. Preliminary analyses found no significant differences among different dispersal ranges, and this range was retained to simplify the comparisons. Although Ben-Hur and Kadmon (2020b) found that dispersal distance could matter in other configurations, it is limited in alpine plants (Morgan & Venn, 2017). For mortality, individuals were removed at each iteration if a uniform random number (0–1) was greater than their response value for that cell. Additionally, individuals were randomly selected and removed while the number of individuals per cell exceeded the potential carrying capacity. Repeated Monte Carlo reproduction and mortality introduced stochasticity. Details of the replications are reported in Appendix S1, Appendix 2: Simulation background, ODD Protocol.

2.2.3 | Observed parameterization

To assess how well the model reproduces the pattern of regional species richness among ranges in the study regions, we parametrized the model to match our empirical study. The number of cells in each simulation is set as close to the number of square kilometres in the represented range as possible for a square grid +/− one row (a grid size of 109 would be represented by a 10×11 simulation grid). Random cells within the grid were defined as non-habitat to retain only the area of alpine grasslands. Thus, the relative areas of the grasslands to the full ranges are the same in the simulations as in the observations, but the cells are not meant to represent square kilometres. The environmental heterogeneity of each range was derived from the climatic, edaphic, and topographic variables by weighting the observed heterogeneities in the empirical analysis by their relative importance (i.e. 40%, 40%, 20%, respectively) and assigning a relative heterogeneity (0–1). We set the carrying capacity, i.e. the number of individuals per cell, using 2 as the lower limit (Baetic System) and scaling relative to the product of warm quarter precipitation and temperature (Appendix S1, Appendix 2: Table A2.2). This limit and the total of 100 virtual species allows efficient computation of the relative species richness among regions for statistical analysis; it is not meant to represent the number of individuals per square kilometre or the number of species per range. We correlated the observed and simulated gamma diversities of the 23 ranges; this pattern of diversity across the ranges, not the absolute values, is used to evaluate the simulation.

2.2.4 | General spatial representations

For the general question of area vs. environmental heterogeneity, we evaluated three spatial representations. Square grids wrapped to tori of varying size and heterogeneity are the primary representation and are styled as islands. Concentric circles within a large grid represent nested areas within a mainland. Multiple nested quadrats represent provinces within a supercontinent (Appendix S1, Appendix 2: Figure A2.4).

For the islands, we used a full factorial design of 10 areas and 10 levels of heterogeneity, even though these included unrealistic combinations of limited area and high heterogeneity and vice-versa for the island representations. We used a sequence of square grids of sizes: 100, 400, 900, 1600, 2500, 3600, 4900, 6400, 8100 and 10,000 cells. The carrying capacity was constant at 9, the mid-point of the observed range. For environmental heterogeneity, we use ranges of 0.1–1.0 in increments of 0.1. Ten replications of the 100 combinations of the squares were run with a new landscape generated each time. By using the same random number seed, the landscapes were the same for all 10 levels of heterogeneity.

For the concentric circles, a sequence of 10 areas were delineated within a single large square for each of the 10 levels of environmental heterogeneity. The radii of the circles were set to closely approximate the same number of cells as the 10 square grids above (100, 4000, … 10,000 cells). The grid was 112×112 cells and the radii of the circles were 5.7–56.42 cells at 5.636 cell increments. This modification allows

consideration of the difference in diversity with area that would be comparable to increasing areas from a point within a continent versus tallying diversity on different islands. The species richness within each successive circle was extracted along with the range of environment.

The second nested design divided a single large area (supercontinent) into six provinces. Each of these had four nested quadrats of increasing area and then these six were accumulated by two, four, and all six provinces giving seven nested areas. For these quadrats, the grid was 120×80 cells, the provinces were 40×40, and the subquadrats were at 100, 400, 900 and 1600 cells and the further clusters at 3200, 6400, and 9600 cells. The species richness and the environmental heterogeneity were tallied within each quadrat, province and cluster.

2.3 | Analyses of simulations

2.3.1 | Virtual microcosms of the 23 ranges

With the grid sizes and heterogeneities parameterized as microcosms of the 23 ranges, we correlated the simulated regional richness for each range with the observed species richness reported by Jiménez-Alfaro et al. (2021).

2.3.2 | General experiments

We examined the projected increase of mean regional richness with increasing heterogeneity across the 10 areas and the increase of mean richness with increasing area across the 10 levels of heterogeneity. We interpret the pattern, especially the slopes of regressions to fit a function within these groups.

To test our second hypothesis, we used a random forest model (RFM; SPSS v29; cf. De'Ath, 2007) with area and environmental heterogeneity as continuous variables, which allows a regression approach and uses accumulated Gini impurities to determine variable importance (Akalin, 2021). Next, we divided the data by area into two equal subsets (smallest and large) and re-ran the same analyses. We analysed RFMs for the islands, concentric circles, and nested quadrats.

2.3.3 | Heterogeneity–effective area trade-off

For the investigation of HEAT, we reduced the environmental resolution of the initialization of the environmental gradient on the grids by rounding the number of decimal places of R_{ix} to 4, 2, or 1 (the default in NetLogo is 16). This modification increased the discreteness of habitats so that we could differentiate discrete vs. continuous heterogeneity, which is known to affect system behaviour (Durrett & Levin, 1994). It may also elucidate how model design can confound ecological interpretation if it induces more instances of the HEAT (cf. Sfenthourakis et al. (2021) for representations of niche). To test our third hypothesis, we counted the proportion of simulation runs in which the species richness in the most heterogeneous environment (1.0) was lower than

in any less heterogenous case in the same replication with the same random number seed. We also refer to results of preliminary analyses with the most discrete habitats and the random distribution of niches and to the single niche for all 100 virtual species.

3 | RESULTS

3.1 | Observed diversity

The regional species richness of the 23 ranges was significantly correlated with several of the spatial and environmental variables (Table 1). The highest r values were with the LogAreaG, LogSoilA, and LogClimG. When these variables were used in a commonality analysis, most of the explained variance was shared among them (Table 2). However, if the shared partitions of the variance explained (61% of the 75%) is allotted among the four independent variables (e.g. 0.017 of the 0.051 of s124 is tallied with each of area, climate, and elevation difference), area is the largest single contributor with a total of 33% (43% of the explained variance) (Figure 1). Our first hypothesis is supported, but a greater role for area is indicated.

3.2 | Simulations

3.2.1 | Observed diversity

The species richness in the simulations of the 23 ranges was significantly correlated with the observations ($r = 0.725$, $p < 0.001$; Appendix S1, Appendix 3: Table A3.1).

TABLE 1 Correlations (Pearson r) between the regional richness of 23 mountain ranges in southern and central Europe and selected environmental values.

Environmental variables	Richness
AreaG	0.586
LogAreaG	0.840
ClimG	0.675
LogClimG	0.842
Rugged	0.347
MaxElev	0.303
ElevDiff	0.555
LogElevDiff	0.224
SoilA	0.660
LogSoilA	0.725
DistX	−0.248
Dist3	−0.109

Abbreviations: G, grassland, not the entire range; ClimG, climate heterogeneity of grassland area; MaxElev, elevation of highest peak of the range; ElevDiff, elevation of highest peak minus that of treeline; SoilA, heterogeneity of soils of the range; DistX, median distance to other ranges; Dist3, distance to the third nearest range.

TABLE 2 The unique (u) and shared (s) contributions of the four independent variables (1: LogAreaG, 2: LogClimG, 3: LogSoilA, 4: ElevDiff) to the explanation of variance in regional species richness determined by commonality analysis.

Independent variables	%variance
u1 (area)	0.107
u2 (climate)	0.011
u3 (soil)	0.014
u4 (elevation diff)	0.010
s12	0.045
s13	0.151
s14	−0.009
s23	0.001
s24	−0.006
s34	0.003
s123	0.100
s124	0.051
s134	0.007
s234	−0.001
s1234	0.264

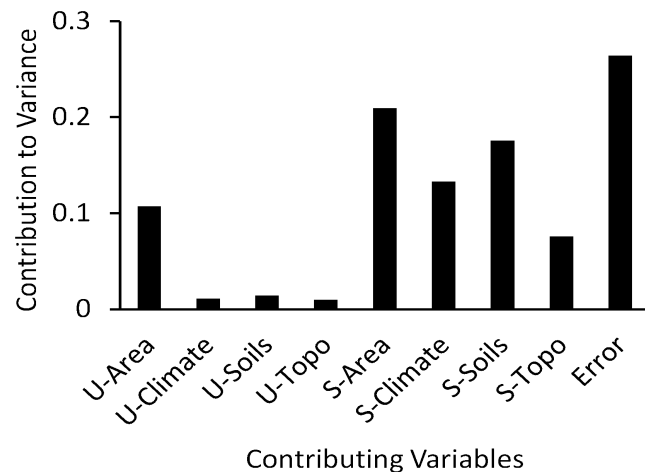*Note*: Negative values indicate suppressor effects.

FIGURE 1 The proportion of variance in regional species richness partitioned to the independent variables in commonality analysis of regression showing the unique (U) and shared (S) contributions. Here, the shared partitions in Table 2 were each divided among the contributing variables equally, and error is the unexplained variance.

3.2.2 | General spatial representations

The regional richness across the standard experiments using islands (independent tori) varied by both area and environmental heterogeneity but was more sensitive to the latter (Figure 2a,b; Appendix S1, Appendix 3: Table A3.2). The projected increases of mean regional richness, with increasing heterogeneity but constant area, were best represented by linear functions, whereas the increases of mean
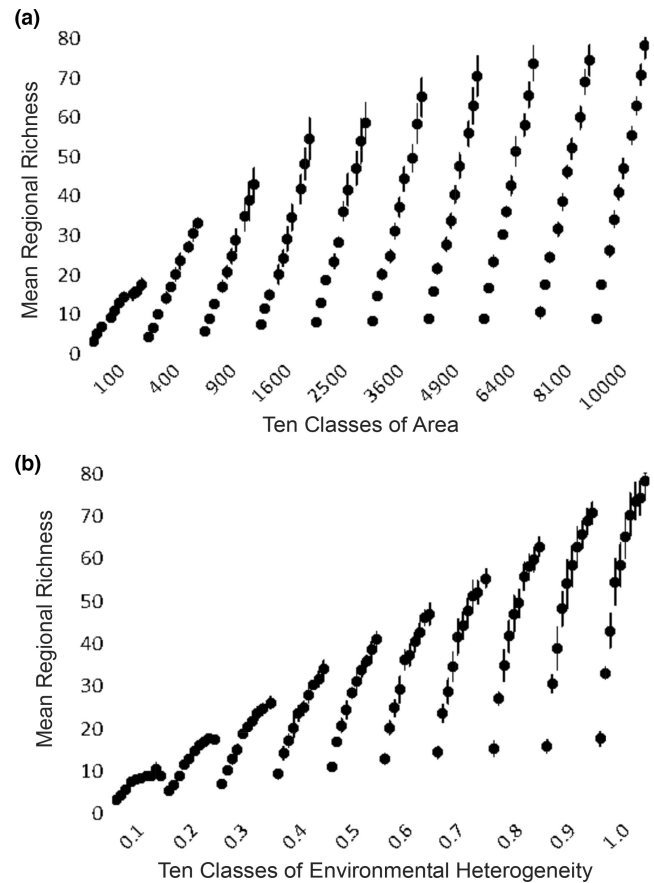

FIGURE 2 The regional species richness of the individual island simulations with (a) the 10 levels of environmental heterogeneity plotted over the 10 areas and (b) the 10 areas plotted over the 10 levels of environmental heterogeneity. The error bars show the 95% CI. The patterns in (a) are consistently linear, while those in (b) are logarithmic.

richness with increasing area but constant heterogeneity were fit by logarithmic functions (Figure 2a,b; Appendix S1, Appendix 3: Table A3.2). The sequence of slopes in each level of area or heterogeneity (from left to right in Figure 2a,b), however, are best fit by a logarithmic function for area but by a linear function for levels of heterogeneity (Figure 3a,b); the R^2s are identical at 0.997.

The simulation results supported our second hypothesis. The RFM for the complete simulation results for the island tori, concentric circles, and nested quadrats revealed more contribution to the variance of regional richness from environmental heterogeneity than from area (Figure 4; RFM details in Appendix S1, Appendix 3: Table A3.3). When the simulation results were divided between the smaller and larger areas, the relative contributions among the smaller ones were similar with slightly increased error. Among the larger areas, the importance of area was reduced, and heterogeneity accounted for more than 90% of the variance. The importance of heterogeneity was greater for the concentric circles than for the island tori and nested quadrats because the heterogeneity was calculated for each concentric circle and so the records were not independent given that the range of heterogeneity was from 10
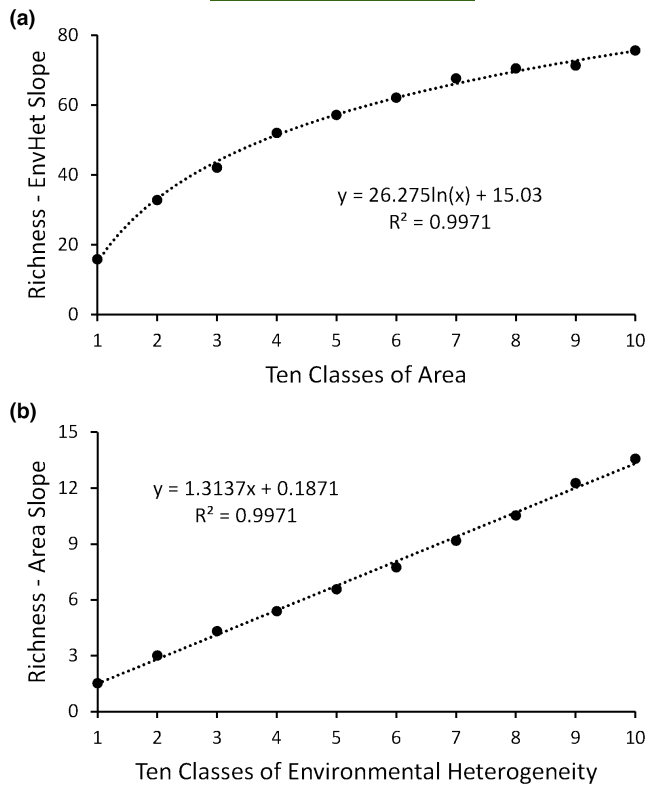
(a)

$$y = 26.275\ln(x) + 15.03$$
$$R^2 = 0.9971$$

(b)

$$y = 1.3137x + 0.1871$$
$$R^2 = 0.9971$$

FIGURE 3 Regressions of each of the 20 groups in Figure 2 (a) Environmental heterogeneity over area and (b) area over environmental heterogeneity: the slopes are fit by logarithmic and linear functions, respectively.
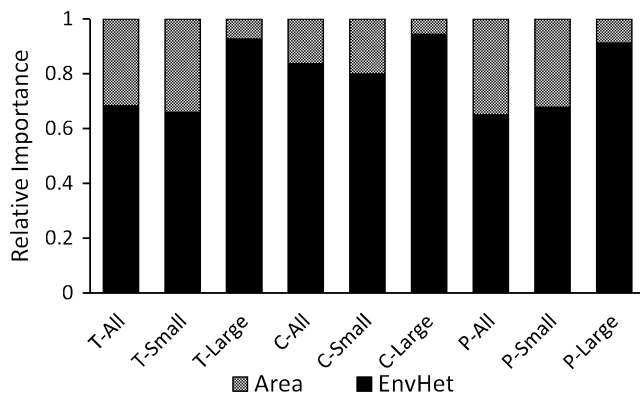

FIGURE 4 The relative importance of area and environmental heterogeneity to the Random Forest Model for the island tori (T), the concentric circles (C), and the nested provinces (P) when the data of all simulations are together or divided into the small and large areas represented in the simulations.

landscapes while those for islands and provinces were from 100 and 60 different landscapes, respectively.

3.2.3 | HEAT

In preliminary analyses with all species having identical niches in the middle of the environmental gradient, regional richness decreased

with increased environmental heterogeneity at all simulated areas, and the unimodal pattern presented by Allouche et al. (2012) is evident with 2 and 3 clusters (Appendix S1, Appendix 3: Figure A3.1). As noted by Sfenthourakis et al. (2021), these are model-selected instances of species being specialists relative to the environmental gradient.

Reducing the environmental resolution of the environment resulted in a decrease in regional richness with an increase in environmental heterogeneity, that is, evidence of HEAT, in a few cases among the smaller areas (100–2500 cells), never in the larger areas (3600–10,000 cells), thus supporting our third hypothesis. Among the smaller areas, it had a unimodal distribution, peaking at 35% of the simulation runs with an area of 200 and a resolution of 2 decimal places. HEAT was less frequent at even lower resolution and smaller areas because overall species richness was low, often a single species. The largest area and smallest resolution at which it occurred was for 2500 cells and 16 decimal places where the overall species richness was much higher and the stochastic loss of a species among the replicates was more likely. HEAT was not evident in preliminary simulations with a random distribution of niche modes (Appendix S1, Appendix 3: Figure A3.1).

4 | DISCUSSION

Although environmental heterogeneity and area can be unified (Triantis et al., 2003), differentiating their separate and shared effects on diversity is an important goal (Ben-Hur & Kadmon, 2020b; Udy et al., 2021). In our observations and simulations for European alpine vascular plant species richness, we found that heterogeneity is more important than area per se, which is the case for many systems worldwide (Stein et al., 2014; Udy et al., 2021), but because of collinearity, the effects are difficult to separate in observational data. The relative importance of area and environmental heterogeneity in explaining diversity in simulations varied with the extent represented. Such scale dependence is expected, but its recognition can elucidate differences among studies and has implications for conservation.

4.1 | Relative influence of area and heterogeneity

In our study system, alpine regional pools are related to historical as well as spatial context and topographic ruggedness (Jiménez-Alfaro et al., 2021) and beta diversity is scale dependent (Malanson, Pansing, et al., 2022). To these reports, we add that regional species richness is better correlated to additional measures of heterogeneity of the environment than to indicators of its direct effect, explaining why most of the explanation was partitioned to shared contributions. The unique and shared components of climatic, edaphic and topographic heterogeneity, when taken together, exceeded that of area (0.423 vs. 0.304). However, the unique contribution of area to regional richness was seven times greater than any of the single measures of heterogeneity for

climate, soils, and topography, and it is their shared contribution to explanation – much of which includes area – that makes them important in our analysis.

Minor differences in their contribution to regional richness were found for indicators of climatic, edaphic, and topographic heterogeneity. These variables had high multicollinearity, and their effects could not be fully teased apart from the observations of 23 ranges. However, the simulation model, which provided a reasonable approximation of the pattern of relative diversity among the mountain ranges given its simplicity, separated the effects of area and heterogeneity. The stronger contribution of heterogeneity in the simulations is expected, given that the design embodies the niche theory of diversity, and yet, area was a consistent driver.

The effects of area are scale dependent because stochasticity is relatively more important in small areas. Small differences in simulation area, from 100 cells to 2500 cells, changed the regional richness significantly, from an average of 11 to 33 species (across all levels of heterogeneity), while a change from 3600 to 10,000 cells changed slightly—35 to 44 species. In contrast, the change from an environmental heterogeneity of 0.1 to 0.5 was 10 to 28 species and from 0.6 to 1.0 it was 33 to 54 species—a difference of 59% vs. 17%. The results in Figure 3a,b further reveal how the effects of environmental heterogeneity per se, as a driver of regional richness, decreases as area increases while the effects of area continue to increase with greater heterogeneity.

The same pattern of a stronger effect of area in provinces than globally (and on islands than mainlands) can be explained by redundancy or the lack thereof. Area was relatively more important than heterogeneity in our representation of islands versus fully nested areas in mainlands. Heterogeneity dominated explanation in fully nested areas on mainlands simulated as concentric circles, but area was more important for regional richness in both other representations: provinces within a supercontinent (nesting is separate within provinces and then accumulates at province-to-supercontinent scale) and islands (non-nested areas). Given that the representation of provinces within a mainland had results more similar to those of islands than concentric circles, we conclude that the role of area was less relevant in a clearly nested analysis. In the nested concentric circles, the same environment was expanded incrementally, and redundancy was duplicated, but while this happens within provinces the further accumulation of provinces in a supercontinent adds new heterogeneity. Our results indicate that this was simply because the importance of redundancy decreases as it is more common.

Focusing only on the most correlated combinations of area and heterogeneity (i.e. both low to both high, e.g. Stein et al., 2014), area and heterogeneity are nearly equal in importance in RFMs and without scale dependence. Thus, the importance of heterogeneity and scale dependence in the full factorial experiments depended on instances of low area and high heterogeneity and/or vice-versa. While the two factors are highly correlated within a specific system, they may be less correlated with a broader range of environments, and heterogeneity is relative to the taxa. For example, alpine grasslands may have greater environmental heterogeneity in a small area than would steppe, and

chalk grasslands support greater specialization than either of those (e.g. Erdős et al., 2018; Zobel, 1992). Where area and heterogeneity covary closely, there is little scope for high heterogeneity to maintain diversity in small areas or for low heterogeneity to suppress it in large areas, and the inverse is also true. In the simulation experiments, however, the two factors did not have identical influences. The nearly linear response of species richness to heterogeneity within levels of area (Figure 3a) contrasted with the logarithmic response to area within heterogeneity (Figure 3b) (cf. Rosenzweig, 1995, as noted above)—and the difference between these two was greatest where either was small (the left-most patterns in Figure 2a,b).

Our preliminary analyses corroborate the reasoning of Sfenthourakis et al. (2021) on the influence of the representation of species niches on environmental gradients on the phenomenon of HEAT. Our simulation also illustrated that this phenomenon can be a function of the discreteness of the representation of the environmental gradient. HEAT occurred in some simulations with a limited number of discrete habitats, but this depended on our representation of niche and so was a limited model result. Whether HEAT will occur in nature will be complicated by actual spatial patterns (Tews et al., 2004). Lastly, lack of HEAT in our smallest simulated areas may be because area and heterogeneity are decoupled (e.g. Triantis & Sfenthourakis, 2012).

4.2 | Implications for conservation

Most of the area of the alpine sky-island grasslands of our study system will be outside their current climate envelopes by 2100, with worst cases in the smaller regions (Malanson, Testolin, et al., 2022). Even if microrefugia, which could mitigate some impacts of climate change on diversity (Körner & Hiltbrunner, 2021; Randin et al., 2009), maintain heterogeneity, our results indicate that a substantial proportion of diversity depends on area per se among small islands, and microrefugia, being micro, cannot provide the redundancy that supports higher diversity. Concurrent losses of heterogeneity and increases in habitat discreteness will exacerbate the potential loss of species. In the smaller ranges, where losses of alpine grassland climate area will be proportionally greatest, the impact on diversity will be dire. Further investigations of scale dependence between areas of microrefugia and the extent of mountain ranges is needed to guide mitigation efforts (Balantic et al., 2021). Responses will need to combine local and regional factors and the combined effect of area and environmental heterogeneity as the best approach to the impacts of projected climate change on diversity.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The vegetation data used in this research are archived at Dryad: https://doi.org/10.5061/dryad.0cfxpnw1h (Jiménez-Alfaro et al., 2021). The climate data are available at Dryad: https://doi.org/doi:10.5061/dryad.kd1d4 and EnviDat (Karger et al., 2018) and the soils data are at ISRIC: https://www.isric.org/explore/isric-soil-data-hub. The specific climate and soils variables used, with their geographic coordinates, and the results of the PCA of climate and soils data, with the shoelace algorithm calculations, and the output of the simulation model are archived at Dryad for review at the Journal of Biogeography. Derived data, that is, the environmental heterogeneity for climate, soils and topography, are included in Supporting Information. The simulation experiment results of species richness are archived at Dryad: https://doi.org/10.5061/dryad.sxksn036g. Examples of the simulation model are at GitHub: https://github.com/gpmalanson/gpmalanson-AvE-experiment/.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.