Scale-dependent niche segregation along dimensions of rocks, vegetation and elevation in sympatric pikas of Ladakh

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Abstract

Microhabitat selection in patchy environments supports the co-existence of closely related species competing for resources. We examined niche partitioning in three sympatric species of pikas, *Ochotona macrotis, Ochotona nubrica,* and *Ochotona ladacensis* from Ladakh, India, that display contrasting lifestyles, social behavior and co-occur at small spatial scales. We used a classical paired quadrat approach to document biologically relevant vegetation and landscape features (niches) likely to support the presence of different species. We used a Bayesian framework to describe niche spaces , estimate niche widths and overlaps between species pairs. In addition, we used a GLM framework to identify factors that promote the presence of different species in the landscape. The rock-dwelling *Ochotona macrotis* was a specialist, exclusively associated with microhabitats offering a good cover of large-sized rocks and no shrubs. The social, *Ochotona nubrica*, was a specialist found across elevations but associated exclusively with mature stands of scrub vegetation (*Caragana sp* in the South-East and *Hippophae sp* in the North-West) occupying a unique niche. The social *Ochotona ladacensis,* although an elevational specialist, was likely to be found in microhabitats of other species characterised by moderate rock cover and low-lying Caragana scrublands, in addition to being found in alpine grasslands and meadows.

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Introduction

The conceptualization of the fundamental and the realized niche (Grinnell 1917, Hutchinson 1957) of species has been particularly valuable to the growth of community ecology (Roughgarden 2009), evolutionary biology (Sexton et al. 2017), and in understanding distribution patterns across space to inform conservation planning (Pulliam 2000, Ahmad et al. 2021, Dvořák et al. 2022). The niche mathematically represents an n-dimensional hypervolume that describes the range of biotic and abiotic factors in which the animal can survive and reproduce (Grinnell 1917, Hutchinson 1957). The width of the niche and the degree to which it can be found in niches of other animals can be used to assess species on the generalist-specialist continuum (Fridley et al. 2007).

Species attributes that promote stable co-existence of ecologically similar species in communities have intrigued researchers for a long time, starting with competitive exclusion experiments in the 1930s (Gause 1936, MacArthur 1958, Hardin 1960, Hutchinson 1961, Slatkin 1974, Hanski and Ranta 1983, Nardone and Gherardi 1997, Sommer 1999). Community assemblages or niches are known to be shaped by abiotic and biotic filtering where physiological limits and biological interactions such as competition for resources and predation limit species occurrence and co-existence (Schoener 1974, Martin 1988, Dunson and Travis 1991, Weiher and Keddy 1995, Weiher et al. 1998, MacRae and Jackson 2001, Stoks and McPeek 2003, Cavender-Bares et al. 2004, Dayan and Simberloff 2005, Bøhn et al. 2008, Pfennig and Pfennig 2009, Colman et al.

2014). In this manuscript we describe the niche space, overlaps and partitioning between three sympatric species of pikas (*Ochotonidae*) from the high elevation trans-Himalayas (3000m-6000m) of Ladakh, India.

Interspecific competition is known to alter the niche width of species and affect community structuring through population sizes of different species (MacArthur 1958, Connell 1961, Mac Nally and Timewell 2005, Luiselli 2006, Bolnick et al. 2010, Stellati et al. 2021). Spatially heterogeneous/patchy environments allow for the co-existence of ecologically/closely related species by alleviating competition through ecological specialization (Hanski 1983, Hanski and Ranta 1983, Holt 1987, Chesson 2000, Amarasekare 2003). This is facilitated by differential habitat/microhabitat selection or use at spatial (Chipps et al. 1994, Satoh and Hori 2005, Malavasi et al. 2007, Tamme et al. 2010, Sillero et al. 2020, Gurvich et al. 2022) and temporal scales (Townsend and Hildrew 1979, Faria and Almada 2001, Castro-Arellano and Lacher 2009, Lea et al. 2020). Although microhabitat selection between closely related species can reduce competition (Majumder et al. in press, Goulart et al. 2009, Lea et al. 2020), it is often hard to establish that competition has driven this selection over and above other biotic and abiotic filtering mechanisms (Shanker 2001, Zhang et al. 2006, Afonso and Eterovick 2007, Crow et al. 2010).

The trans-Himalayas of Ladakh, India, are home to asocial rock-dwelling (*Ochotona macrotis: OM*) and social burrowing species (*Ochotona ladacensis: OL, Ochotona nubrica: ON*). While *OM* is found in rocky talus and scree slopes in alpine deserts (2300m-6000m), *ON* is a burrowing species that uses thorny vegetation, rocks when availbale (2800m-5300m) and with (Pfister 2004, Wilson and Mittermeier 2016, Smith et al. 2018). *OL,* on the other hand, is associated with barren xeric alpine valleys at high elevations characterised by cushion plants and sedges (Pfister 2004, Wilson and Mittermeier 2016, Smith et al. 2018) (4200m-5400m). A photographic representation of these microhabitats reveals differences and similarities of niches of different species (Figure 1). While *OM* and *OL* (clade *Conothoa)* have diverged ~5mya, these species have diverged from *ON* (clade *Ochotona*) 13mya (Wang et al. 2020, Lissovsky et al. 2022). Assuming that closely related species share similar physiological requirements, we would expect that *OM* and *OL* use similar microhabitats when compared to *ON* (Dahal et al. 2020).

In this study, we describe the ecological niche space of different species of sympatric pikas in Ladakh and address if they use different microhabitats. In addition, we examine how various ecological factors drive pika presence at high elevations in Ladakh, India, by documenting microhabitat level features (variables related to rocks and vegetation) and topographic features (elevation, slope, aspect) at different spatial scales. Studies on Neotropical snakes (Corrêa Nogueira et al. 2019) and Austalian songbirds (Harmáčková et al. 2019) found evidence for scale-dependent phenomena of niche spaces and overlaps between species but such studies of niches at different spatial scales are generally rare. A well-defined study at varying spatial scales would not only provide a framework to describe niches of species, address evolutionary drivers of such choice, but also allow for exploration of proximate factors that drive presence and directly feed back into conservation planning (Lian and Jianping 2005, Edgel et al. 2014). Pikas are high-elevation specialists under threat of extirpation due to climate change, and describing their niches will provide baseline data for effective policy-making in the trans-Himalayas (Beever et al. 2010, 2011, Dahal et al. 2020).

Methods

2.1 Determining pika occurrence - Appropriate microhabitats were visually inspected for signs of pika activity (fecal pellets, haypiles, and burrows). A 10m*10m quadrat was laid centered around each identified site. In each quadrat, variables about rocks, vegetation, and topographic features were documented (Table S1). In addition to each occurrence plot, a random paired plot was laid 50m away (compass direction determined by a uniformly generated random number bound between 1 and 360). For social pikas, colony boundaries were identified using outermost burrows, and paired plots were laid outside the colony.

2.2 Extraction of high-resolution topographic information from remotely sensed data - For mapping altitude, a Digital Elevation Model (30m) for the tiles of our interest was downloaded from the Bhuvan, Indian Geo Platform of ISRO (https://bhuvan.nrsc.gov.in/home/index.php). The raster was further processed in ArcMap 10.5 (ESRI 2022) to give slope and aspect, which represent relevant ecological attributes of a landscape that animals are known to use to select sites for residence. NDVI values (30m) for each plot location were obtained for the months of July-August (Summer) and November-December (Winter) dating back nine years (2013 to 2021), from Landsat 8 imagery (USGS) with the least cloud cover, using Google Earth Engine (Gorelick et al. 2017). These were further processed to provide additional variables concerning NDVI (Table S1).

2.3 Sampling sites - Based on logistics and pilot surveys, sampling locations were chosen across elevational distribution ranges of the three pika species (Figure 2, Figure 3). Since we aimed to understand ecological factors that shape pika presence at a broad scale, plots were laid in different locations for each species (Figure 2) (South-East Ladakh - 88 plots; North-West Ladakh - 66). Sampling was done in zones of sympatry and supplemented with sampling in zones of allopatry to capture the niche breadth of all species. The regions sampled included South-East Ladakh (part of the Qinghai-Tibetan plateau; 4000kmsq) and North-West Ladakh (Ladakh and Zanskar ranges; 8000kmsq).

2.4 Generalised Linear Models (GLMs) - To identify ecological factors that support the presence of different species of pikas at a broader scale, quadrats sampled across species and sites (n=148) were pooled and scored for a binary presence/absence variable for each species (for instance presence and absence plots of *ON* and *OL* were treated as absence points for *OM*). Such an approach is helpful as it is informative regarding where a species is likely or unlikely to be present. We modeled the presence of pikas at sites using logistic regressions with plot variables (Table S1) as predictors using the 'glm' function in the R package 'arm' (R core team 2021, Gelman and Su 2021).

Landscape features and vegetation structure were noticeably different across sites (Figure 9), with huge-sized boulder rocks at low elevations in North-West Ladakh (Thanh et al. 2010), including sea buckthorn along rivers and in South-East Ladakh, the extensive cover of *Caragana* , cushion plants, and small-sized scree rocks at high elevations. We, therefore, modeled the presence of these species at three different spatial extents: a) South-East and North-West Ladakh (controlling for differences in landscape and vegetation), b) Ladakh (across the entire landscape). Since only OM and ON are found in North-West Ladakh, only the presence of these species was modeled at this spatial scale. At the South-East Ladakh scale, the occurrence of all three species was modeled as they co-occur in this landscape.

Due to problems associated with sample size, all variables additively could not be subject to a stepwise/backward selection algorithm. To resolve this problem, we use a modified version of the purposeful selection framework (Bursac et al. 2008, Zhang 2016). The workflow used is depicted below:

1. Predictor variables that affected presence were identified using univariate logistic regressions and plots (one predictor and one binary response variable). All variables that explained the occurrence of a species in these models ($p<0.05$) were additively used to model occurrence (Model 1: Statistical model). In addition, all variables with a p-value cut-off of 0.25 and other variables that were biologically relevant (based on field observations) were additively used to model the occurrence (Model 2: Purposeful model) following Zhang (2016). Finally, a third model was constructed with predictors (p-value < 0.25 in univariate regressions) binned into different ecological classes (Table S2) to depict the different landscape-level features (Model 3: sub-model) that could influence pika presence.
2. A stepwise regression (StepAIC) was run on all three models to pick models that best explain the occurrence (based on the three species of interest). When AIC values varied marginally across sub-models in ecological classes, all predictors across models were considered for further analysis.
3. For the sub-model alone, variables from all the best sub-models across different ecological classes were additively used to model presence using a stepwise regression for the second time. While doing so, care was taken to add/replace biologically relevant variables (based on field experience and literature) even if they were dropped during the sub-modeling process.
4. Best models across modeling approaches were compared and analyzed. Finally, biologically relevant interactions (based on field observations) were evaluated based on AIC scores. Goodness of fit tests (Hosmer and Lemeshow 1989) were performed to assess model fits.

2.5 Comparison of niche overlaps and niche width between species at broad and regional scales - A dataset was constructed by filtering out all absence points and including only variables that were both biologically (based on natural history observations) and statistically important (based on univariate regressions for each species) for the presence of each species (OM - variables related to rocks and geography; ON - variables related to vegetation and shrubs in particular; OL - variables related to vegetation, elevation) (variables highlighted in blue on Table S2). This dataset was subjected to a PCA analysis to reduce dimensionality and to visualize the variation along eigenvectors. The PCA revealed the separation of broad niches along different axes of rocks, vegetation, elevation, and NDVI. Variables related to vegetation (perc_vegetation, height_tallgrass_reeds, height_shrub, average NDVI in summer) and rocks (perc_rocks) loaded onto PC1, while PC2 and PC3 were driven byloaded on by only one variable, elevation and variance in winter NDVI respectively (cos2 >0.5).

Since three PC axes explained 55% of the total variance in the dataset, only three dimensions of the PC transformed points were considered for further analysis of niche overlaps and niche width. We used the NicheRover package on R using a bayesian based probabilistic estimation of niche space, overlaps, and width (Swanson et al. 2015). Directional overlaps were computed by a specified number of Monte Carlo draws from the parameter list ($\alpha = 0.95$) that indicated the probability of finding 'species A' in the niche space of 'species B .'The niche width was obtainedcalculated by calculating the posterior distribution of niche size by species (niche size for every posterior sample drawn) (Swanson et al. 2015). Niche estimation following the methods described was performed at two scales (Broad scale: All of Ladakh, three species representing three niches) and (Regional scales: North-West Ladakh and South-East Ladakh representing five niches).

Results

Comparison of niche overlaps and niche width between species at broad and regional scales

Broad scale: At the larger spatial scale of Ladakh, the elliptical projections of niche space indicated that the three species separated best along the first two dimensions, albeit with significant overlaps (Figure 4). The niche overlap analysis suggested that OL was very likely to be found in the microhabitats that are inhabited by*ON* (mean = 40 %) and *OM* (mean= 50%) (Figure 5).Both OM and ON were less likely to be found in microhabitats inhabited by other species (mean < 15%) (Figure 5). The n-dimensional niche width constructed was different across species (Pr(>F) = <2e-16 ***, F value = 6541, df = 2), with OL having the smallest niche, OM having an intermediate-sized niche, and ON having the largest niche as evidenced by Turkey HSD tests (Figure 6).

Regional scales: When the species were subdivided based on location (OL South-East Ladakh, ON North-West Ladakh, ON South-East Ladakh, OM North-West Ladakh, OM South-East Ladakh), elliptical projection of niche spaces indicated significant overlaps between niches of ON and OL in the South-East, the niche of OM in the South-East and the North-West, and ON in North-West Ladakh being distinct with no significant overlaps with any other niche (Figure 7). The niche overlap analysis suggested that all species across geographic areas had unique niches and were unlikely to be found in microhabitats of other species (Figure 8). The niche width of species across geographic areas was different at the regional scale (Pr(>F) = <2e-16 ***, F value = 9570, df = 4) and revealed contrasting patterns to those recovered at the broad scale. Tukey HSD tests suggested that the niche width of OM in the North-West was the largest, followed by ON and OL in the South-East, having the second and third largest niches, respectively (Figure 9). The niche width of ON and OM in the South-East did not differ (diff = 2.68, p adj = 0.089) and were among the smallest niches in comparison (Figure 8).

Ochotona macrotis

Univariate models **-** Comparison of univariate models at different scales prior to model building revealed that the variables low percentage cover of vegetation, greater percentage of rocks, greater percentage of large sized rocks, and more number of large-sized rocks were important for predicting the presence of OM across all scales (Table C1). It also indicated unique variables that were important at each spatial scale (Table C1):

- At the Ladakh scale, presence was associated with a greater slope.
- At the South-East Ladakh scale, presence was associated with more extensive coverage of class 2 rocks (+).
- At the North-West Ladakh scale, presence was associated with consistently lower NDVI.

All the univariate models run are presented here (Table S3, Table S4, Table S5).

Multivariate models - At each spatial scale, models constructed were subjected to a stepwise regression analysis to pick the best additive models using different methods. The purposeful modeling approach (Model 2) consistently produced the best models across spatial scales. It included variables significantly associated with presence in univariate regressions at regional scales, such as the percentage cover of large-sized rocks and the number of large-sized rocks (Table 1). At the Ladakh spatial scale, the presence of OM was driven by a higher cover of large rocks, a greater number of large-sized rocks, and lower NDVI in summer (Table 1). At the South-East Ladakh spatial scale, the occurrence was primarily driven by a higher cover of large rocks, a greater number of large-sized rocks, higher elevation, lower cover of shrubs, and consistently low NDVI in winter (Table 1). At the North-West Ladakh scale, the occurrence was driven by many variables, with no variables related to rocks, vegetation, or geographic features strongly influencing the presence of the species (Table 1).

Ochotona nubrica

Univariate models - Comparison of univariate models at different scales prior to model building revealed that more relative percentage of bush cover, more number of shrubs, a greater height of shrubs, and large mature stands of tall grass and reeds were significant for predicting the presence of ON across all scales (Table C2). At the larger Ladakh scale, variables related to rocks (negatively) and NDVI across seasons (positively) were important in explaining the presence of*ON* (Table C2). In the North-West, presence was associated with NDVI (positively) and reflected greener habitats that the species occupies. Details of univariate models run can be found in Supplementary material (Table S6, Table S7, Table S8).

Multivariate models - At the Ladakh scale, the purposeful model (Model 2) produced the best results; the sub-modeling approach (Model 3) was best for the South-East, while at the West-Ladakh scale, all three modeling approaches produced equally good results (Table 2). At the Ladakh spatial scale, variables that predicted the absence of the species included cover and number of large-sized rocks, and variables that predicted the presence of the species, such as the cover of shrubs and NDVI, were important (Table 2). In the South-East, only variables related to vegetation and mainly shrubs were important in explaining the presence of the species (Table 2). In the North-West, different NDVI variables (for different modeling approaches) and mature stands of tall grass and reeds were necessary to explain the species' presence, although the species was restricted to large mature stands of Sea buckthorn (Table 2).

Ochotona ladacensis

Univariate models - At the Ladakh spatial scale, many variables related to rocks (lower percentage cover of rocks, lower percentage of large-sized rocks, lower number of large-sized rocks), heights of plants (low herb and forb height, tall cushion plants) were important in determining the presence of the species (Table C3). At the South-East Ladakh scale, only topographic variables such as elevation and slope significantly predicted presence (Table C3). All univariate models run are presented in Supplementary information (Table S9, Table S10).

Multivariate models - At both spatial scales, the purposeful modeling approach best predicted the occurrence of the species (Table 3). Variables that strongly predicted the absence of the species and those that predicted their presence were important in explaining where the species was most likely to be found. At both scales, the presence of OL was associated with a lower cover of rocks of different sizes, a lower number of large-sized rocks, a higher relative percentage of cushion plants, lower heights of shortgrass-sedges and shrubs, high elevation, and a more prominent aspect.

Discussion

The study set out to describe ecological niche spaces of three sympatric species of pika (*Ochotona macrotis:* OM, *Ochotona nubrica:*ON, and *Ochotona ladacensis:* OL), examine niche overlaps and widths in the context of ecological specialization under interspecific competition. In addition, it aimed to understand ecological factors that support the presence of these species at different spatial scales in the Ladakh Trans-Himalayas (3100m - 5200m) to inform conservation policy making.

Comparison of niche overlaps and niche width between species at broad and regional scales

At the broad scale (All of Ladakh, three species, three niches), OL shared a substantial portion of its niche (>%40) with OM and ON but had a small niche width given that it was elevational restricted. ON and OM, however, shared very little of their niche with other species and had large niche widths, given that they were found in a diversity of microhabitats.

At the regional scale (South-East and North-West Ladakh, three species, five niches), species shared very little of their niche with others, suggesting that at smaller spatial scales, all species were unique in the microhabitats they utilized, mirroring findings in Australian songbirds (Harmáčková et al. 2019) and sharp-nosed snakes (Corrêa Nogueira et al. 2019). OM had the largest niche width at the broad scale (generalist) and some of the smallest niche widths in the South-East (specialists). This is likely to have occurred due to natural variation in topography and landscape features across sites, with the species being found in a wide variety of microhabitats in the North-West compared to the South-East. ON had intermediate niche width at the broad scale, while at the regional scale, it had intermediate (North-West) and small (South-East) niche widths. This is reflective of the exclusive association of the species with tall mature stands of *Caragana sp.* exclusively in South-East Ladakh and with *Hippophae sp.* in the North-West, but inhabiting two very different microhabitats at the broad scale (also explains slight deviation from multivariate normal distributions in density plots at the broad scale). On the other hand, OL had the smallest niche width at the broad scale (high elevation specialist) and an intermediate niche width at regional scales. The species is restricted in elevational distribution but occurs in different microhabitats such as alpine meadows/grasslands and Caragana scrublands at these elevations.

Identifying important ecological factors drive presence of different species - Ecological factors contributing to different species' niches were used to model presence. At different spatial scales, different variables were significant in predicting the presence of a species. Such scale-dependent phenomena have been poorly explored in describing niche spaces and overlaps between species (Corrêa Nogueira et al. 2019).

At the Ladakh (broad) scale, OM was found in places with a good cover of large-sized rocks, a high number of large-sized rocks, and a low cover of tallgrass-reeds (Table 4).

The model suggested that presence was also driven by elevation and cover of rocks of class size two but not those of class size three (Table 4). This is likely an artifact of our sampling design (species found in the elevation bands 3000m-6000m) or a problem of finely dissecting ecological variables which doesn't majorly affect our understanding of how species partition microhabitats. It is worth noting that low cover of tallgrass-reeds was the only variable related to vegetation that appeared in the best model. This suggests that refuges are more critical than resources for microhabitat selection for the species and agrees with the literature on other rock-dwelling species *O. roylei*(Bhattacharyya et al. 2015) and *O. princeps* (Hall et al. 2016). However, it remains to be explored if refuges associated with large-sized rocks offer thermoregulatory benefits to animals across seasons, as shown for *O. princeps*(Hall et al. 2016).

At the same scale, ON was likely to occur in areas with high shrub cover, a higher number of shrubs, and a greater height of shrubs and other vegetation while actively avoiding areas with high rock cover (Table 4). Our field observations indicated that ON exclusively associates with areas with mature stands of scrub vegetation*Caragana* sp. at high elevations and sea buckthorn (*Hippophae rhamnoides*) at low elevations. While there are reports of the species using rocks as refuges (Smith et al. 2010, Wilson and Mittermeier 2016), we failed to observe such behavior and documented the use of forms instead (unpublished data).

OL was likely to occur at high elevations characterized by short plants (stunted growth) on alpine meadows/grasslands, low-lying *Caragana* , and cushion plants while avoiding areas with a high cover of rocks (Table 6).

This study describes, for the first time, niche spaces and overlaps between three sympatric species of pika from Asia. It illustrates that sympatric pika communities in Ladakh, India, segregate into different niches along rocks, vegetation, and elevation axes. There is a lot to gain from measuring niche space, overlaps, and widths at different spatial scales since it helps us understand how competition shapes niches and communities. This also provides opportunities for conservation planning for pikas in Ladakh's rapidly developing landscape.

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Figure 1 : Typical microhabitats of different species of pikas at Ladakh.

Ochotona macrotis microhabitats

Ochotona ladacensis microhabitats

Ochotona nubrica microhabitats

Figure 2: Map of regions sampled in Trans-Himalayas of Ladakh UT (blue polygons).

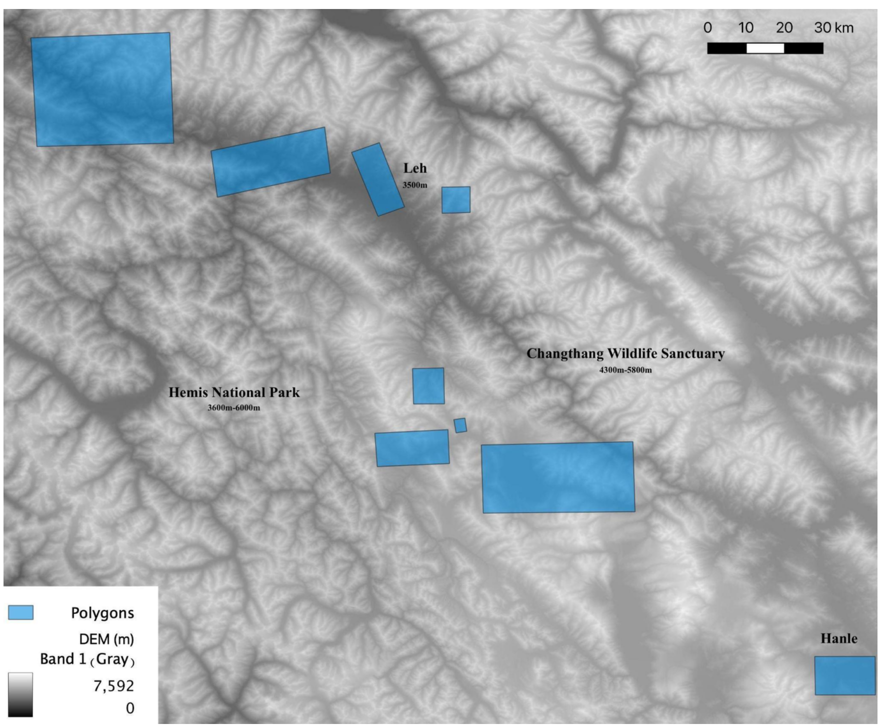

Figure 3 : Elevational distribution of presence and absence plots laid in the study across species. OL - Ochotona ladacensis, OM - Ochotona macrotis, ON - Ochotona nubrica.

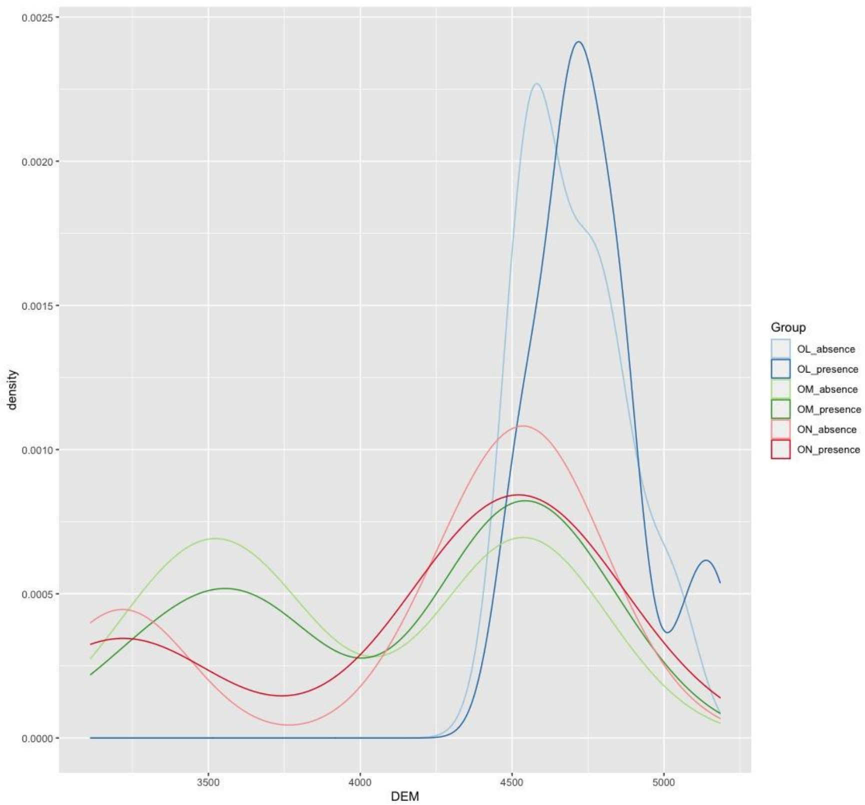

Figure 4 : Ten random elliptical projections of niche space for each species and pair of PC transformed axes (elliptical plots). Also displayed are one-dimensional density plots (lines) and two-dimensional scatterplots. Smoothed histograms (density plots) indicate a small deviation from normality for the species *O.nubrica* and *O. ladacensis.*

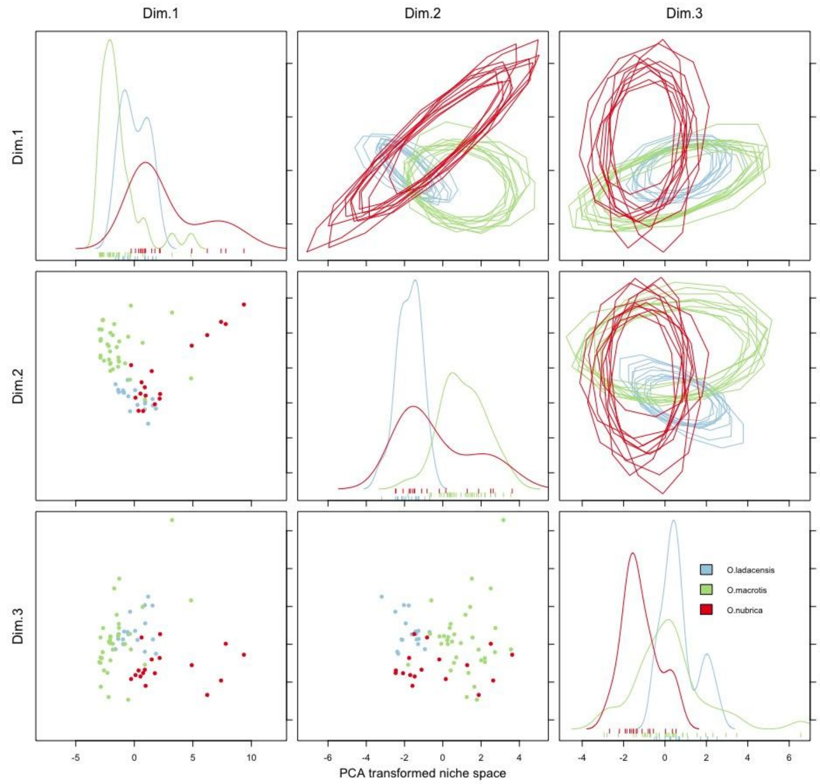

Figure 5. Posterior distribution of the probabilistic niche overlap metric (%) for a specified niche space of 95%. The figure represents the directional probability of finding species 1 (row) in the niche of species 2 (column). The posterior means and 95% credible intervals are displayed in the figure.

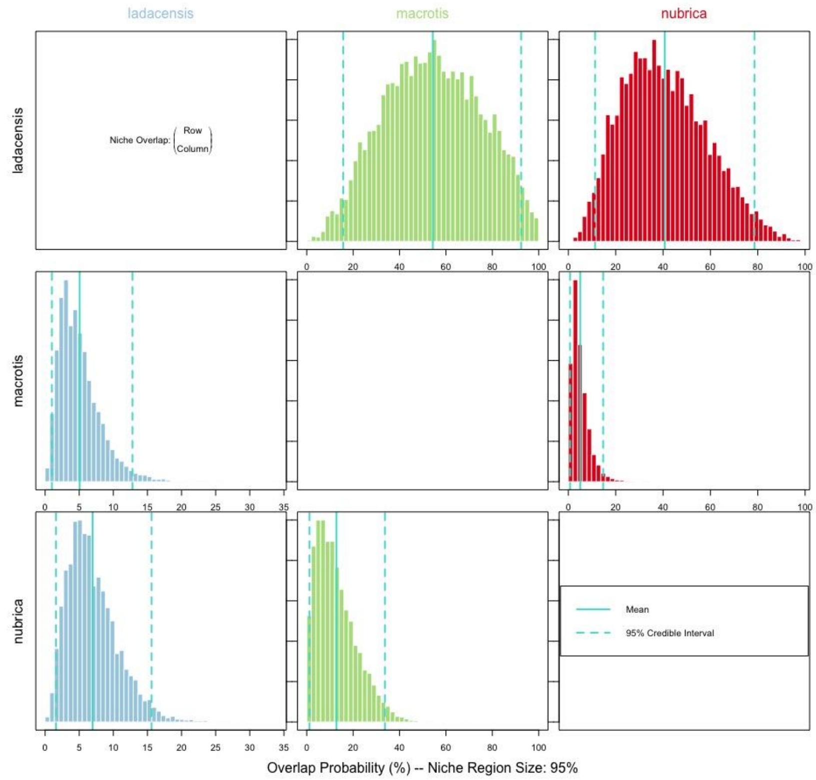

Figure 6 : Niche width of species (in this case, a 3 dimensional volume - first 3 PC axes) discerened from presence points of each species.

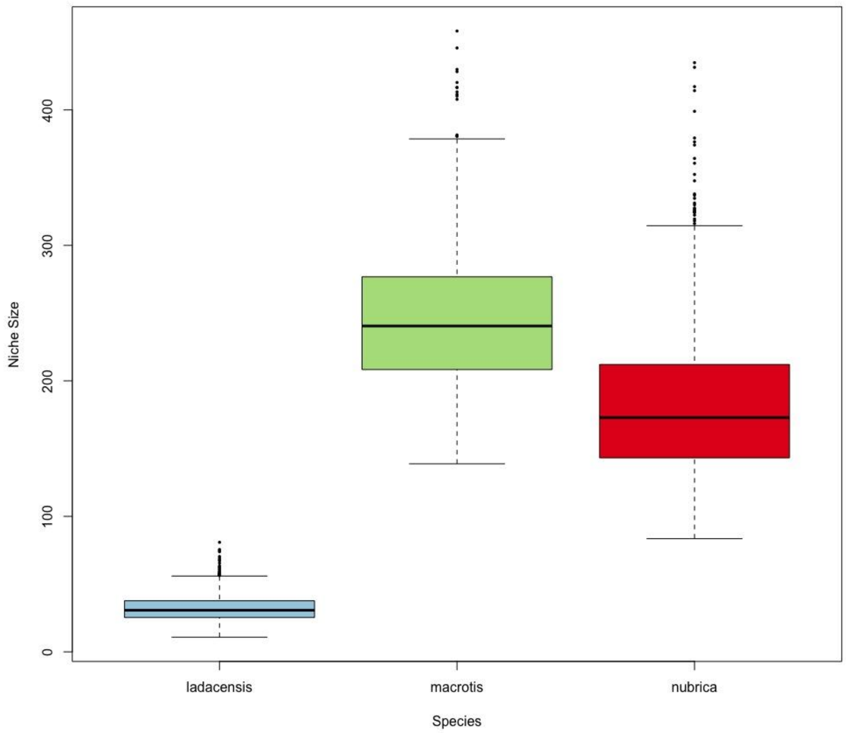

Figure 7 : Ten random elliptical projections of niche space for each species subdivided by location and pair of PC transformed axes (elliptical plots). Also displayed are one-dimensional density plots (lines) and two-dimensional scatterplots. Smoothed histograms (density plots) indicate a small deviation from normality for the species

O. ladacensis.

Legend : OL - *O.ladacensis* , ON - *O.nubrica* , OM -*O.macrotis* .

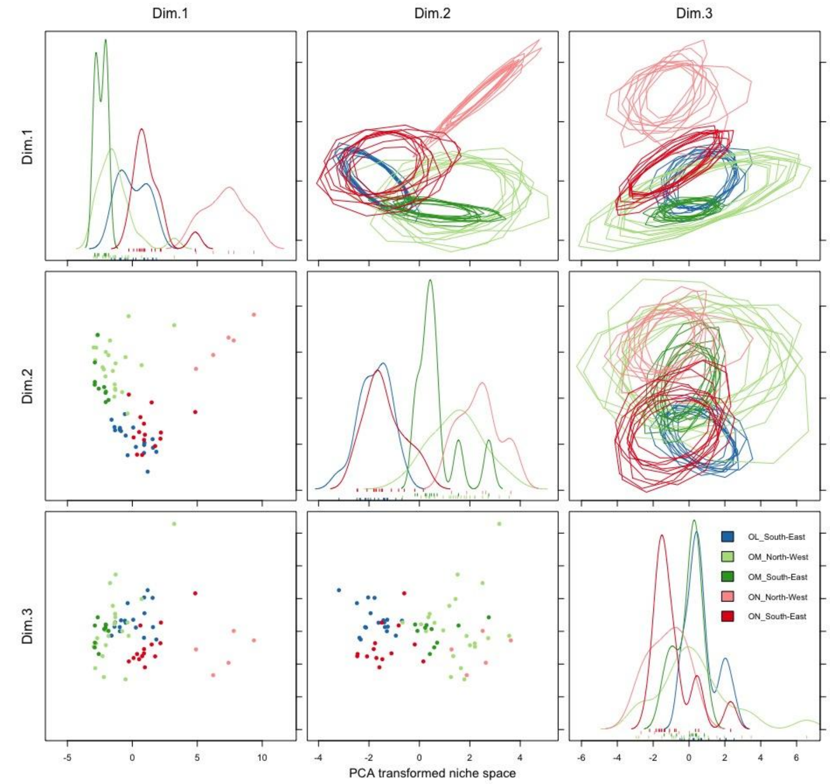

Figure 8: Posterior distribution of the probabilistic niche overlap metric (%) for a specified niche space of 95%. The figure represents the directional probability of finding species 1 (row) in the niche of species 2 (column). The posterior means and 95% credible intervals are displayed in the figure.

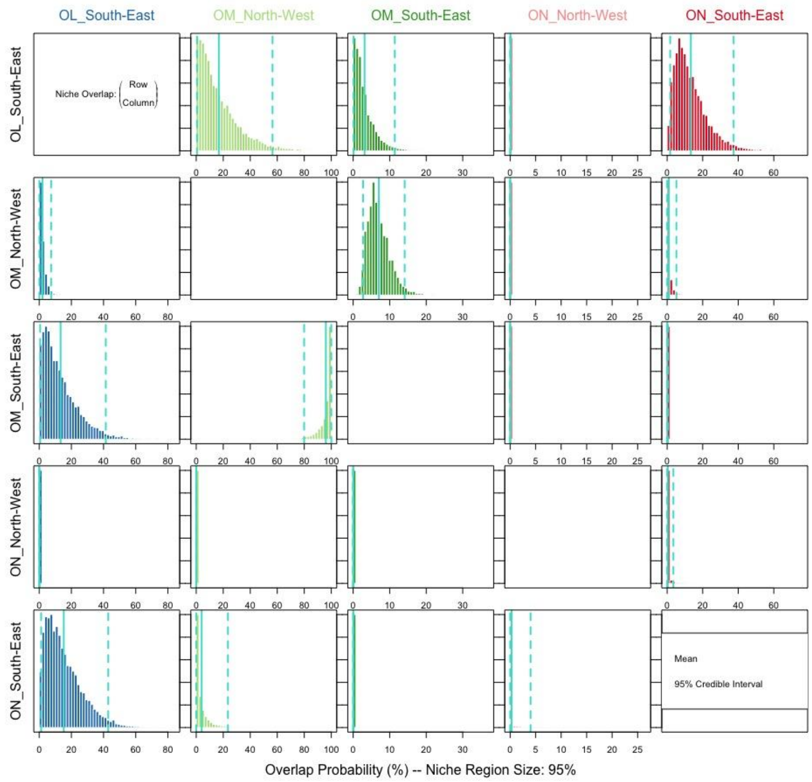

Figure 9 : Niche width of species subdivided by location (in this case, a 3 dimensional volume - first 3 PC axes) discerened from presence points of each species in different areas of Ladakh.

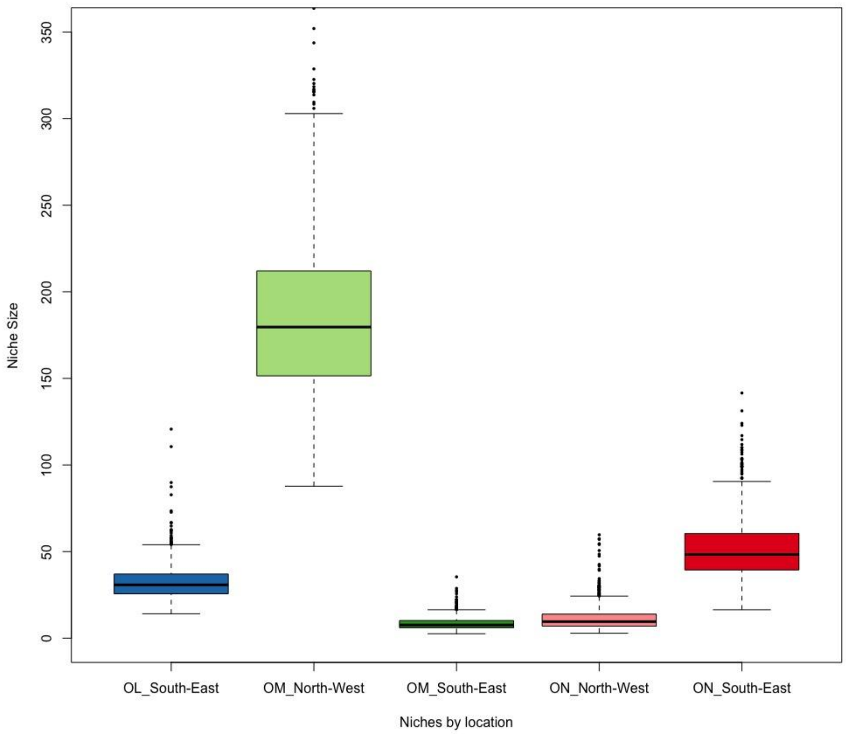

Table 1: Best multivariate models found using the StepAIC function across different modelling methods (see Model 1, Model 2 and Model 3 in Methods) and spatial scales for *Ochotona macrotis* . Within each spatial level, the best model and the approach has been highlighted.

Spatial Level: Ladakh

Modelling framework	**Best model**	**AIC**	**Top contributors to model**
Statistical model	macrotis ˜ perc_rocks + num_4rocks + DEM.elevation + x (NDVI_Winter)	94.25	
Purposeful model	macrotis ˜ perc_2rocks + perc_4rocks + num_4rocks + perc_herb_forb + perc_shrub + height_tallgrass_reeds + x (NDVI_Winter) + x (NDVI_Summer) + stdev (NDVI_Summer)	89.41	perc_4rocks num_4rocks x (NDVI_Summer)

Sub-model	macrotis ~ perc_2rocks + perc_4rocks + num_4rocks + perc_herb_forb + perc_shrub + perc_tallgrass_reeds + height_tallgrass_reeds + x (NDVI_Winter) + x (NDVI_Summer) + stdev (NDVI_Summer)	88.5	perc_4rocks num_4rocks x (NDVI_Summer)
Spatial Level: South-East Ladakh Modelling framework	**Spatial Level: South-East Ladakh Best model**	**Spatial Level: South-East Ladakh AIC**	**Spatial Level: South-East Ladakh Top contributors to model**
Statistical model	macrotis ~ perc_3rocks + perc_4rocks + DEM.elevation	29.74	
Purposeful model	macrotis ~ perc_rocks + perc_3rocks + perc_4rocks + num_4rocks + perc_vegetation + perc_shrub + stdev (NDVI_Winter)+ DEM.elevation	18	Perc_4rocks num_4rocks DEM.elevation Perc_shrub stdev (NDVI_Winter)
Sub-model	macrotis ~ perc_3rocks + perc_4rocks + DEM.elevation	29.74	
Spatial Level: North-West Ladakh Modelling framework	**Spatial Level: North-West Ladakh Best model**	**Spatial Level: North-West Ladakh AIC**	**Spatial Level: North-West Ladakh Top contributors to model**
Statistical model	macrotis ~ num_4rocks + perc_4rocks + x (NDVI_Winter)	45.94	

Purposeful model	macrotis ~ perc_bareground + perc_4rocks + num_3rocks + num_4rocks + perc_vegetation + perc_shrub + perc_herb_forb + perc_tallgrass_reeds + height_shrub + height_herb_forb + height_tallgrass_reeds + num_tallgrass_reeds + num_shortgrass_sedge + num_3rocks + perc_bareground + x (NDVI_Winter) + x (NDVI_Summer) + stdev (NDVI_Summer) + x (Δ NDVI) + DEM.elevation	38	All variables are equally important
Sub-model	macrotis ~ num_4rocks + perc_4rocks + perc_tallgrass_reeds + num_shortgrass_sedge Average.Delta.NDVI	45.5	

Table 2: Best multivariate models found using the StepAIC function across different modelling methods (see Model 1, Model 2 and Model 3 in Methods) and spatial scales for *Ochtona nubrica* . Within each spatial level, the best model and the approach has been highlighted.

Spatial Level: Ladakh

Modelling framework	**Best model**	**AIC**	**Top contributors to model**
Statistical model	nubrica ~ perc_vegetation + perc_rocks + num_3rocks + num_4rocks + num_shortgrass_sedge + perc_herb_forb + perc_shrub + height_tallgrass_reeds + height_shrub + height_trees + Slope + x (NDVI_Winter)	26	

Purposeful model	nubrica ~ perc_vegetation + perc_3rocks + perc_4rocks + perc_herb_forb + perc_shrub + height_shrub + x (NDVI_Winter) + x (NDVI_Summer)+ x (Δ NDVI)	20	All variables are equally important besides variables related to rocks.
Sub-model	nubrica ~ perc_3rocks + perc_4rocks + perc_herb_forb + perc_shrub + x (NDVI_Summer) + num_shrub + height_shortgrass_sedge + height_tallgrass_reeds + height_shrub	20	All variables are equally important besides x (NDVI_Summer)
Spatial Level: Changthang Modelling framework	**Spatial Level: Changthang Best model**	**Spatial Level: Changthang AIC**	**Spatial Level: Changthang Top contributors to model**
Statistical model	nubrica ~ num_shrub + perc_herb_forb + perc_shrub + height_tallgrass_reeds + height_shrub + Average.NDVI_Nov_Dec	20.12	
Purposeful model	nubrica ~ perc_bareground + perc_3rocks + perc_shrub + height_herb_forb + height_shrub + Average.NDVI_Nov_Dec	14	
Sub-model	nubrica ~ perc_vegetation + perc_shrub + x (NDVI_Winter)+ height_shrub	10	All variables are equally important
Spatial Level: West Ladakh Modelling framework	**Spatial Level: West Ladakh Best model**	**Spatial Level: West Ladakh AIC**	**Spatial Level: West Ladakh Top contributors to model**
Statistical model	nubrica ~ height_tallgrass_reeds + stdev (NDVI)	6	All variables are equally important

Purposeful model	nubrica ˜ height_tallgrass_reeds + x (Δ NDVI)	6	All variables are equally important
Sub-model	nubrica ˜ x (NDVI_Summer) + height_tallgrass_reeds	6	All variables are equally important

Table 3: Best multivariate models found using the StepAIC function across different modelling methods (see Model 1, Model 2 and Model 3 in Methods) and spatial scales for *Ochotona ladacensis* . Within each spatial level, the best model and the approach has been highlighted.

Spatial Level: Ladakh

Modelling framework	**Best model**	**AIC**	**Top contributors to model**
Statistical model	ladacensis ˜ num_4rocks + DEM.elevation	80.95	
Purposeful model	ladacensis ˜ perc_bareground + perc_vegetation + perc_rocks + perc_1rocks + perc_4rocks + num_4rocks + perc_trees + height_shortgrass_sedge + DEM.elevation + Aspect + x (NDVI_Winter)	63.99	All variables equally important
Sub-model	ladacensis ˜ perc_1rocks + num_4rocks + height_shrub + DEM.elevation + Aspect	73.37	
Spatial Level: Changthang	**Spatial Level: Changthang**	**Spatial Level: Changthang**	**Spatial Level: Changthang**
Modelling framework	**Best model**	**AIC**	**Top contributors to model**
Statistical model	ladacensis ˜ DEM.elevation + Slope	89.94	
Purposeful model	ladacensis ˜ perc_1rocks + perc_4rocks + height_shrub + DEM.elevation + Slope	71.93	perc_1rocks perc_4rocks DEM.elevation Slope
Sub-model	ladacensis ˜ perc_rocks + perc_1rocks + perc_4rocks + perc_cushionplant + height_shrub	79.5	