Weak support for the abundant niche-centre hypothesis in North American birds

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Abstract

Species may be more abundant in the centre of their geographic range or climatic niche (the abundant-centre hypothesis). Recently, Osorio-Olvera *et al.* (2020) reported strong support for the niche abundant-centre relationship. We demonstrate here that methodological decisions strongly affected perceived abundant-centre support. Upon re-analysis, we show that abundant-centre relationships are quite rare.

The spatial distribution of abundance has long fascinated ecologists who searched for general rules governing where species occur and the density at which they are found (McGill *et al.*, 2007; Sagarin & Gaines, 2002). Particularly controversial rules are the abundant-centre and abundant-niche centre hypotheses, which predict abundance to decrease gradually from the centre to the margins of species geographic ranges and ecological niches respectively (Brown, 1984; Pironon *et al.*, 2017)). Both theories have received mixed empirical support (Martínez-Meyer *et al.*, 2013; Sagarin & Gaines, 2002; Dallas *et al.*, 2017) and limited theoretical development (Osorio-Olvera *et al.*, 2019; Holt, 2019). Moreover, recent analyses highlighted that tests of these hypotheses were sensitive to the quality of the input data and the methodological approach considered (Santini *et al.*, 2019).

Osorio-Olvera *et al.* (2020) analyze data from the North American Breeding Bird Survey (BBS) to test for a negative correlation between species abundance and the distance to their climatic niche centroid. Counter to recent findings questioning its generalizability (Sagarin & Gaines, 2002; Dallas *et al.*, 2017; Santini *et al.*, 2019), the authors find general support for the hypothesis and propose that the distance to species climatic niche centroid (quantified using minimum volume ellipsoids) could represent a reliable and simple new metric to predict the current and future distribution of species abundance. However, we show that, by (i) considering the full species environmental niche, (ii) reporting non-significant relationships and (iii) selecting models with the best fit only, overall conclusions may differ greatly.

To estimate the niche, Osorio-Olvera and colleagues contrast bird occurrence records with 10,000 background points sampled randomly all over the Americas including Canada and South America, i.e., a methodological approach that the authors point in the discussion as a potential reason why previous studies failed to support the abundant-niche centre relationship (Santini *et al.*, 2019). However, many of the species considered in the study also occur in other continents (e.g. *Ardea alba*, *Corvus corax*), and some only share a very small portion of the range in the study area (e.g. *Thalasseus maximus*, *Aramus guarauna*). We calculated geographic and climatic niche overlap of the BBS data with the BirdLife International data (BirdLife International, 2017), demonstrating a clear influence on the estimation of the geographic range and climatic niche boundaries, as well as their centroids (Figure 1). This subsequently affects the abundant-niche centre relationship, as discussed in Soberón *et al.* (2018). Oddly, many of the bird species whose geographic ranges are underestimated [mean (sd) of geographic range overlap = 55(27)%] and whose niches have been underestimated [mean (sd) of niche overlap = 53(23)%] also exhibit significant negative abundant-centre relationships, putatively supporting the hypothesis.

The strongest support for the abundant-niche centre relationships comes from Osorio-Olvera *et al.* (2020) estimating the species niche as a minimum volume ellipsoid (MVE) by considering more than 4000 combinations of climatic variables, including all 19 commonly-used bioclimatic variables together with the first 15 PCA components of a PCA based on the same bioclimatic variables. The authors use every possible combination of two and three niche axes to estimate the niche. We identify two main issues associated with this procedure.

First, the authors report results only for models showing significant abundant-niche centre relationships, omitting non-significant correlations (Figure 2a). This issue is not only present in the fit MVE models, but also in the 2 and 3 feature models using convex hulls or MVEs, which makes Figure 3 of Osorio-Olvera et al. (2020) quite a biased view of the abundant-niche centre relationship. In fact, by including non-significant correlations, the mean abundant-niche centre relationship across all model sets becomes quite weak ($\bar{\rho} + -sd$ = -0.08 +− 0.01), and many species exhibit significantly positive abundant-niche centre relationships (Figure 2b). Including these non-significant results is important, in our view, and strongly influences the resulting perceived support for the abundant-centre pattern (Figure 2b). Our re-analysis suggests that only between 37% and 45% of species have negative abundant-centre relationships, regardless of approach used (see https://figshare.com/s/8fadf780810e73d44623), while the majority of the estimated relationships are either positive or non-significant. Interestingly, this low empirical support is consistent with previous findings for the geographic interpretation of the hypothesis (Pironon *et al.*, 2017; Sagarin & Gaines, 2002).

Second, while the authors train an average of 1,852 models per species to calculate MVEs, they perform no form of model selection. This functionally treats the poorest fit MVE and the best fit MVE as equivalent, provided the model produced a significant abundant-centre relationship. When non-significant results are included, and only best models are retained, the overall pattern changes substantially (Figure 2; but note the niches are still biased to data in North America). When only the best fit models are considered, 115 out of 379 species had significant abundant-niche centre relationships, with a mean correlation coefficient of -0.07. Some of these best models had higher omission rates than what Osorio-Olvera *et al.* (2020) considered. Removing these models reduces the number of species down to 303 species, of which 94 had significantly negative abundant-niche centre relationships, while 180 and 29 had non-significant or significantly positive relationships, respectively (Figure 2c). A large part of the presentation of the results in Osorio-Olvera *et al.* (2020) is dedicated to species that meet the expectations and exhibit higher abundance in areas closer to the centre of their niche (Fig. 1 and 2 in Osorio-Olvera *et al.* (2020)), we note that a less biased overview of their findings shed doubts on the putative support for the abundant niche-centre hypothesis.

The study from Osorio-Olvera *et al.* (2020) highlights the timely need for disentangling the complex relationship between species ecological niche, geographic distribution and demographic performance (Holt, 2019; Bohner & Diez, 2020). Explaining the convergence and divergence of results of studies exploring occurrence and abundance patterns is key for improving our understanding of biodiversity and ability to predict its response to ongoing changes in the global environment.

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142 # Figures

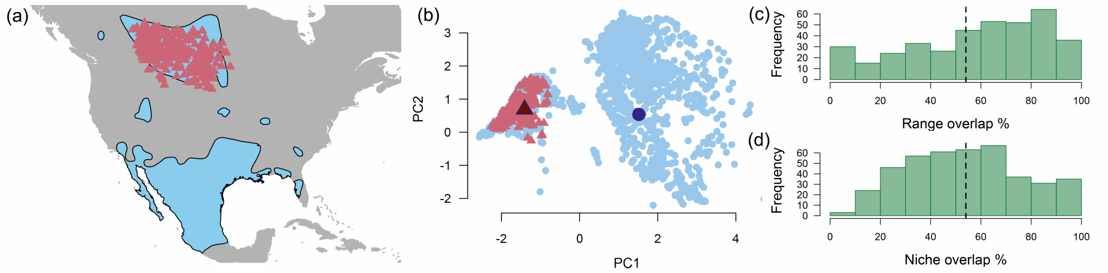

Figure 1: Mismatch in geographic and niche estimate between abundance data used in Osorio-Olvera *et al.* (2020) and the full resident and breeding range distribution of species, estimated IUCN range polygons. We acknowledge, as others previously have Soberón *et al.* (2018), that IUCN polygons may not capture a species actual range. **a**) Sprague's pipit (*Anthus spragueii*) IUCN geographic range (in blue) and sample data to estimate the niche (in red); **b**) First two PCA axes of all bioclimatic variables showing environmental values considered in the study (red triangles) and those estimated considering the cells in the IUCN range (blue dots). The darker and larger triangle and circle represent the estimated centroids of the two hypervolumes; **c**) Distribution of geographic range overlap between convex hulls drawn around abundance estimates and the IUCN ranges for all species considered in the study; **d**) Distribution of niche overlap between convex hulls drawn around abundance estimates and grid cells within the IUCN ranges for all species in the study. Niche overlap and niche centroids were estimated using the hypervolume package Blonder *et al.* (2015).

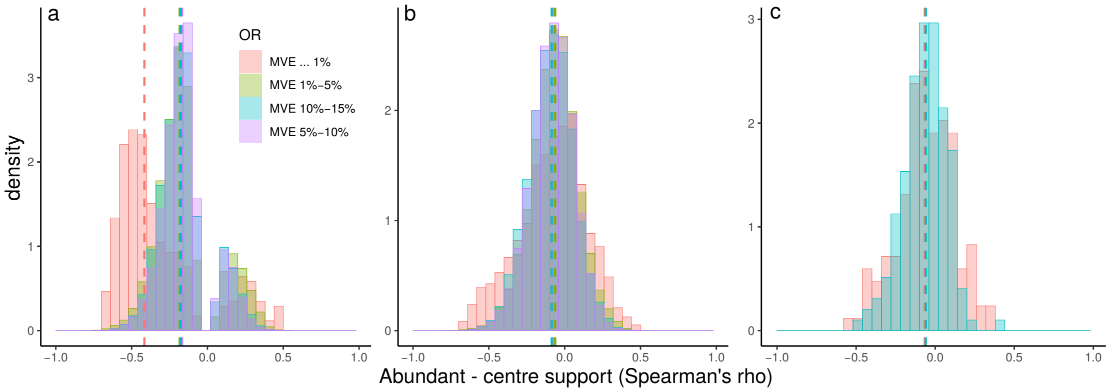

Figure 2: Variation in support for the abundant-niche centre hypothesis across North American birds as a function of analytical decisions involved in the formation of over 700,000 models of species Minimum Volume Ellipsoids (MVEs). **a**) the reproduced results from Osorio-Olvera *et al.* (2020) showing predominantly negative abundant-centre relationships, especially when omission rates were low; **b**) the effect of including non-significant abundant-niche centre relationships. **c**) only considering the best fit MVE model for a given species instead of using all fit models, while also considering that the best fit model could have a non-significant abundant-centre relationship.