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Research

Midpoint attractor models resolve the mid-elevation peak in Himalayan plant species richness

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The midpoint attractor (MPA) models of species richness integrate a unimodal environmental favourability gradient and neutral effects forced by geometric constraints and thus extend the ecologically neutral mid-domain model. However, both alternative MPA algorithms assume that underlying environmental favourability peaks within the modelling domain. Here, we used elevational distribution data for 1054 plant species occurring in northwest Himalaya to explore species richness gradients and MPA performance in species groups defined by biogeography, taxonomy and life-form. MPA models achieved an excellent fit, but the two MPA algorithms produced contrasting estimates of MPA location, especially for species groups with richness originating in lowlands. Therefore, we propose a modification of the MPA model accounting for the environmental favourability peak outside the study domain to reflect these situations. Biogeographic origin was more decisive for MPA location than taxonomic or life-form classification, indicating relatively low climatic niche conservatism in plants.

Keywords: elevational gradient, geometric constraints, Himalayas, mid-domain effect, midpoint attractor, neutral theory, null models, species ranges, species richness peak, vascular plants

Introduction

Species diversity patterns along elevational and latitudinal gradients have long fascinated scientists, from the time of von Humboldt to the present day (Lomolino 2001). The monotonic decrease of diversity with increasing elevation was a generally accepted and universal pattern attributed to the general decrease of temperature with elevation, but the conflicting evidence of humped-shaped species diversity patterns resulted in a search for alternative explanations of empirical diversity patterns (Rahbek 1995, 2005). A mid-elevation peak was found more frequently in dry climates, where productivity at low elevations is limited by increasing aridity caused by high evaporation rates and low precipitation (McCain 2009). Furthermore, anthropogenic ecosystem disturbances have been concentrated mostly in lowlands, with reported negative effects

on biodiversity (Nogués-Bravo et al. 2008). However, the observed mid-elevation diversity peak may just be an artefact of the sampling effort or the method used to estimate elevational diversity patterns from available observations (Colwell and Hurtt 1994, Grytnes and Vetaas 2002). When the species range is estimated from point-samples, it is likely that the absolute range would be underestimated and this consequently causes the underestimation of actual diversity, especially at the domain margins and when the sampling effort is limited.

A simple and ecologically neutral explanation for a diversity peak at middle elevations emerged with the concept of 'mid-domain effect' (MDE), using only geometric constraints and random placement of species ranges within these constraints (Colwell and Hurtt 1994, Colwell and Lees 2000). MDE predicts the formation of symmetrical, hump-shaped distributions just by random overlap of species ranges placed within the domain. The MDE thus represents an ecologically neutral null model, simulating a richness pattern within a bounded domain when species range placement is not governed by climate suitability or any other ecological gradient. The support for MDE varies widely among studies, according to the geographic extent and the organism group studied (Dunn et al. 2007). Generally, the MDE prediction is more likely to fit empirical richness patterns when species ranges of the studied species group (relative to domain size) are large and when the scale of analysis is large (Jetz and Rahbek 2001, Dunn et al. 2007). Range location within a bounded domain is more restricted by geometric constraints for large-ranged species groups; therefore, their overlap in the middle of the domain tends to produce a stronger mid-domain richness peak. In practice, large-ranged species yielding a better MDE fit are expected when the environmental gradients are weak (Colwell et al. 2005) or under conditions of high environmental tolerances of the modelled species group (Rangel and Diniz-Filho 2005). In contrast, small-ranged (relative to domain size) species are usually found along prominent gradients with sharply changing environmental conditions; such systems are accordingly less prone to the influence of MDE. Better fit found in studies on large spatial scales may be caused by weaker correlations between environmental gradients (e.g. temperature, water availability) and the geographic domain, especially for continental-scale latitudinal studies compared to local elevational studies (Dunn et al. 2007). A weaker role for climatically controlled processes then leaves more 'space' for neutral processes.

While MDE quickly attained recognition by biogeographers, it had also been strongly criticised (Zapata et al. 2005, Currie and Kerr 2008, but see Colwell et al. 2004, 2005). MDE opponents stressed the conceptual difficulties in defining domain boundaries, as well as purported latent effects of environmental factors on the range size frequency distribution used to generate mid-domain null models (Hawkins et al. 2005) or evidence that the water-energy hypothesis can provide a better fit to empirical richness gradients than MDE (Hawkins et al. 2003). It is true that, with the exception of islands and other domains with sharp ecophysiographic boundaries (e.g. freshwater lakes), practically no other parts of the terrestrial surface have effective hard boundaries. This seems to be the major constraint for the application of MDE in practice, thus prompting the question of how to define the domain and its boundaries. In general practice, the lowest elevation of land surface in the study area (usually the sealevel) is considered the lower domain limit. In contrast, the decision where to set the upper limit is more arbitrary – it can be the elevation of the highest summit in the area and also the physiological limit for survival of the organisms studied (Grytnes 2003a, Zapata et al. 2005). The growing body of macroecological studies on diversity distributions reveals that they cannot define the modelling domain unambiguously and are accordingly cautious in interpreting their results. Currently, there seems to be a consensus that the effects of geometric constraints can jointly influence the observed richness pattern together with other ecological drivers of diversity, and the neutral effect of domain boundaries can eventually be separated and quantified. In fact, MDE is not important for what it does explain but rather for what it does not. The unexplained residuals from the MDE model require further explanation because they may include deterministic, non-random and biologically relevant drivers (Colwell and Lees 2000).

To overcome the limitations of MDE, the midpoint attractor (MPA) model was recently developed. This model extends the conceptual framework of MDE by replacing an ecologically neutral uniform distribution of potential midpoint positions within the domain with a MPA with Gaussian distribution (Colwell et al. 2016). The MPA model is more flexible than MDE because the Gaussian attractor allows MPA to fit also skewed hump shapes, peaking outside of the centre of the domain. The Gaussian attractor has two parameters A and B; the parameter A identifies the position of the peak of the Gaussian distribution function and the parameter B is the standard deviation of the Gaussian distribution function, that is an inverse measure of an attractor's strength. The distribution function is truncated by the limits of the domain. The position and shape of the MPA can be interpreted as an ecologically meaningful shared 'optimum', favouring diversity of the studied taxa, shifting the MPA model from purely neutral towards a model with biological meaning.

However, even the MPA model has limitations and assumptions that must be considered. Artefacts in underlying empirical data (e.g. incomplete sampling of species diversity and arbitrary decisions about where to set domain boundaries), may confound the model fit and interpretation. Furthermore, species whose fundamental niche extends beyond the environmental gradient present in the domain will have their realised range truncated, and therefore one or both of their range boundaries will likely be aligned with the domain boundary (Grytnes 2003a, Feeley and Silman 2010). The presence of such species may cause deviations from the neutral distribution of midpoints. To compensate for truncated species ranges, Colwell et al. (2016) proposed a modification of the primary MPA algorithm. While the primary MPA model (hereafter called MPA 1) uses a doubly

truncated normal distribution as a midpoint sampler, a modified MPA algorithm (MPA 2, aka 'spreading dye' algorithm in Colwell et al. 2016) samples midpoints from the complete Gaussian distribution and then adjusts midpoints of the species with ranges exceeding domain boundaries to the position closest to the respective domain boundary that will exactly keep the complete species range within the domain boundaries. Both variants prevent the simulated species ranges from overlapping domain boundaries, but the second approach increases the probability that the species range limit is placed directly at the domain limit. While Colwell et al. (2016) claimed that fit between empirical and modelled richness was comparable or better using Algorithm 2 for most datasets involved, the consequences of model selection on estimated model parameter values and their interpretation were not sufficiently discussed.

The basic assumption underlying the MPA is the existence of a universal, unimodal gradient of environmental favourability that underlies the realised richness patterns in a bounded domain. In reality, the ecological niche of taxonomically or functionally related groups of organisms tends to be similar, and this niche conservatism is mirrored in the pattern of species richness along elevational and latitudinal gradients (Peterson et al. 1999, Wiens and Graham 2005), but for distinct taxonomic or functional groups the relevance of particular climatic drivers may largely differ. Water-energy balance measures like actual evapotranspiration and water deficit or climatic extremes (e.g. monthly temperature minima and maxima) are usually considered the most relevant climatic variables controlling plant species ranges and richness (Hawkins et al. 2003, Šímová et al. 2011). While the average temperature universally decreases with elevation, other climatic measures potentially controlling species richness exhibit more complex relationships to elevational gradients (Körner 2007, McCain and Grytnes 2010). Thus, the selection of a species group entering the model affects the resulting species richness curve and, consequently, model performance. The decision of how to define a species group used for richness assessment is usually made ad hoc; mostly according to taxonomic or life-form criteria (Zhou et al. 2019). For plants, studies dealing with elevational richness gradients generally consider either all vascular plants (Grytnes and Vetaas 2002, Grytnes 2003b) or selected functional or taxonomic groups, such as ferns (Watkins et al. 2006, Colwell et al. 2016), epiphytes (Cardelús et al. 2006), trees (Carpenter 2005, Rana et al. 2019) or palms (Bachman et al. 2004). However, studies aiming to directly address differences among these groups are surprisingly scarce (Grytnes and Beaman 2006, Peters et al. 2016, Rana et al. 2019).

In this paper, we use a comprehensive dataset on vascular plant distribution from the Ladakh region in the western Himalaya to explore diversity patterns along an elevational gradient spanning more than 3500 m. We tested the performance of the MDE and MPA models, addressing elevational diversity patterns in the area, where the lower domain boundary is defined geographically, while the upper domain boundary is set physiologically and therefore represents a hard boundary (sensu Colwell and Hurtt 1994). Specifically, we aimed to find an optimal model setting for fitting and interpreting the species richness pattern along the elevational gradient. We then used the optimal model to decompose the effects of geographic constraints, sampling bias, species functional grouping, phylogenetic structure and biogeographic origin on realised species richness patterns.

Methods

Study region

We studied diversity patterns along an elevation gradient in northwest Himalaya, Ladakh region, India (Fig. 1). This region is partly isolated from adjacent areas by two biogeographical barriers – glaciated mountain ranges of Great Himalaya to the south and Karakoram Range to the northwest. To the east, the region is connected to the Tibetan plateau. Orographic barriers are also responsible for a strong rain-shadow effect, causing overall aridity in the region, with total annual precipitation often below 100 mm year^{-1}. Elevations with available unglaciated land area stretches from 2650 to ca 7050 m a.s.l., but the highest occurrence of vascular plants currently known is from 6150 m a.s.l. (Dvorský et al. 2015). Combined effects of low temperature stress and aridity restrict regional species ranges and dominant life-forms (Dvorský et al. 2017). The prevailing vegetation is treeless because of high aridity, except for shrubby formations along streams. At higher elevations, where the water regime is more balanced due to the decrease in evapotranspiration, low temperature is the dominant limiting factor (Dvorský et al. 2015).

Species data

We compiled information on species occurrence on the elevational gradient in the study region using two datasets of plant occurrence data: a dataset of 95 812 georeferenced floristic records from the study region collected on 4062 sites in surveys conducted by L. Klimeš (LK) in years 1997–2006 and from 7187 floristic records from field surveys led by J. Doležal (JD) in years 2008–2015 (Fig. 1). Field survey made by LK aimed to systematically explore floristic diversity of the region and to cover the geographic and elevational extent of the Ladakh, including remote areas far from the roads. Sampling took place during the short growing season (July–September each year). LK chose the sampling sites in the field ad hoc with the aim to cover the whole diversity of vegetation types in the region. For each sampling site, LK recorded a complete species list of vascular plant species growing in 1 ha area. Surveys by JD focused primarily on explorative plant trait data collection along the elevational transects with emphasis on species upper range limits and therefore a variable number of plant individuals was recorded at each site. Elevation for each site was recorded according to handheld GPS or barometric altimeter. The total extent of the study area covered by field sampling is ca 50 000 km², and the
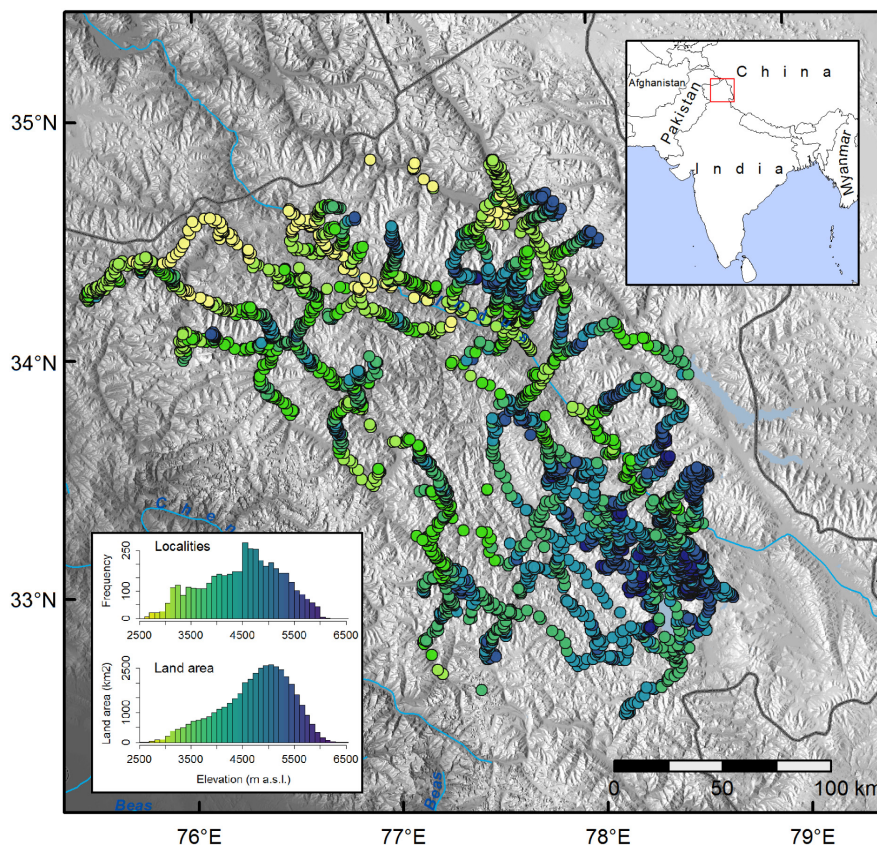
Figure 1. Study area with sampling localities. Inset histograms show sampling effort and terrestrial land area by 100 m elevation bands.

vertical range covered by sampling stretches from 2650 m a.s.l. in the Suru Valley in northwest Ladakh to 6150 m a.s.l. in the Changthang region, in eastern Ladakh.

Before conducting the analyses, we excluded all cultivated plant species and taxonomically unresolved records. This selection resulted in a dataset comprising 90 464 records of 1054 plant species, used for further analyses. For each species, we identified the elevation of its lowest and highest occurrence in the dataset.

To complement this empirical elevational distribution realised within our study region, we extracted species elevational range limits realised in adjacent regions (Supporting information) from published floras and online databases. Specifically, we used the Flora of Pakistan (<www.tropicos. org/Project/Pakistan>), the Flora of China (<www.eFloras. org>), the Flora of Nanga Parbat (Dickoré and Nüsser 2000), the Himalayan Uplands Plant database (Dickoré 2011) and the Global Biodiversity Information Facility (GBIF, <www. gbif.org>). Elevational records from the GBIF were rounded to the nearest hundred m a.s.l. to match the resolution reported in published floras and other databases. Unreliable records based mostly on historical reports (e.g. proclaimed elevation more than 1000 m apart from elevational extremes reported by other data sources for the same focal species) were discarded. We used information on elevational ranges realised outside the study region only for interpretation of the results based on regional elevational ranges.

To assess the contribution of various species groups to the overall diversity pattern, we classified the species according to the following criteria: family level taxonomic grouping, biogeographical affinity and life-form (annuals, graminoids, forbs, shrubs and trees). Detailed classification of species and the rules applied are given in the Supporting information.

Data analyses

We defined our domain by the extent of elevations inhabited by plants within our study area. The low elevation limit at 2650 m a.s.l. was aligned with the geographic extent of the study, therefore representing a 'soft boundary' (sensu Colwell and Hurtt 1994), while the upper domain limit at 6150 m a.s.l. was determined by climatic tolerance of vascular plants, therefore representing a 'hard boundary' (Dvorský et al. 2016). For model fitting, we transformed elevation values to unit domain values and back-transformed these values for the interpretation of results.

To calculate empirical elevational species richness (ESR), we used the interpolation method, assuming that each species was continuously present at all elevations between its extreme occurrences (Grytnes and Vetaas 2002). ESR was then calculated as the number of overlapping species ranges in 100 evenly spaced positions along the elevation gradient.

We performed two independent analyses to reveal how ESR is affected by sampling bias and uneven distribution

of planimetric area along the elevational gradient. First, we calculated ESR from species ranges based on a limited number of observations. We subsampled floristic records used for ESR calculation to mimic a limited sampling effort. We used sequences of sub-samples consisting of 5–95% records sampled randomly without replication from the full dataset. We repeated this procedure 1000 times and calculated the median ESR for each sampling intensity. Second, we calculated species richness in elevational bands using incidence data from point-samples and applied corrections for sampling effort and total land area. This method is less sensitive to elevational richness pattern distortion close to domain boundaries (Grytnes and Vetaas 2002). We calculated uncorrected empirical richness as the number of species present in 35 elevational bands (100 m each). To account for sampling effort, we calculated total species richness using the incidence-based asymptotic richness estimator (aka Chao2, Chao et al. 2014) from the iNEXT R package (Hsieh et al. 2019), based on occurrence data at sampling sites. To account for potentially confounding species–area effects in fixed elevation belts, we divided the elevation gradient into 35 variable elevational bands with equal total unglaciated terrestrial land area in each band. Elevation range in equal-area bands ranged from 45 to 632 m. To compensate both for uneven sampling and for land area in each belt, we calculated Chao2 estimate for incidence data also from these equal-area belts.

To disentangle neutral drivers of ESR from a gradient of environmental favourability, we employed MPA models (Colwell et al. 2016). We compared the performance of MPA models to the ecologically neutral MDE, which simulates random range placement within a domain (Colwell and Lees 2000). Because MPA models were introduced recently and their performance had not been widely tested on independent datasets so far, we decided to explore four alternative settings of MPA in order to find an optimal solution and to describe the consequences of model design on fitted MPA parameters.

To fit the MDE model, we randomly sampled midpoint positions for each species from a uniform probability density distribution function restricted to the interval of values that limits the randomised range placement within the modelling domain: on the unit domain is this interval defined by [half range; 1 – half range] (Colwell and Hurtt 1994). We repeated the sampling 1000 times and recorded the median and the 95% confidence interval (2.5 and 97.5 percentiles) from species richness predicted by MDE models at 100 evenly spaced positions along the elevation gradient.

The MPA models suppose that the species richness gradient is generated by an underlying midpoint density that follows a Gaussian distribution and is limited by geometric constraints. MPA uses Bayesian inference to optimise the Gaussian attractor of midpoint density defined by two parameters: the parameter A, which controls the location of the attractor's peak, and parameter B, which is the standard deviation of the attractor, controlling the strength of the attractor. The attractor distribution is truncated by domain limits. We implemented both variants of MPA as proposed

by Colwell et al. (2016), differing in the way they draw midpoints during Bayesian parametrisation of attractor parameters in order to prevent simulated range from overlap with the domain boundary. Algorithm MPA 1 uses a doubly truncated Gaussian probability density function for midpoints, where truncation is adjusted individually according to the range size of each species, to prevent sampled ranges from extending beyond domain limits. Algorithm MPA 2 uses a Gaussian probability density function for midpoints truncated by domain limits, and only if the sampled midpoint position results in range truncation by domain limits (i.e. the distance of midpoint from the closest domain limit is less than half of the elevational range), it is adjusted to the closest possible position (half range distance from the domain limit) which prevents range overlapping with the domain boundary. The resulting midpoint density distribution function, therefore, corresponds to a censored normal distribution. This setting favours placement of midpoints at positions where range limits exactly reach the domain boundary.

For both MPA 1 and MPA 2 algorithms, we tested two different settings: first, with MPA parameter A values restricted to the unit [0, 1] interval (i.e. constrained to lie within the domain) and parameter B restricted to the unit [0, 1] interval, henceforth referred to as algorithm MPA 1a and MPA 2a, respectively. This first setting for A and B corresponds to the original setting used by Colwell et al. (2016). In the second setting, we allowed MPA parameter A to fall outside the domain limits, within an interval restricted to [−0.5, 1.5], and we allowed the MPA to be weaker by allowing attractor parameter B to be drawn from a broader interval [0, 2] (algorithm MPA 1b and MPA 2b). This second setting therefore allows MPA to be located below/above actual domain limits, which is a possible scenario in our study area, where the lower domain limit is determined by the geographic extent of the study and the centre of diversity may potentially lie below the actual lowest elevation found within the study area. Regardless of the limits for the MPA parameters, the same rules were applied for truncation/censoring of the resulting probability density function by geometric constraints.

We implemented MPA models using Bayesian inference through 'RStan' (Stan Development Team 2018). Flat priors were used to define both parameters. For Bayesian inference of the parameters of the Gaussian attractor, we used a direct likelihood function for midpoint distribution, instead of using a goodness-of-fit measure for empirical species richness as proposed by Colwell et al. (2016). However, predicted species richness (PSR) values were stored for post hoc evaluation of model performance. Our approach gives equal weight to each species, whereas the original approach gives proportionally more weight to wide-ranged species because they contribute more to richness patterns. We used four chains and 1000 iterations for warm-up and 1000 post-warm-up iterations, with a thinning factor of five, resulting in 800 draws used for model inference. We stored the posterior mean and 95% credible interval values of distributions of estimated MPA parameters A and B, and median and 95% credible

intervals for PSR values at 100 evenly spaced positions along the elevation gradient for each model.

For model performance evaluation, we calculated four goodness-of-fit measures based on median PSR and ESR: Pearson correlation (cor), mean absolute error (MAE), root mean squared error (RMSE) and normalised RMSE (RMSE divided by total species richness).

We fitted MDE and MPA models to the full species list and to subsets of species, with species groups selected according to taxonomic classification at family level, biogeographic affinity and life-form (Supporting information). Only groups comprising more than 10 species were used for model fitting. We tested the effects of decomposition of the total diversity into these species groups on MPA model fit. We quantified between-group variability in MPA position as the standard deviation of MPA parameter A and variability in attractor strength as average MPA parameter B, using posterior mean parameter estimates for the selected species groups. We used randomised species classification (randomisation without replication) to provide a null expectation, given the numbers and sizes of the species groups are equal to the actual groups. We expected that, if our grouping criteria were ecologically relevant, the variability in MPA parameter A (attractor position) would be higher and the average MPA parameter B (inverse measure of attractor strength) would be lower than the null expectation. Increased variability in parameter A indicates differentiation of midpoint positions between the groups and a smaller parameter B indicates higher homogeneity of midpoint positions within the groups. We used a one-tailed F-test to test our hypothesis that variability of MPA parameter A will be higher and a one-tailed paired t-test to test the hypothesis that average MPA parameter B will be lower for empirical parameter estimates compared to null expectations for ecologically differentiated species groups.

All statistical analyses were performed in R 3.4.4 (<www.r-project.org>); R code implementing all four variants of MPA models can be found in the electronic Supporting information.

Results

From 1054 species, 177 species (16.8%) had their lower range limit within 100 m of the lower domain boundary, but only seven species (0.7%) had their upper range limit within 100 m of the upper domain boundary (Fig. 2). The empirical species richness curve was unimodal and positively skewed, peaking at 3875 m a.s.l. (0.35 on unit domain) with a maximum richness of 660 species (Fig. 3). Towards higher elevations, species diversity declined and reached zero below the physical limit of available unglaciated land-area at high elevations.

Sampling bias

Random subsampling of the species-occurrence dataset affected the shape of the ESR (Fig. 3). Richness estimates
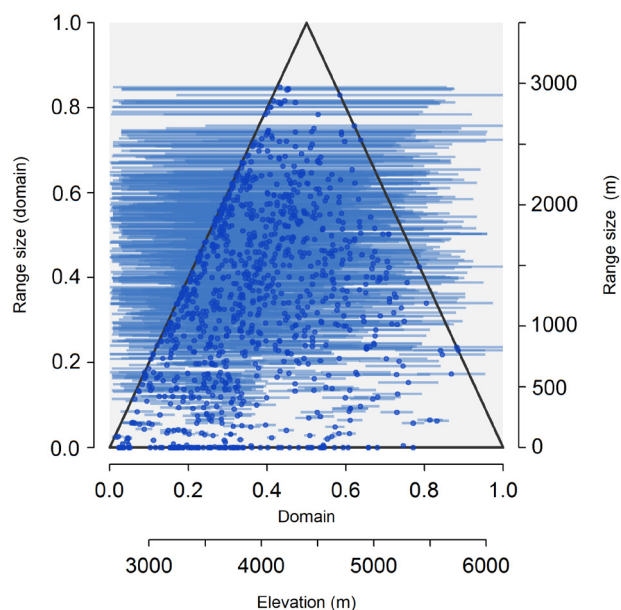

Figure 2. Empirical species ranges of vascular plants growing in Ladakh. The position of the species range midpoint (x-axis) is plotted by points against its range size (y-axis). Horizontal lines display species ranges defined by minimum and maximum elevation of occurrence. The triangle bounds possible locations of midpoints within the domain.

based on the interpolation method at the domain margins proved to be the most sensitive to simulated sampling effort bias. The lower regions of the elevational domain were more sensitive to sampling effort bias than the upper regions: 50% reduction of sampling intensity resulted on average in 27% species richness reduction in the lower elevation belt (below 2970 m a.s.l.), 12.6% reduction in the middle elevation belt (4240–4560 m a.s.l.) and 22.8% reduction in the upper elevation belt (above 5830 m a.s.l.). The shape of the ESR converged as sampling effort increased: reducing sampling effort by 10% resulted in 4.1, 2 and 4.1% species richness reduction for lower, middle and upper elevational belts. With very limited sampling effort (<10% of the original dataset), the ESR became more symmetric, with its peak at 4030 m a.s.l., close to the domain centre at 4400 m a.s.l.

Species richness estimates from point-samples in elevational bands also produced hump-shaped patterns (Fig. 4). Applying an asymptotic estimate (Chao2) for total species richness in elevational bands conserved a hump-shaped pattern, with a maximum of 711 species (SE = 34) estimated for the elevational band 3550–3650 m a.s.l. (Fig. 4b). When band planimetric area was equalised, the hump was less pronounced, reaching maximum values in the 3280–3500 m a.s.l. band, both for observed (615 species) and sampling-intensity corrected (764 species, SE = 32) species richness (Fig. 4c–d).

Model performance

Full dataset
MDE prediction produced a symmetrical, parabolic curve, which reproduced the empirical species richness pattern
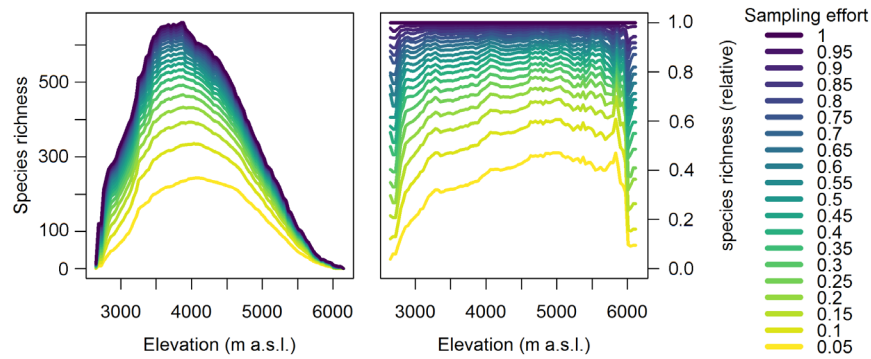
Figure 3. Species richness of vascular plants along an elevational gradient in Ladakh. Species richness was estimated with different levels of sampling effort using the range interpolation method. Sampling bias is most pronounced at domain margins and in the lower part of the gradient. Absolute (left) and relative to the full dataset (right), species richness was estimated using randomly selected fractions (0.05–1.0) of all species occurrence records.

poorly, underestimating diversity at lower elevations and overestimating diversity at upper elevations (Fig. 5a, f). All MPA models fitted the empirical species richness well, with algorithm MPA 1b providing best results (Fig. 5). Algorithms MPA 1 and 2 differed only slightly in the goodness-of-fit metrics, but they provided significantly different estimates of MPA parameters (Table 1). MPA position estimated by MPA 1b was situated below the lower domain limit. Algorithm MPA 2b produced MPA position estimates similar to those produced by algorithm MPA 2a, with the attractor centred approximately at the observed peak of diversity.
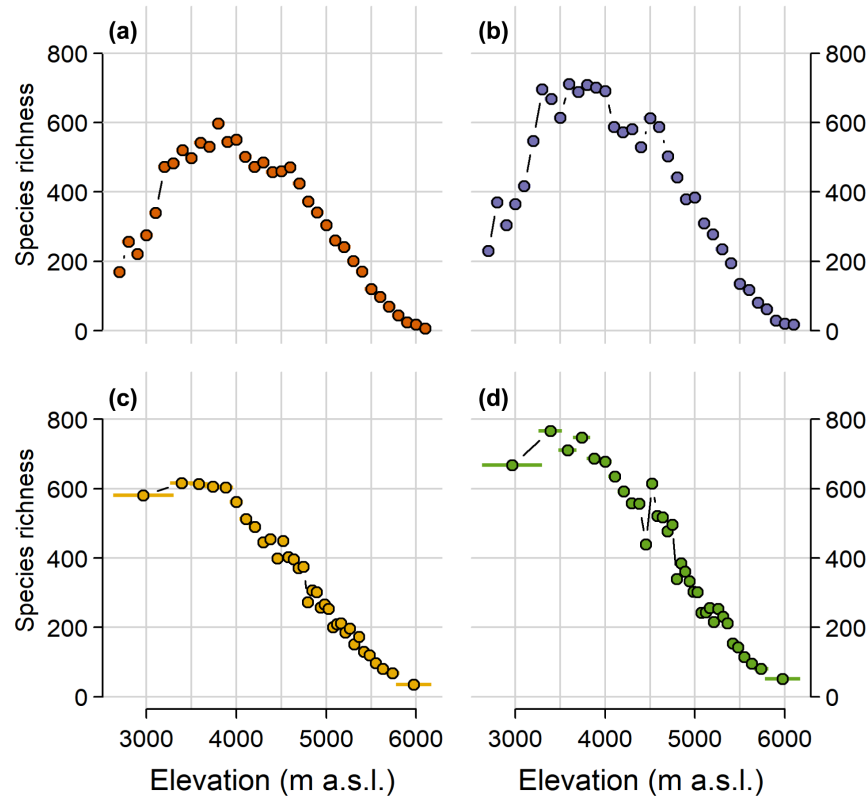

Figure 4. Estimated species richness using point-samples in 35 elevational bands, (a) using equally spaced 100 m elevational bands, (b) using equally spaced 100 m elevational bands corrected for sampling intensity using the asymptotic richness estimator Chao2, (c) using variable bandwidth with equal planimetric land area, (d) using variable bandwidth with equal planimetric land area corrected for sampling intensity using the asymptotic richness estimator Chao2. Horizontal whiskers indicate the width of the elevational bands used.
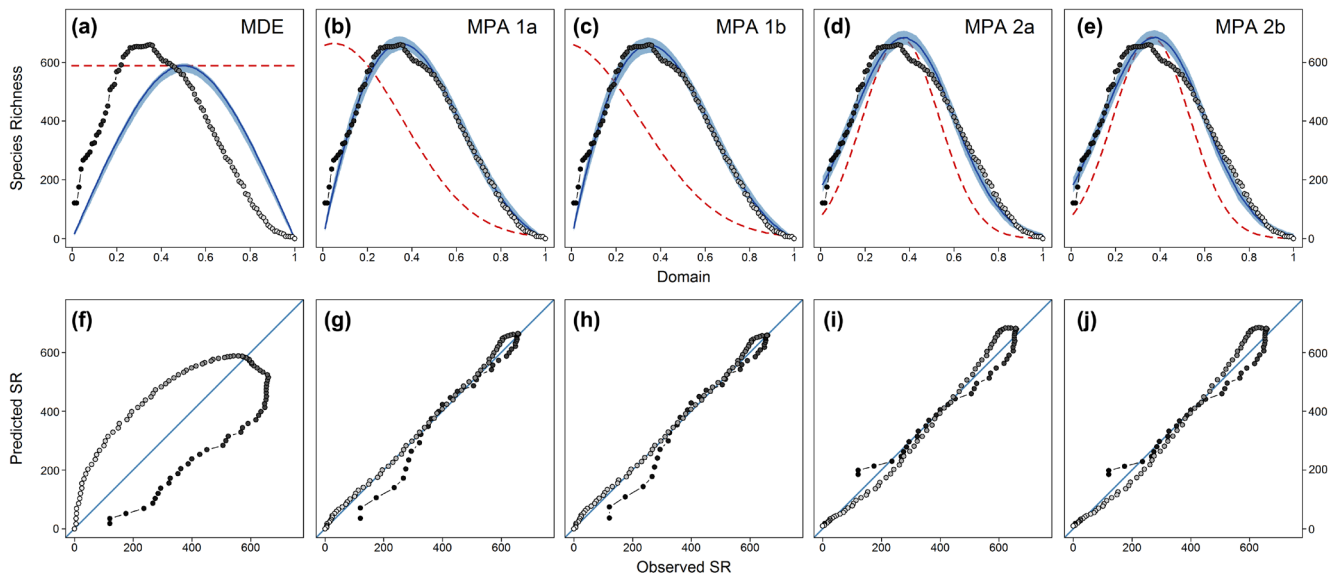
Figure 5. Observed elevational species richness and null model predictions for MDE model (a, f), MPA 1a (b, g), MPA 1b (c, h), MPA 2a (d, i) and MPA 2b (e, j). Upper panels (a–e) show empirical richness (dots), predicted species richness by null models (blue line and light blue area for median and 95% confidence/credible interval), and the probability function of the midpoint attractor (dashed red line). Lower panels (f–j) display observed versus predicted species richness and the 1:1 line. While the MDE model provided a poor fit to the empirical richness, all variants of the MPA models provided an excellent fit.

Species grouping

Splitting the dataset into species groups significantly affected MPA shape parameters (Fig. 6), but goodness-of-fit measures were on average worse than for whole vascular plant richness (Supporting information).

Grouping based on life-form resulted in a marginally significant effect on the variance of attractor positions (parameter A) only for model MPA 2b (p = 0.066), but marginally significant effects on attractor strength (parameter B) were found for all four MPA models (Table 2). The difference from random expectation in absolute numbers was, however, the largest among the tested grouping criteria, but the low number of life-form groups (n = 5) resulted in low test power.

Grouping based on biogeographical affinity significantly affected both attractor position and strength in all MPA models. Attractor location for Eurasian, Mediterranean, Eurasian and Cosmopolitan biogeographic elements was estimated below the lower domain limit by the model MPA 1b. In contrast, the MPA for Tibetan elements was located at 5290 m a.s.l., far above MPA of other biogeographic groups (Fig. 6).

Taxonomic grouping by families marginally affected the variance of attractor position (parameter A) only in the MPA 1a model and affected attractor strength (parameter B) in models MPA 2a and MPA 2b (Table 2). Attractor position estimated by MPA 1b for 13 out of 23 families was below the domain limit. The highest attractor position was reported consistently by all MPA models for Saxifragaceae. A very weak attractor (MPA 1b parameter B > 3000 m) was reported for four families (Brassicaceae, Crassulaceae, Papaveraceae and Saxifragaceae).

Discussion

Empirical observations and sampling bias

Underestimation of species ranges leads to underestimated diversity, especially close to domain boundaries, when the interpolation method for richness estimation is used (Grytnes and Vetaas 2002). Although sampling effort was very intensive in this study, empirical species ranges may still be slightly

Table 1. Estimated parameters and model performance for evaluated richness models using the full set of species. Parameter A controls the Gaussian MPA location (in m a.s.l.); parameter B controls strength (standard deviation, in m) of the Gaussian MPA. Fit between observed and predicted elevational richness is presented by goodness-of-fit measures: Pearson correlation (corr); mean absolute error (MAE); root mean squared error (RMSE) and normalised root mean squared error (nRMSE).

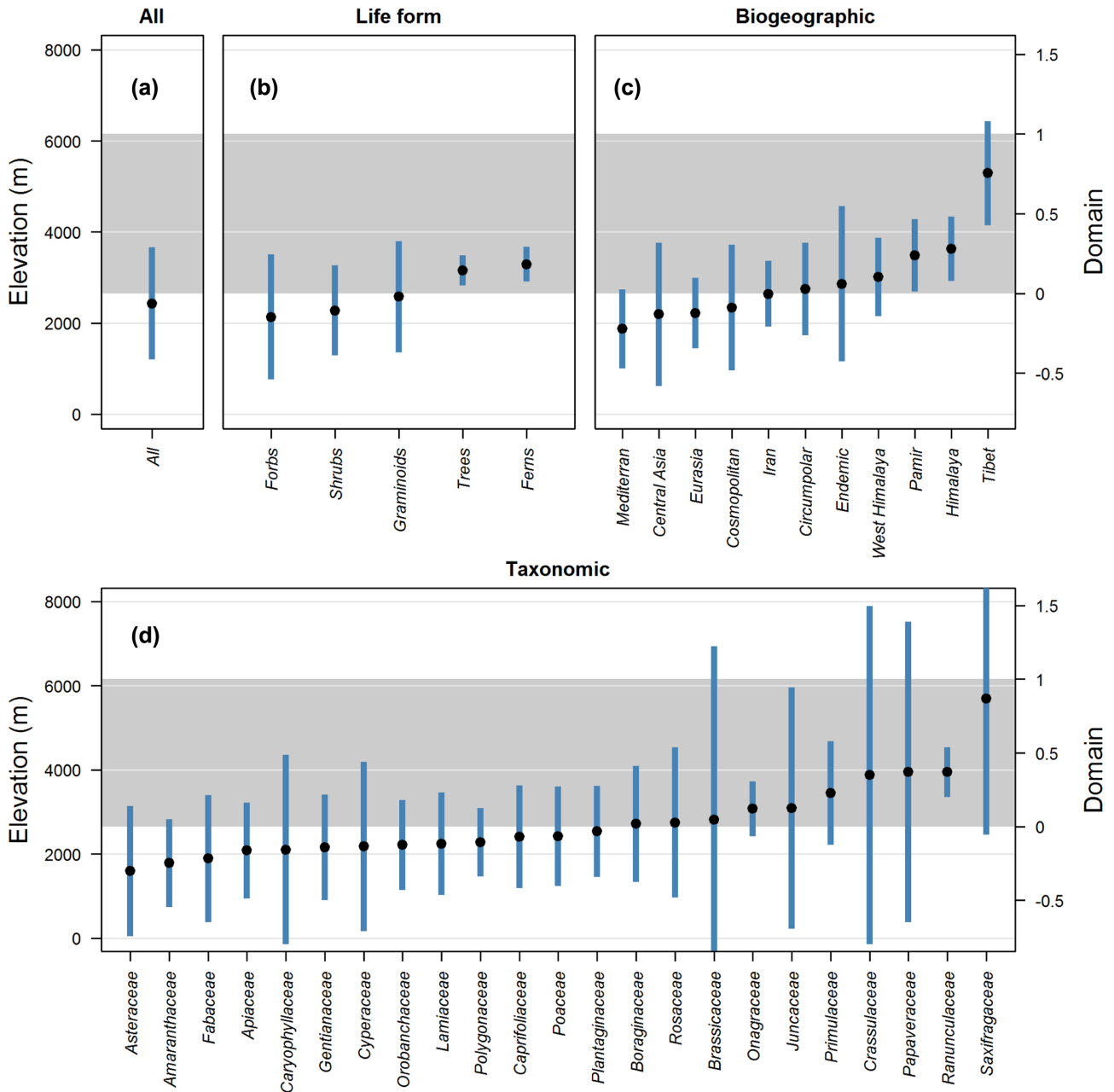| Richness model	Param. A mean (95% CI)	Param. B mean (95% CI)	corr	MAE	RMSE	nRMSE
MDE	–	–	0.718	140.88	155.74	0.148
MPA1a	2848 (2659; 3114)	1078 (946; 1185)	0.993	17.66	25.86	0.025
MPA1b	2431 (1324; 3044)	1229 (989; 1595)	0.994	16.67	24.49	0.023
MPA2a	3913 (3873; 3949)	600 (570; 630)	0.990	26.03	32.90	0.031
MPA2b	3913 (3876; 3948)	600 (570; 632)	0.990	26.02	32.94	0.031

Figure 6. Estimated midpoint attractor position (points) and strength (bars) using the MPA 1b model for (a) the full dataset and species grouped according to (b) the life-form, (c) biogeographic elements and (d) taxonomic groups (families). Gaussian midpoint attractor position (parameter A) is plotted by dots and its strength (standard deviation of Gaussian attractor) (parameter B) as a vertical blue bar. The shaded area depicts domain limits. Note that if a midpoint attractor is located below the lower domain limit, only a monotonically decreasing portion of the Gaussian curve was used for midpoint sampling.

underestimated. Simulation of less intensive sampling effort in this study showed that empirical species richness in the lower part of the elevational gradient is more sensitive to range underestimation with limited sampling, while in the upper part of the elevational gradient, estimated diversity was less affected (Fig. 3). Nevertheless, a hump-shaped richness pattern remained apparent for alternative point-sample-based richness estimation, even when adjusted for sampling effort (Fig. 4). When we corrected for land area using equal-area bands, the

hump was less pronounced but still apparent, peaking at 3280–3500 m. Therefore, we conclude that the unimodal elevational richness pattern has a real basis, controlled either by neutral processes or by underlying climate gradients, or both.

MDE and MPA models

The MDE model, which can be considered as an ecologically neutral null model of the species richness gradient on

Table 2. Variability in parameter estimates among different species groups classified according to the life-form, biogeographic element and taxonomic families. The effects of grouping on the variance of attractor location (parameter A) were tested with an F-test and a t-test was used to test the effects on attractor strength (parameter B).

Groups	Model	Parameter A					Parameter B				
		SD (obs)	SD (rnd)	F-value	p-value	Signif.	Avg. (obs)	Avg (rnd)	t-value	p-value	Signif.
Life-form (n = 5)	MPA1a	208.5	19.4	0.81	0.579		714.8	1160.4	−1.97	0.060	(.)
	MPA1b	518.0	40.0	1.46	0.362		857.4	1688.4	−1.71	0.082	(.)
	MPA2a	217.4	62.5	5.38	0.066	(.)	480.6	703.6	−2.05	0.055	(.)
	MPA2b	230.9	109.1	1.82	0.287		498.4	926.4	−1.70	0.082	(.)
Biogeographic (n = 11)	MPA1a	621.9	146.7	17.97	< 0.001	***	826.8	1025.3	−2.97	0.007	**
	MPA1b	950.9	344.7	7.61	0.002	***	1048.8	1355.9	−2.95	0.007	**
	MPA2a	342.1	86.5	15.63	< 0.001	***	541.5	643.1	−3.26	0.004	**
	MPA2b	380.0	134.5	7.98	0.001	**	572.3	672.3	−2.72	0.011	*
Taxonomic (n = 23)	MPA1a	536.5	382.1	1.97	0.060	(.)	1115.2	1212.6	−0.69	0.249	
	MPA1b	931.8	714.2	1.70	0.110		1773.2	1846.5	−0.26	0.400	
	MPA2a	250.1	200.3	1.56	0.153		594.0	794.5	−2.84	0.005	**
	MPA2b	267.2	313.9	0.72	0.772		637.2	1111.3	−2.91	0.004	**

Statistical significance: 0 *** < 0.001 ** < 0.05 (.) < 0.1.

a geometrically constrained domain, failed to accurately reproduce the observed, positively skewed diversity pattern. Despite the positive correlation between MDE prediction and empirical richness (r = 0.72), all MPA models performed substantially better than the MDE model. The MPA models almost perfectly fitted the empirical species richness curves, regardless of the MPA algorithm used. The full set of regional vascular plant species richness was matched with a correlation coefficient r > 0.99, reached by all four alternative MPA models. However, the model MPA1b achieved the best fit regarding all goodness-of-fit measures applied. The advantage of MPA models lies in the inclusion of both ecologically neutral effects represented by geometric constraints and an ecologically informative MPA with two parameters, which effectively regulates the shape and location of the predicted richness pattern and represents environmental favourability for the studied species group.

Notably, the fitted shape parameters of MPAs were sensitive to the model algorithm used. The MPA model parameters A and B were restricted to a unit range in the original work of Colwell et al. (2016), but we see no strict reason for this limitation, because the centre of diversity may lie in specific cases outside the domain, especially when the studied region covers only a part of the elevational gradient. When we allowed the MPA to be located outside the domain (model MPA 1b), the model fit to the data slightly increased and the estimated attractor position (parameter A) for all species was situated at 2430 m a.s.l., about 220 m below the domain limit. When the MPA peak is situated below the domain limit, the resulting probability density function truncated by the domain limits is the monotonically decreasing part of the Gaussian curve. When this is true, then the existence of a peak of empirical species richness within the domain must be caused by neutral processes linked to geometric constraints, in conjunction with an approximately Gaussian distribution of environmental favorability for the group in question.

The MPA probability function of the MPA 2 algorithm places species ranges directly at domain boundaries with substantially higher probability than the MPA 1 algorithm because it uses a censored rather than a truncated probability density function. In contrast, the MPA 1 algorithm compensates for the truncation of the MPA distribution by shifting the MPA to lower elevations; in the case of MPA 1b (attractor position is not restricted by domain limits), the estimated MPA was actually situated below the lower domain limit for most analysed datasets: the whole flora, for 13 families, for four biogeographic groups and for three life-forms (Supporting information). The maximum difference in estimated MPA position between the MPA 1b and MPA 2b models for the same species group was as much as 2250 m. The discrepancy between models was accentuated when we fitted species groups with a centre of diversity in lower elevations, probably as a consequence of a high proportion of truncated ranges. The sensitivity of MPA parameters to model assumptions indicates that the midpoint position must be interpreted with caution, particularly if a substantial portion of evaluated species ranges reaches domain limits. Although many species in our dataset have a lower range boundary at or close to the lower domain limit, the algorithm MPA 1 performed slightly better than MPA 2. This is in contrast to Colwell et al. (2016), who favoured the second algorithm, but the datasets used in their study contained usually only a few sampling sites along the elevation gradient (5–70 sites), and therefore, it was more likely that the observed species ranges would be alligned exactly with the lower domain limit. Because the interpretation of the underlying MPA probability function is also more straightforward for algorithm MPA 1, we recommend this algorithm for further use.

We also question the restriction of parameter B to unit definition range as proposed by Colwell et al. (2016). There is no strict mathematical reason for such restriction; this limitation in Colwell et al. (2016) was empirically chosen because higher values did not yield better fits. Theoretically, if parameter B was set to infinity, then the MPA 1 would be equal to MDE. In several instances, we found that the estimated value for parameter B exceeded the unit interval in the MPA 1b

models for certain species groups, when the a priori range for parameter B was set to the [0, 2] interval. This result indicates low climatic control on midpoint placement for these groups, or, in other words, high ecological plasticity of these groups. However, a priori restriction of the model parameters may be useful when the Bayesian model fails to converge.

Ecological interpretations

The absolute decline of species richness towards high elevations is presumably determined by low temperature, as has been experimentally confirmed from our study region (Klimeš and Doležal 2010, Dvorský et al. 2016). Conditions above the elevation of the highest vascular plant occurrence at 6150 m a.s.l. are clearly inhospitable: annual mean temperature falls below −10°C, and freezing temperatures occur every single day of the year (Klimeš and Doležal 2010, Dvorský et al. 2015). The upper limits of plant species in this area belong to the highest records on Earth (Dvorský et al. 2015), and we repeatedly searched for plants growing above the highest known plant occurrence, but thus far with negative results. We are therefore confident that the upper range limits used in this study are not truncated because of the geographic extent of our study area, but represent a hard boundary set by species' physiological tolerance.

In contrast, species richness at the lowest elevations may be depressed by increasing aridity, but not so strictly as by the low temperatures at upper domain limits (Dvorský et al. 2017). Climate in the lower parts of Ladakh is arid, but even moisture-demanding species can find suitable habitats along streams and on occasional spring fens. Therefore, we assume that drought limitation may rather affect relative species abundances than their absolute range limits. However, the decline in species richness towards the lower domain limit has several potential non-biological explanations: elevations below 3000 m a.s.l. in the study region are geographically restricted to valleys of the Indus, Dras and Shyok rivers in the northwest part of the region (Fig. 1). It is thus possible that species growing in comparable elevations in adjacent regions are truly missing from the same elevations in Ladakh, simply because of dispersal limitations and/or stochastic extinctions of small local population, following the principles responsible for species–area relationship. This idea is also supported by the less pronounced richness peak calculated by the bin method with equal-area bins than by the method with fixed elevational bins.

To assess how common range truncation by geographic constraints may be, we conducted a literature survey on species range limits in adjacent regions. We identified 615 species (60% of the total plant diversity in Ladakh) that were reported from lower elevations in other regions than their actual lowest elevation of occurrence in Ladakh in our dataset. This finding provides additional support to our conclusion that environmental favourability is monotonically decreasing with elevation within our study domain as was predicted by the MPA model, and the observed decrease in species richness towards low elevations has other reasoning

than climate. This inference is not in conflict with an estimated hump-shaped pattern of diversity by asymptotic point-sample estimates for elevational bands (Fig. 4), because this approach adjusted only for sampling bias and species–area relationships but not for the neutral effects of geometric constraints. Likewise, Grytnes and Vetaas (2002), in a study from Nepal, concluded that the observed hump-shaped diversity pattern is a product of a linearly decreasing underlying trend and domain boundaries.

Species groups

The fit of MPA models to the full set of species was almost perfect; therefore, dataset separation into distinct species groups by their taxonomy, biogeographic affinity or life form could not have improved the overall model fit. On the contrary, we observed a slightly worse fit for separately fitted groups than for the whole plant diversity of the area. Nevertheless, the evaluation of models for species subsets revealed considerable variation in attractor shape parameters among the groups (Fig. 6). We interpret the perfect fit to the full species set, despite the presence of ecologically distinct species groups, as an analogy to the central limit theorem, which predicts that regardless of the distribution of separate samples, the summation converges towards normal distribution (Šizling et al. 2009). This is likely why the Gaussian attractor is so successful in MPA models. The only model parameter that suggests that ecological divergence among species groups contributes to the overall richness pattern is the inflated (for all species, compared to within groups) attractor parameter B, regulating the strength of the attractor. When we separated species to groups using various grouping criteria, the strength of the MPA generally increased (parameter B decreased).

Species groupings based on their biogeographical affinity had the greatest divergence among them, for attractor positions and strength. This is not surprising because climatic niche mirrors both elevational and latitudinal range. Similarly, Rana et al. (2019) concluded that trees with different biogeographic affinity in east Himalaya greatly differed in their elevational predominance, but the mixing of groups in middle elevations could not explain the formation of the richness peak.

Surprisingly, phylogenetic signal in attractor parameters was relatively weak. With the exception of the Saxifragaceae, the positions of the MPA overlapped and the strength of MPAs was relatively weak. Variability in thermal tolerances within taxonomic groups at the rank of family is obviously still high, probably because of rapid evolution of adaptations to low-temperature stress (Araújo et al. 2013, Liu et al. 2020). Notably, the 12 species found at elevations above 6000 m a.s.l. belonged to six different families. This evolutionary convergence illustrates well the limited niche conservatism with respect to thermal tolerances at the level of family (cf. Prinzing et al. 2001).

Classification based on life-form provided seemingly surprising results: the MPA in the MPA 1b model for trees was

located higher than for forbs, graminoids or shrubs (Fig. 6b). This result may seem contradictory, but only at first glance: MPA strength was much higher for trees, which means that their midpoints are restricted to elevations around 3000–3500 m a.s.l., while the midpoints of the latter life-forms are distributed more evenly along the elevational gradient. Drought limitation and human pressure may be responsible for a steeper decline of tree species richness at low elevations as compared to other groups, while physiological constraints control the upper tree-line (Dolezal et al. 2019).

Here we compared fit to separate models for each group, but integration of species grouping into one model is potentially feasible. The question is, what then should be the optimisation criterion, when the fit to the empirical richness of our less complex model treating all species together is equal or even better than the fit to sets of coherent species groups? Resolving this issue is critical for understanding the ecology of species, otherwise hidden within the universal richness gradient.

Conclusions

MPA, but not MDE, models proved to be useful for fitting and interpreting empirical richness data. However, MPA models must be interpreted with caution because model parameters are sensitive to the setting of a model algorithm and the two parameters of the MPA interact in their effects on the resulting shape of predicted richness curves.

Using the best performing MPA model, we found that the empirical unimodal skewed species richness pattern of vascular plants in the Himalaya is jointly driven by a decreasing climatic suitability gradient and by neutral domain boundary effects. Sampling bias is a potential source of richness underestimation, especially at the geographically truncated domain boundaries, but with our extensive dataset, it played a minor role. The inclusion of ecologically distinct groups did not decrease goodness-of-fit measures, but it weakened the strength of the MPA. According to differences in MPA parameters among species groups, the main distinction criterion was biogeographic affinity, rather than taxonomic rank or life-form.

Author contributions

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