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Population ecology

Ecological niche structure and rangewide abundance patterns of species

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Spatial abundance patterns across species' ranges have attracted intense attention in macroecology and biogeography. One key hypothesis has been that abundance declines with geographical distance from the range centre, but tests of this idea have shown that the effect may occur indeed only in a minority of cases. We explore an alternative hypothesis: that species' abundances decline with distance from the centroid of the species' habitable conditions in environmental space (the ecological niche). We demonstrate consistent negative abundance–ecological distance relationships across all 11 species analysed (turtles to wolves), and that relationships in environmental space are consistently stronger than relationships in geographical space.

1. Introduction

An important paradigm in ecology concerns population abundance trends across species' geographical distributions [1]. It has been argued that abundances are highest at the geographical centres of species' distributions, and lowest along the periphery [2–4]; this notion has been used to predict extinction probabilities [5,6] and is prominent in the conservation biology literature [7,8]. Nonetheless, empirical tests of this idea have yielded mixed results: the geographical distribution–abundance relationship is not straightforward, and many exceptions have emerged [9,10].

Explanations of observed abundance variation across species' ranges invoke dispersal mechanisms in source-sink systems [11] and fitness responses to variation in critical habitat variables [4]. Ultimately, however, geographical abundance patterns should reflect, at least in part, the extent to which niche requirements are fulfilled at each site [12], such that 'niche' is the N-dimensional hypervolume within which populations can be self-maintained indefinitely [13]. Maguire [14] proposed that the niche has an internal structure where optimal conditions are at the centroid of the hypervolume; if this is true, then geographical abundance patterns across ranges respond to the arrangement of environmental conditions relative to the niche centroid across landscapes.

Ecological niche modelling was developed principally for characterizing distributions of species, but has had little connection to underlying population-biological processes [15,16]. Although theoretical treatments have addressed the distributional consequences of these processes [17–21], no empirical studies have as yet linked niche model outputs rigorously to population processes [19,20]. The niche modelling framework offers an alternative viewpoint on the central–peripheral question: as with other recent efforts [22,23], population processes can be examined in both geographical and ecological dimensions simultaneously. Here, we re-examine the question of abundance patterns, comparing relationships between

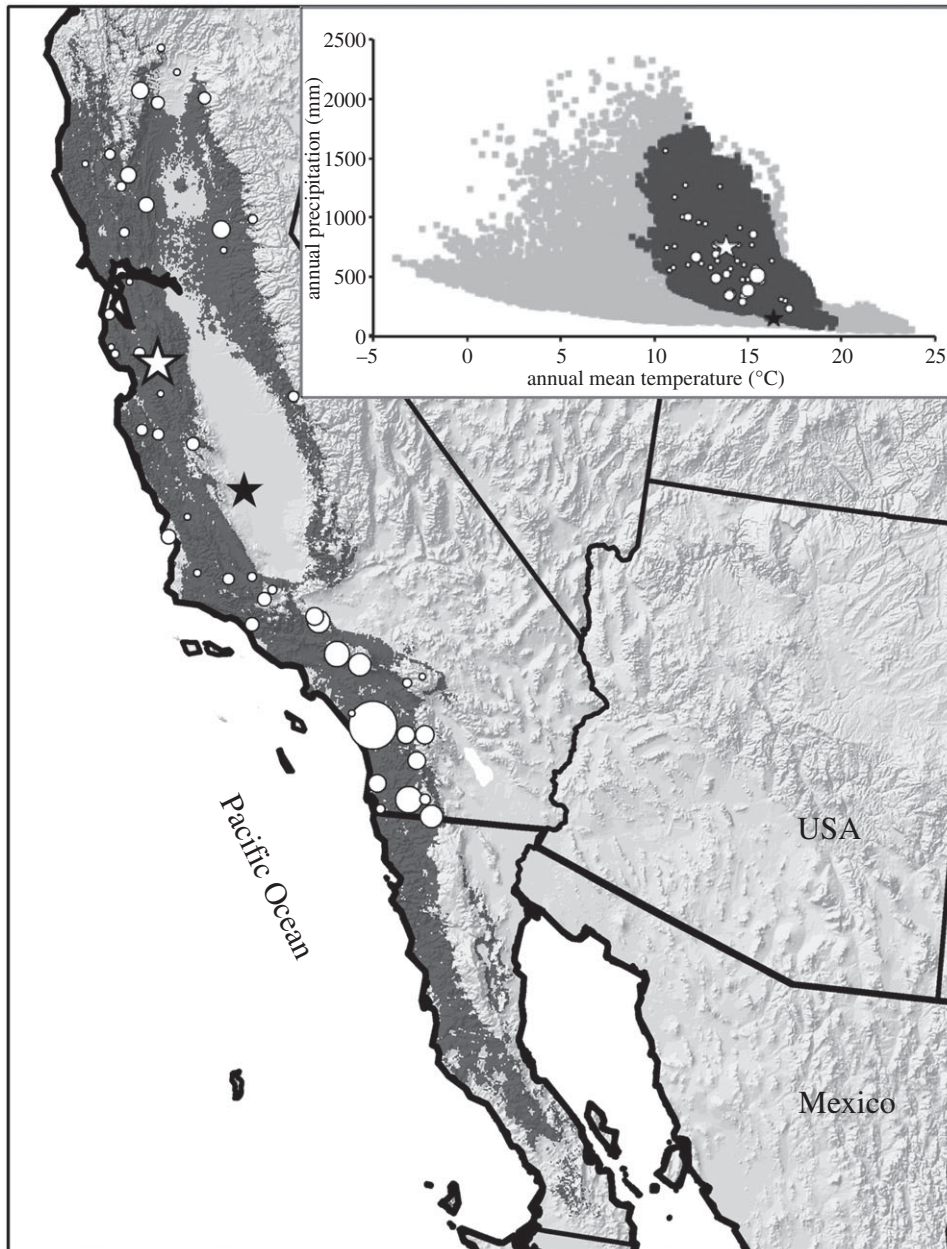


Figure 1. Geographical and environmental distribution of the California thrasher (*Toxostoma redivivum*). Map of western North America showing known occurrences with abundance information (white dots; dot sizes indicate numbers of individuals per route), the geographical centroid of the species' distribution (black star), modelled distribution (dark grey) and the geographical location of the environmental centroid of the ecological niche (white star). Inset: visualization of the distribution of the species in a space of annual mean temperature and annual precipitation, showing environments across western North America (light grey), environments modelled as suitable for the species (dark grey), abundance occurrences of this species (white dots; dot sizes indicate numbers of individuals per route), environmental conditions at the centroid of the species' geographical distribution (black star) and the centroid of niche in environmental space (white star).

abundance and geographical centrality with those between abundance and *environmental* centrality.

2. Material and methods

To develop tests of abundance as a function of distances to centroids of species' distributions in geographical and environmental spaces, we required data for each species at an array of sites, plus independent data on occurrences with which to calibrate models. Abundance data for four bird species (*Toxostoma redivivum*, *Calamospiza melanocorys*, *Spiza americana*, *Hylocichla mustelina*) were derived from the North American Breeding Bird Survey [24]; we used route totals averaged over 1968–2004. Other taxa and data sources included wintering populations of the sandpiper *Tryngites subruficollis*; individuals per trap-night for the mice *Peromyscus leucopus* and *P. maniculatus*; survey publications (individuals per park) for wolves *Canis lupus*; individuals per 100 km² for jaguars *P. onca*;

and individuals per hectare for the turtle *Clemmys guttata* and the howler monkey *Alouatta palliata* (see electronic supplementary material, appendix S1). In each case, we sought species occurrence data independent of the sources of abundance information, thereby providing a way to calibrate ecological niche models in the data resources served by the Global Biodiversity Information Facility (GBIF; www.gbif.org). Sources for all data are in electronic supplementary material, appendix S1; as necessary, textual locality descriptors were georeferenced via electronic databases [25].

Raster-format data for modelling included the 19 'bioclimatic' dimensions in WorldClim [26], plus elevation, slope and topographic index from Hydro-1K [27], which were resampled to 2–20 km resolution, with finer resolutions for species with smaller distributions to provide sufficient detail.

Ecological niches were modelled, using GARP [28] OPEN MODELLER Desktop v. 1.1.0 (<http://openmodeller.sourceforge.net/>). GARP estimates niches in environmental dimensions by relating

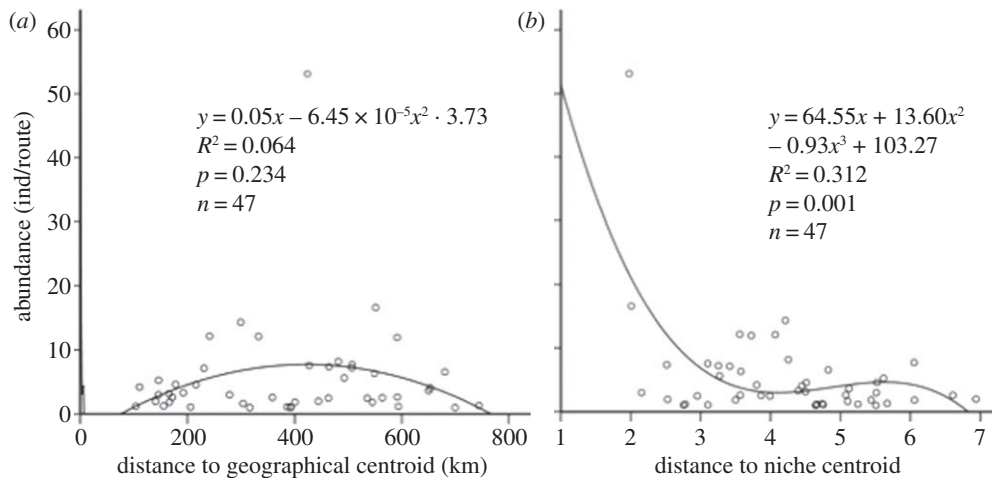


Figure 2. Relationships between abundance and distances to (a) geographical and (b) environmental centroids for the California Thrasher (*Toxostoma redivivum*).

characteristics of known occurrences to those of points randomly sampled from across the study region in order to develop decision rules that summarize factors associated with the species' presence [28,29]. For each species, 100 replicate models were built; the 20 with lowest omission retained, and the 10 closest to median area predicted suitable were summed as a final consensus model (modified from Pearson *et al.* [30]). Finally, we thresholded model predictions to produce binary maps by establishing the level at which 90 per cent of input occurrence points are included in the prediction. GARP's predictive abilities have been tested [31–33], and it typically produces results on par with other methodologies [34]. Our data and the GARP models are deposited in the University of Kansas Repository and made available at <http://hdl.handle.net/1808/10061> [35].

To characterize niches, we combined environmental variables with model prediction in ArcGIS v. 9.3 (ESRI, Redlands, CA, USA), producing a grid with an attributes table summarizing unique environmental combinations across the study region. We identified grid cells corresponding to points where we had abundance data, transformed environmental variables to standard normal variates and calculated the centroid in environmental space as the mean value of suitable pixels in each environmental dimension. We then calculated Euclidean distances from all pixels to the ecological niche centroid; for comparison, we calculated distances from all points to the geographical centroid, with geographical distributions drawn from diverse 'extent of occurrence' resources (see electronic supplementary material, appendix S1). We related observed abundances to both of these distance measures via regression (best fit of exponential, logarithmic, power, cubic or linear); we also used a bootstrapping routine in R that uses 1000 simulations using 70 per cent of records for training and 30 per cent for testing. We calculated proportions of test records falling within 95% CIs as a probability value measuring performance of the model.

3. Results

As an exemplar, we chose the California thrasher (*Toxostoma redivivum*), the species used by Grinnell [36] to develop the concept of niches (figure 1). For this species, we found no significant association between abundance and distance to the geographical centroid ($R^2 = 0.064$, $p = 0.234$; figure 2a). Centroid distance in environmental space, however, showed considerable explanatory power for abundances ($R^2 = 0.312$, $p = 0.001$; figure 2b): populations farther from the niche centroid in environmental space were smaller in numbers. Hence, distance in environmental space explained considerable variation in abundance, whereas geographical distance to the centre of the species' distribution did not.

Parallel analyses used 10 additional species with body masses spanning three orders of magnitude (table 1). In 10 of 11 cases, significant ($p < 0.05$) negative abundance–environmental distance relationships existed; regressions explained 7–69% of overall variation and there was no significant dependence of R^2 on sample sizes ($p = 0.178$). By contrast, abundance–geographical distance relationships were not significant in seven of 11 species, and R^2 -values were lower in nine of 11 species (0.005–0.327; table 1).

4. Discussion

Our results suggest that the geographical 'abundant-centre hypothesis' [4,10] is not causal. It 'works' by happenstance when geographical ranges and ecological niches coincide in their central tendencies. Instead, we posit that ecological niches play a role in defining more than range limits [18,37]: the geographical structure of species' abundance patterns [38] maps onto patterns of centrality in ecological niche space [12,14].

The observed inverse relationships between abundance and distance to the centroid are generally nonlinear in nature (except for the turtle). This realization implies that: (i) sites presenting optimal niche conditions support many more individuals than most occupied sites [12]; and (ii) optimal niche conditions are relatively narrow, such that few sites hold suitable conditions for maintaining large populations [12]. Implications of this asymmetry for population biology are profound: because more individuals are produced in highly suitable areas, migration rates to suboptimal sites are higher, limiting adaptation to novel conditions and reinforcing niche conservatism [18,21,39].

We also found exceptions to the general trend. First, for the migrant buff-breasted sandpiper the abundance–niche centroid relationship was inverse but not significant. Analyses for this species were conducted across the wintering distribution; the rest of the species were analysed across breeding distributions. Some migratory species shift ecological niches between seasons [40], responding to different requirements; it is thus possible that the winter niche of this species is less climatically driven, but this possibility needs further exploration. Lastly, the spotted turtle presented an inverse linear relationship, suggesting that optimality of sites reduces monotonically rather than abruptly. This result, however, may be an artefact of small sample sizes ($n = 14$), clearly lacking a detailed representation of population size variability across the species' geographical range.

Table 1. Relationships between population abundances and distances to geographical and environmental centroids in 11 species. 'Pixel size' refers to the spatial resolution of environmental variables used for analyses. 'Regression' indicates the form of the curve that best fit the data when a significant relationship was found. 'Predictive power' refers to the bootstrap-based assessment of ability to anticipate abundances for data records omitted from particular analyses.

common name	species	n for abundances	pixel size (km)	body mass (g)	geographical range centroid distance			ecological niche centroid distance				
					regression	R ²	p	regression	R ²	p	predictive power	predictive power
California thrasher	<i>Toxostoma redivivum</i>	48	2	86	—	0.064	0.234	0.012 ± 0.016	$y = -64.55x + 13.60x^2 - 0.931x^3 + 103.3$	0.312	0.001	0.152 ± 0.054
lark bunting	<i>Calamospiza melanocorys</i>	277	10	40	$y = -0.502x + 0.001x^2 - 3.6 \cdot 10^{-7}x^3 + 181.9$	0.068	<0.001	0.052 ± 0.018	$y = 209.1(-0.494)^x$	0.161	<0.001	0.102 ± 0.016
dickcissel	<i>Spiza americana</i>	709	10	26	$y = 102.2(-0.003)^x$	0.327	<0.001	0.262 ± 0.019	$y = 36.98(-0.356)^x$	0.081	<0.001	0.073 ± 0.010
wood thrush	<i>Hylocichla mustelina</i>	699	10	45	—	0.005	0.073	0.002 ± 0.002	$y = -20.191x - 68.22x^2 + 43.87x^3 + 9.404$	0.083	<0.001	0.003 ± 0.002
buff-breasted sandpiper	<i>Tryngites subruficollis</i>	36	7	60	$y = 0.969(0.001)^x$	0.275	<0.001	0.047 ± 0.040	—	0.134	0.198	0.164 ± 0.045
white-footed mouse	<i>Peromyscus leucopus</i>	55	10	23	—	0.063	0.340	0.007 ± 0.007	$y = 9.027(-1.153)^x$	0.074	0.045	0.016 ± 0.013
deer mouse	<i>Peromyscus maniculatus</i>	54	20	20	—	0.050	0.105	0.034 ± 0.037	$y = -47.82x + 9.666x^2 - 0.551x^3 + 74.659$	0.234	0.006	0.095 ± 0.094
gray wolf	<i>Canis lupus</i>	28	10	60 000	$y = 0.020x - 3.17 \cdot 10^{-6}x^2 - 8.552$	0.215	0.048	0.024 ± 0.035	$y = 33.086x - 3.695x^2 - 50.19$	0.255	0.025	0.154 ± 0.092
jaguar	<i>Panthera onca</i>	29	10	78 000	—	0.136	0.292	0.116 ± 0.084	$y = 10.94x - 2.362x^2 + 0.139x^3 - 9.674$	0.281	0.038	0.184 ± 0.078
howler monkey	<i>Alouatta palliata</i>	10	2	5200	—	0.134	0.819	0.145 ± 0.140	$y = -9.101x - 0.763x^2 + 26.937$	0.691	0.016	0.255 ± 0.230
spotted turtle	<i>Clemmys guttata</i>	14	10	1000	—	0.106	0.541	0.069 ± 0.095	$y = -1.638x + 10.409$	0.440	0.010	0.446 ± 0.142

The abundant (geographical) centrality idea has been a paradigm in biogeography for decades [2,7,8,41,42]. However, support for this idea as a general relationship has been unclear [9,10]. The environmental centrality result, on the other hand, has both a conceptual underpinning [14,38], and now empirical support.

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