

# **Evaluating ecological uniqueness over broad spatial extents using species distribution modelling**

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**Abstract:** Local contributions to beta diversity (LCBD) can be used to identify sites with high ecological uniqueness and exceptional species composition within a region of interest. Yet, these indices are typically used on local or regional scales with relatively few sites, as they require information on complete community compositions difficult to acquire on larger scales. Here, we investigated how LCBD indices can be predicted over broad spatial extents using species distribution modelling and examined the effect of scale changes on beta diversity quantification. We used Bayesian additive regression trees (BARTs) to predict warbler species distributions in North America based on observations recorded in the eBird database. We then calculated LCBD indices for observed and predicted data and compared the site-wise difference using direct comparison, a spatial association test, and generalized linear regression. We also examined the relationship between LCBD values and species richness in different regions and at various spatial extents. Our results showed that species distribution models provided uniqueness estimates highly correlated with observed data. The form and variance of the LCBD-richness relationship varied according to the region and the total extent size. The relationship was also affected by the proportion of rare species in the communities. Therefore, sites identified as unique over broad spatial extents may vary according to regional characteristics. These results show that species distribution modelling can be used to predict ecological uniqueness over broad spatial extents, which could help identify beta diversity hotspots and important targets for conservation purposes in unsampled locations.

## **1 Introduction**

2 Beta diversity, defined as the variation in species composition among sites in a geographic re-  
3 gion of interest (Legendre, Borcard, and Peres-Neto 2005), is an essential measure to describe  
4 the organization of biodiversity through space. Total beta diversity within a community can be  
5 partitioned into local contributions to beta diversity (LCBD) (Legendre and De Cáceres 2013),  
6 which allow the identification of sites with exceptional species composition, hence unique biodi-  
7 versity and potential conservation value. Sites with unique community composition often differ  
8 from those with high species richness, possibly as they harbour rare species or help maintain  
9 beta diversity (da Silva, Hernández, and Heino 2018; Heino et al. 2017; Landeiro et al. 2018).  
10 Hence, focusing on uniqueness can prove helpful as a complementary approach to species rich-  
11 ness (Heino and Grönroos 2017; da Silva, Hernández, and Heino 2018; Yao et al. 2021; Dubois,  
12 Proulx, and Pellerin 2020). However, the use of LCBD indices is currently limited in two ways.  
13 First, LBCD indices are typically used on data collected over local or regional scales with rela-  
14 tively few sites, for example, on fish communities at intervals along a river or stream (Legendre  
15 and De Cáceres 2013). Second, LCBD calculation methods require complete information on  
16 community composition; thus, they are inappropriate for partially sampled sites (e.g., where  
17 data for some species are missing or uncertain) and cannot directly provide assessments for un-  
18 sampled ones. Accordingly, this method is of limited use to identify areas with exceptional  
19 biodiversity in regions with sparse sampling. However, predictive approaches offer an oppor-  
20 tunity to overcome such limitations, as computational methods often uncover novel ecological  
21 insights from existing data (Poisot et al. 2019), including in lesser-known locations and on larger  
22 spatial scales.

23 Species distribution models (SDMs) (Guisan and Thuiller 2005) can bring a new perspective to  
24 LCBD studies by filling in gaps in community composition data to perform analyses on broader  
25 scales. Single-species SDMs aim at predicting the distribution of a species in unsampled loca-  
26 tions based on information (such as environmental data) from sampled locations with reported  
27 occurrences. Many approaches allow going from single-species SDMs to a whole community on  
28 which to evaluate community-level metrics, yet their relevance has not been explicitly evaluated  
29 for ecological uniqueness and LCBD indices. The most straightforward approach is stacked

30 distribution models (S-SDMs) (Ferrier and Guisan 2006; Guisan and Rahbek 2011). Single-  
31 species SDMs are first performed separately, then combined to form a community prediction on  
32 which community-level analyses can be applied. S-SDMs tend to overestimate species richness  
33 (Dubuis et al. 2011; D'Amen et al. 2015; Zurell et al. 2020), which could result from threshold-  
34 ing the probabilities into presence-absence data before stacking the species distributions (Cal-  
35 abrese et al. 2014). Summing the occurrence probabilities without applying a threshold is an  
36 alternative (Calabrese et al. 2014), but it may limit some analyses as it does not return species  
37 identities for every site (Zurell et al. 2020), as is required with LCBD calculations. In com-  
38 parison, joint species distribution models (JSDMs)(Pollock et al. 2014) try to improve predic-  
39 tions by incorporating species co-occurrence or shared environmental responses into the mod-  
40 els. However, these models do not always improve community-level predictions compared to  
41 S-SDMs (Zurell et al. 2020). Spatially explicit species assemblage modelling (SESAM) (Guisan  
42 and Rahbek 2011), hierarchical modelling of species communities (HMSC) (Ovaskainen et al.  
43 2017), and Bayesian networks (BN) (Staniczenko et al. 2017) are other alternatives that could  
44 yield better community predictions than S-SDMs. On the other hand, they add methodological  
45 and computational overload, impeding their use for broad spatial extents. Moreover, their rele-  
46 vance for community prediction is often validated against extensive work on species richness.  
47 By comparison, ecological uniqueness and LCBD indices have rarely been used in predictive  
48 frameworks. Therefore, S-SDMs may prove an appropriate first step to establish some prediction  
49 baselines.

50 Combining LCBD indices with a predictive approach through SDMs will allow measuring  
51 uniqueness over broader spatial extents, across continuous landscapes, and on a higher num-  
52 ber of sites than what has previously been studied. LCBD scores have typically been used at  
53 local or regional scales with relatively few sites (up to 60 sites on extents covering 10 km to 400  
54 km, Legendre and De Cáceres 2013; da Silva and Hernández 2014; Heino et al. 2017; Heino  
55 and Grönroos 2017). Some studies did use the measure over broader, near-continental extents  
56 (Yang et al. 2015; Poisot et al. 2017; Taranu, Pinel-Alloul, and Legendre 2020), but the total  
57 number of sites in these studies were relatively small (maximum 51 sites). Recent studies also  
58 investigated LCBD and beta diversity on sites distributed in contiguous grids or as pixels, hence

59 uniform sampling intervals and no spatial gaps, but these did not cover large extents and a high  
60 number of sites (up to 1250 sites and 6 km<sup>2</sup>, Tan et al. 2017, 2019; Legendre and Condit 2019;  
61 D'Antraccoli et al. 2020). Two recent studies have, however, adopted promising predictive ap-  
62 proaches on regional extents. First, Niskanen et al. (2017) predicted LCBD values of plant  
63 communities (and three other diversity measures) on a continuous scale and a high number of  
64 sites (> 25,000) using Boosted Regression Trees (BRTs). However, they modelled the diversity  
65 measures directly after calculating them on a smaller number of sampled sites. Second, Vascon-  
66 celos, Nascimento, and Prado (2018) used ecological niche models (ENMs) to predict anurans  
67 ecological niches according to actual and forecasted environmental conditions, then calculated  
68 the LCBD values on the predictions to identify biodiversity hotspots. Using this approach, pre-  
69 dicted LCBD values are calculated in a way closer to the original formulation. This development  
70 of predictive techniques is exciting, especially as it could be pushed a step further to continental  
71 extents, a higher number of sites, and more species occurrences using SDMs and massive data  
72 sources. Still, it should be accompanied by an investigation of the determinant of ecological  
73 uniqueness in such conditions.

74 Measuring ecological uniqueness from LCBD indices over broad spatial extents and spatially  
75 continuous data also raises the question of which sites will be identified as exceptional and for  
76 what reason. The method intends that sites stand out and receive a high LCBD score whenever  
77 they display an exceptional community composition, be it a unique assemblage of species with  
78 high conservation value or a community richer or poorer than others in the region (Legendre  
79 and De Cáceres 2013). Both the original study and many of the later empirical ones have shown  
80 a negative relationship between LCBD scores and species richness (Legendre and De Cáceres  
81 2013; da Silva and Hernández 2014; Heino et al. 2017; Heino and Grönroos 2017), although  
82 other studies observed both negative and positive relationships at different sites (Kong et al.  
83 2017) or quadrats (Yao et al. 2021). Some studies showed that the direction of the relationship  
84 is related to the percentage of rare species in the community (da Silva, Hernández, and Heino  
85 2018; Yao et al. 2021). However, beta diversity and species rarity are both concepts that depend  
86 on scale. For instance, total beta diversity increases with spatial extent (Barton et al. 2013) and  
87 varies because of higher environmental heterogeneity and sampling of different local species

88 pools (Heino et al. 2015). Therefore, the LCBD-richness relationship and the effect of rare  
89 species on LCBD values should be investigated over broad spatial extents, as they might not be  
90 constant across scales.

91 Here, we examined whether species distribution models (SDMs) can be combined with local  
92 contributions to beta diversity (LCBD) to assess ecological uniqueness over broader spatial ex-  
93 tents. We also investigated the effect of scale changes on beta diversity quantification. We first  
94 predicted species distributions on continental scales using extended occurrence data from eBird  
95 and Bayesian additive regression trees (BARTs). We then quantified uniqueness with the LCBD  
96 measure for both predicted and observed data. Next, we examined the site-wise difference us-  
97 ing direct comparison, a spatial autocorrelation test, and generalized linear regression. We then  
98 investigated the relationship between uniqueness and species richness for different regions and  
99 scales and according to the proportion of rare species.

## 100 Methods

### 101 Occurrence data

102 We used occurrence data from eBird (Sullivan et al. 2009) downloaded through the eBird Basic  
103 Data set from June 2019 (eBird Basic Dataset 2019). We restricted our analyses to the New  
104 World warbler family (*Parulidae*) in North America (Canada, the United States, Mexico). eBird  
105 is a semi-structured citizen science data set, meaning that observations are reported as checklists  
106 of species detected in an observation run (Johnston et al. 2020). Observers can explicitly specify  
107 that their checklist contains all species they could detect and identify during a sampling event, in  
108 which case it is labelled as a “complete checklist.” Using complete checklists instead of regular  
109 ones allows researchers to infer non-detections in locations where detection efforts occurred,  
110 which offers performance gains in species distribution models (Johnston et al. 2020). Therefore,  
111 we selected the data from the complete checklists only. Our final data set comprised 62 warbler  
112 species and 22,974,330 observations from 9,103,750 checklists. Warblers are a diverse group  
113 with many species, are popular among birders given their charismatic aspect, and are widely  
114 distributed in various habitats across North America.

115 **Environmental data**

116 Our environmental data consisted of climatic data from WorldClim 2.1 (Fick and Hijmans 2017)  
117 and land cover data from the Copernicus Global Land Service (Buchhorn et al. 2019). We  
118 restricted these data to a spatial extent comprised between -145.0 and -50.0 degrees of longitude  
119 and between 20.0 and 75.0 degrees of latitude. First, the WorldClim data consist of spatially  
120 interpolated monthly climate data for global land areas. We used the standard BIOCLIM variables  
121 (Booth et al. 2014) from WorldClim 2.1, which represent annual trends, ranges, and extremes  
122 of temperature and precipitation, but selected only 8 out of the 19 ones to avoid redundancy  
123 (bio1, bio2, bio5, bio6, bio12, bio13, bio14, bio15). We downloaded the data at a resolution of  
124 10 arcminutes (around 18 km<sup>2</sup> at the equator), the coarsest resolution available, which should  
125 mitigate potential imprecision in the eBird data regarding the extent of the sampled areas in  
126 each observation checklist. Moreover, some studies have argued that coarser resolutions lead  
127 to less overestimation of species richness and better identification of bird biodiversity hotspots  
128 given the patchiness of observation data (Hurlbert and Jetz 2007). We acknowledge that using an  
129 arcminutes-based resolution means that the surface area of our pixels will not be equal depending  
130 on the latitude.

131 Second, the Copernicus data are a set of variables representing ten land cover classes (e.g., crops,  
132 trees, urban areas) and measured as a percentage of land cover. The data are only available at  
133 a finer resolution of 100 m. We coarsened them to the same ten arcminute resolution as the  
134 WorldClim data by averaging the pixels' cover fraction values. We removed two variables (moss  
135 and snow) from our predictive models as their cover fraction was 0% on all sites with warbler  
136 observations.

137 **Species distribution models**

138 We converted the occurrence data to a presence-absence format compatible with community  
139 analyses. We considered every pixel from our ten arcminutes environmental layers as a site and  
140 then verified, for each species, if there was a single observation in every site. Finally, we recorded  
141 the outcome as a binary value: present (1) if a species was ever recorded in a site and absent (0) if

142 it was not. Complete checklists help ensure that these zeros represent non-detections, rather than  
143 the species not being reported; hence we considered them as absence data, similar to Johnston  
144 et al. (2020), although we recognize that there exists a doubt on whether these truly represent  
145 non-detections.

146 We predicted species distribution data on continuous scales from our presence-absence data  
147 using Bayesian Additive Regression Trees (BARTs) (Chipman, George, and McCulloch 2010),  
148 a classification and regression trees method recently suggested for species distribution modelling  
149 (Carlson 2020). BARTs are based on an ensemble of trees, similarly to Boosted Regression Trees  
150 and Random Forest, but follow a sum-of-trees model and a Bayesian framework. Trees are first  
151 constrained as weak learners by priors regarding structure and nodes, then updated through an  
152 iterative Bayesian backfitting Markov Chain Monte Carlo (MCMC) algorithm which ultimately  
153 generates a posterior distribution of predicted classification probabilities (Chipman, George,  
154 and McCulloch 2010; Carlson 2020). In the context of species distribution modelling, BARTs  
155 showed high performance when compared to other predictive algorithms (Konowalik and Nosol  
156 2021; Tytar and Baidashnikov 2021). We first performed BARTs separately for all species and  
157 estimated the probability of occurrence in all the sites of our region of interest using the posterior  
158 median. We then converted the results to a binary outcome according to the threshold that  
159 maximized the True Skill Statistic (TSS) for each species, as suggested by Carlson (2020).

## 160 Quantification of ecological uniqueness

161 We used the method of Legendre and De Cáceres (2013) to quantify compositional unique-  
162 ness from overall beta diversity for both the observed and predicted data. First, we assembled  
163 the presence-absence data by site to form two site-by-species community matrices, one from  
164 observed data, called  $Y$  (39,024 sites by 62 species), and one from predicted data, called  $\hat{Y}$   
165 (99,382 sites by 62 species). Next, we measured species richness per site as the number of  
166 species present. Finally, we removed the sites without any species from the predicted matrix  
167  $\hat{Y}$ , for a new total of 85,526 sites (this was unnecessary for the observed matrix  $Y$ ). We then  
168 applied the Hellinger transformation to both matrices in order to compute beta diversity from  
169 the community composition data (Legendre and De Cáceres 2013). We measured total beta di-

170 versity as the variance of each community matrix and calculated the local contributions to beta  
171 diversity (LCBD), which quantify how much a specific site (a row in each matrix) contributes  
172 to the overall variance in the community (Legendre and De Cáceres 2013). High LCBD values  
173 indicate a unique community composition, while low values indicate a more common species  
174 set. We note that our LCBD values, which add up to 1 because the values are divided by the  
175 total sum-of-squares of the data matrix, were very low given the high number of sites in both  
176  $Y$  and  $\hat{Y}$ . However, the relative difference between the scores in one set matters more than the  
177 absolute value to differentiate their uniqueness.

## 178 Comparison of observed and predicted values

179 We performed three verification to compare the richness and uniqueness estimates obtained  
180 from our predicted distributions to those obtained with the eBird occurrence data. First, we  
181 performed a direct comparison by subtracting the richness and LCBD estimates obtained from  
182  $Y$  (the observed data) from the estimates obtained from  $\hat{Y}$  (the predicted data). To do so, we  
183 used the richness estimates as-is but modified the LCBD values to achieve a non-biased com-  
184 parison, given that the values were initially calculated on sets of different lengths. Therefore,  
185 we recomputed the LCBD scores only for the sites for which we had occurrences in both  $Y$  and  
186  $\hat{Y}$ , which mostly corresponded to the sites in  $Y$ , minus a few sites where the SDMs predicted no  
187 species occurrence. We then plotted the richness and LCBD differences to examine their spatial  
188 distributions. Second, we performed the modified  $t$  test from Clifford, Richardson, and Hemon  
189 (1989) to assess the correlation between the observed and predicted estimates and test for spatial  
190 association. We performed the test separately for the richness and the LCBD estimates. Third,  
191 we performed Generalized Linear Models between the observed and predicted estimates and  
192 plotted the deviance residuals to examine their spatial distribution. We used a negative binomial  
193 regression with a log link function for the richness estimates and a beta regression with a logit  
194 link function for the LCBD values, similar to Heino and Grönroos (2017) and Yao et al. (2021).

195 **Investigation of regional and scaling variation**

196 To investigate possible regional and scaling effects, we recalculated LCBD values on various  
197 subregions at different locations and scales. First, we selected two subregions of equivalent size  
198 (20.0 longitude degrees by 10.0 latitude degrees) with contrasting richness profiles and corre-  
199 sponding to different ecoregions to verify if the relationship between species richness and LCBD  
200 values was similar. The first subregion was in the Northeast (longitude between -80.0 and -60.0,  
201 latitude between 40.0 and 50.0), was mostly species-rich (for both the observed and predicted  
202 data), and corresponded to the Eastern Temperate Forests level I ecoregion (Commission for  
203 Environmental Cooperation 1997). The second subregion was in the Southwest (longitude be-  
204 tween -120.0 and 100.0, latitude between 30.0 and 40.0), was mostly species-poor, and covered  
205 Mediterranean California, North American Deserts, Temperate Sierras, and Southern Semi-  
206 Arid Highlands ecoregions (Commission for Environmental Cooperation 1997). Second, we  
207 recalculated the LCBD indices at three different extents, starting with a focus on the Northeast  
208 subregion and progressively extending the extent to encompass the Southwest subregion. We did  
209 these two verifications with both the observed and predicted data but only illustrate the results  
210 with the predicted data as both were qualitatively similar.

211 **Proportion of rare species**

212 We investigated the effect of the proportion of rare species in the community on the direction  
213 of the relationship between species richness and LCBD values in our Northeast and Southwest  
214 subregions. Following De Cáceres et al. (2012) and Yao et al. (2021), we classified species  
215 as rare when they occurred in less than 40% of the sites in each subregion. We calculated the  
216 proportion of rare species for every site. We then grouped the sites for both subregions depend-  
217 ing on whether they were part of an ascending or a descending portion in the LCBD-richness  
218 relationship. Given that the relationship sometimes displays a curvilinear form with a positive  
219 quadratic term (Heino and Grönroos 2017; Tan et al. 2019), we separated the ascending and  
220 descending portions based on the species richness at the site with the lowest LCBD value (us-  
221 ing the median richness if there were multiple sites). This value corresponds to the inflection  
222 point of the relationships. For example, the lowest LCBD value was 7.045e-05 in the Northeast

223 subregion and the corresponding richness was 23. All the sites with more than 23 species were  
224 assigned to the ascending portion, and all the sites with 23 species or fewer were assigned to the  
225 descending portion. In the Southwest subregion, the lowest LCBD value and its corresponding  
226 richness were 5.438e-05 and 12, respectively. We then mapped the ascending and descending  
227 groups to view their spatial distribution. We also examined the distribution of the rare species  
228 proportions in both groups using a kernel density estimation plot. Similar to our previous veri-  
229 fication, we performed this analysis with both observed and predicted data but once again only  
230 illustrate the results with the predicted data as both were qualitatively similar.

## 231 Software

232 We used *Julia v1.6.1* (Bezanson et al. 2017) for most of the project and *R v4.1.0* (R Core Team  
233 2021) for some specific steps. We used the *Julia* package `SimpleSDMLayers.jl` (Dansereau and  
234 Poisot 2021) as the basic framework for our analyses, to download the WorldClim 2.1 data, and to  
235 map our results through the package's integration of `Plots.jl`. We also used `StatsPlots.jl` to  
236 produce the kernel density estimation plots in our rare species analysis. We computed the LCBD  
237 indices with our own function implemented in *Julia*, whose results were verified by comparison  
238 to the `beta.div` function from the package `adespatial` (Dray et al. 2021) in *R*. We used the *R*  
239 packages `auk` (Strimas-Mackey, Miller, and Hochachka 2018) to extract and manipulate eBird  
240 data, `embarcadero` (Carlson 2020) to perform the BART models, `vegan` (Oksanen et al. 2019) to  
241 apply the Hellinger transformations, and `SpatialPack` (Vallejos, Osorio, and Bevilacqua 2020)  
242 to perform the modified *t* test (with the function `modified.ttest`) from Clifford, Richardson,  
243 and Hemon (1989). We used `MASS` (Venables and Ripley 2002) and `betareg` (Cribari-Neto  
244 and Zeileis 2010) to perform the negative binomial and beta regressions, respectively. We also  
245 used `GDAL` (GDAL/OGR contributors 2021) to coarsen the Copernicus land cover data. All  
246 the scripts required to reproduce the analyses are archived on Zenodo (<https://doi.org/10.5281/zenodo.6024392>).

248 **Results**

249 **Species distribution models generate relevant community predictions**

250 Species richness from observation data (Fig. 1a) was higher on the East Coast and lower on  
251 the West Coast, with many unsampled patches in the North, South, and Central West. Richness  
252 results from SDM data (Fig. 1b) displayed higher richness on the East Coast and sites with few or  
253 no species up north and in the Central West. There was no clear latitudinal gradient in richness  
254 but rather an East-West one. Landmarks such as the Rockies and croplands in the Central West  
255 (which should be species-poor habitats) were notably visible on the maps, separating the East  
256 and West. LCBD scores from observation data (Fig. 1c) were low on the East Coast and higher  
257 on the border of sampled sites in the Central West. They were also higher in the North and in  
258 the South where observations were sparser. Results from SDM predictions were qualitatively  
259 similar (Fig. 1d), with lower LCBD values in the East and more unique sites in the Central West,  
260 Central Mexico, and some Northern regions. There was no clear latitudinal gradient, and the  
261 East-West contrast, while present, was less clear than on the richness maps.

262 [Figure 1 about here.]

263 The modified *t* test of Clifford, Richardson, and Hemon (1989) showed a high correlation be-  
264 tween the observed and predicted estimates of richness and uniqueness, as well as a statistically  
265 significant spatial association between the values. For species richness, the correlation coeffi-  
266 cient was 0.777, the *F*-statistic was 20.007, and the p-value was 6.093e-04. For LCBD scores,  
267 the correlation coefficient was 0.518, the *F*-statistic was 40.083, and the p-value was 5.528e-09.

268 The difference between the observed and predicted estimates (predicted richness - observed  
269 richness and predicted LCBD - observed LCBD) showed opposite geographic distributions for  
270 species richness and ecological uniqueness (Fig. 2). Predicted richness estimates were higher  
271 than observed estimates on the East Coast, on the West Coast and in Mexico but were lower than  
272 observed estimates in the Central West (Fig. 2a). Predicted LCBD estimates, on the other hand,  
273 were lower than observed estimates on the East Coast and higher in the Central West (Fig. 2b).

274 Regression residuals showed similar geographic distributions to their corresponding difference  
275 values (Fig. 3).

276 [Figure 2 about here.]

277 [Figure 3 about here.]

## 278 **Uniqueness displays regional variation as two distinct profiles**

279 The relationship between LCBD values and species richness displayed contrasting profiles in  
280 species-rich and species-poor regions (Fig. 4). In the species-rich Northeast region , LCBD  
281 scores displayed a mostly decreasing relationship with species richness, with a slightly curvi-  
282 linear form and increase of values for very rich sites. The sites with the highest LCBD values  
283 were the species-poor sites while the species-rich sites displayed scores. The Southwest subarea  
284 showed a different relationship with a sharper initial decline and a larger increase as richness  
285 reached 20 species. The sites with the highest LCBD values were the poorest in terms of species  
286 richness, as in the Northeast region, but the species-rich sites were proportionally more unique  
287 in the Southwest region. Total beta diversity was higher in the Southwest subregion (0.417) than  
288 in the Northeast (0.179), indicating higher compositional differences between the sites.

289 [Figure 4 about here.]

## 290 **Uniqueness depends on the scale on which it is measured**

291 The LCBD-richness relationship showed important variation when scaling up and changing the  
292 region's extent (Fig. 5). For smaller extents, starting with a species-rich region, the relationship  
293 is well defined, mostly decreasing but notably curvilinear (with a lesser increase for richness  
294 values higher than the median). However, as the extent increases and progressively reaches  
295 species-poor regions, the relationship broadens, displays more variance, and loses its curvilinear  
296 aspect while keeping a decreasing form. Total beta diversity was higher when increasing the  
297 spatial extent, going from 0.121 to 0.284 and 0.687.

298 [Figure 5 about here.]

299 **Uniqueness depends on the proportion of rare species**

300 The proportion of rare species per site differed depending on the classification in the ascending or  
301 descending portions of the LCBD-richness relationship (Fig. 6). The proportion of rare species  
302 was higher in the sites corresponding to the ascending portions of the relationships (shown in 4)  
303 than in the sites corresponding to the descending portions for both subregions. The classification  
304 of the sites in the two portions showed a clear latitudinal gradient in the Northeast subregion,  
305 while it was distributed in patches in the Southwest subregion (Fig. 6).

306 [Figure 6 about here.]

307 **Discussion**

308 Our results showed a decreasing relationship between species richness and LCBD values on  
309 broad spatial extents (Fig. 5c) but also highlighted that the exact form of this relationship varies  
310 depending on the region and the spatial extent on which it is measured. Our species-rich North-  
311 east subregion (Fig. 4a) showed a decreasing relationship, very similar to previous studies, and  
312 slightly curvilinear, as described by Heino and Grönroos (2017) and Tan et al. (2019). This  
313 result for warbler species is in line with the original study on fish communities (Legendre and  
314 De Cáceres 2013) and with following ones on insect metacommunities (da Silva and Hernández  
315 2014; Heino et al. 2017; Heino and Grönroos 2017), dung beetles (da Silva, Hernández, and  
316 Heino 2018; da Silva, Bogoni, and Heino 2020), aquatic beetles (Heino and Alahuhta 2019),  
317 stream macroinvertebrates (Sor, Legendre, and Lek 2018), stream diatoms (Vilmi, Karjalainen,  
318 and Heino 2017), multi-trophic pelagic food webs (phytoplankton, zooplankton, fish) (Taranu,  
319 Pinel-Alloul, and Legendre 2020), temperate forest trees (Tan et al. 2019), mammals (da Silva,  
320 Bogoni, and Heino 2020), wetland birds (de Deus et al. 2020), and various phylogenetic groups  
321 (plants, lizards, mites, anurans, mesoinvertebrates) (Landeiro et al. 2018). However, it was  
322 originally argued that the negative relationship was not general or obligatory (Legendre and De  
323 Cáceres 2013). Different LCBD-richness relationships have also been observed, with both pos-  
324 itive and negative relationships for different sites or taxonomic groups in some studies (Kong et

325 al. 2017; Teittinen et al. 2017), as well as a negative relationship with the number of common  
326 species but a positive relationship with the number of rare species (Qiao et al. 2015).

327 Our results further show that the relationship may depend on the region's richness profile, as  
328 the relationship was different in our species-poor Southwest subregion, with a sharper initial  
329 decrease (Fig. 4b). Therefore, the curvilinear form may depend on how pronounced the contrast  
330 is between the region's median richness and its richest ecologically feasible sites. The increasing  
331 part of the curvilinear form for higher richness values was also more pronounced in our results  
332 (Fig. 4a,b; Fig. 5c) than in previous studies (e.g., Tan et al. 2019), which reinforces the idea that  
333 the relationship and its curvilinear form may vary depending on the region.

334 The variation in the LCBD-richness relationship when extending the study extent showed that  
335 the uniqueness patterns highlighted are not necessarily the same depending on the scale on which  
336 it is used (Fig. 5). The relationship progressively lost its clear definition and curvilinear form  
337 as the East and West profiles merged, creating a new distinct profile with more variation and  
338 no curvilinear form. Therefore, aggregating too many different sites might possibly mask some  
339 patterns of uniqueness in species-rich sites. Total beta diversity, on the other hand, showed the  
340 variation expected from previous studies, increasing with spatial extent (Fig. 5) (Barton et al.  
341 2013; Heino et al. 2015). Its value was high at the continental scale (0.687) but lower than what  
342 has been observed in some studies (e.g., 0.80 on macroinvertebrate communities in the Lower  
343 Mekong Basin by Sor, Legendre, and Lek 2018).

344 Our results confirm that the proportion of rare species in the community may affect the direc-  
345 tion of the relationship between species richness and ecological uniqueness (Fig. 6). da Silva,  
346 Hernández, and Heino (2018) suggested that the proportion of rare and common species in the  
347 communities determines whether the relationship will be negative, non-significant, or positive.  
348 Yao et al. (2021) showed an association between the direction of the relationship and the pro-  
349 portion of rare species, with sites with a lower proportion (between 60% and 75% in their case)  
350 displaying a negative relationship and sites with a higher proportion (around 85%) showing a  
351 positive one. Our results further show that sites associated with a positive relationship within a  
352 curvilinear one tended to have a higher rare species proportion (Fig. 6). This also implies that  
353 the proportion of rare species was higher in species-rich sites than in species-poor ones in both

354 our Northeast and Southwest subregions. Further work should attempt to disentangle the effects  
355 of the rare species proportion and the region's richness profile.

356 Our results showed that SDM models provide richness and uniqueness predictions highly cor-  
357 related to the occurrence data while filling gaps in poorly sampled regions (Fig. 1). The results  
358 showed a statistically significant spatial association between predicted and observed estimates  
359 despite correcting for autocorrelation using the modified *t*-test from Clifford, Richardson, and  
360 Hemon (1989). A positive autocorrelation on large distances indicates aggregates or structures  
361 repeating through space (Legendre and Fortin 1989). This is consistent with our results, as the  
362 distribution of richness and uniqueness values was visibly spatially structured in both our ob-  
363 served and predicted data (Fig. 1). Nonetheless, it is possible that the autocorrelation in the  
364 predicted values could represent an artifact of the predictive models (capturing the spatial struc-  
365 ture from the environmental variables, for example), and might not represent the true autocor-  
366 relation expected for the uniqueness estimates. Further work could verify this by quantitatively  
367 comparing the autocorrelation and spatial structures in the observed and predicted uniqueness  
368 estimates.

369 Predicted values also tended to underestimate uniqueness in species-rich regions and overesti-  
370 mate it in species-poor ones, with the opposite trend for species richness (Figs. 2, 3). Overpre-  
371 diction of richness using S-SDMs was reported previously (Dubuis et al. 2011; D'Amen et al.  
372 2015; Zurell et al. 2020). No comparable baseline exists for predictions of LCBD values, as  
373 our study is the first to compare LCBD estimates from observed and predicted data in such a  
374 way. However, some studies showed that LCBD distributions were spatially structured across  
375 sampling sites (da Silva, Hernández, and Heino 2018). On the other hand, the spatial structure  
376 in our results did not exactly concord with the one reported by Heino and Alahuhta (2019), who  
377 showed a negative relationship between LCBD values and latitude for diving beetles commu-  
378 nities in Northern Europe. In comparison, our LCBD scores increased both in the North and  
379 South (Fig. 1), hence did not strictly increase with latitude, and also showed a clear East-West  
380 gradient. Overall, our distribution results (Figs. 1, 2, 3) also have implications for conservation,  
381 as they confirm that species richness and ecological uniqueness measured from LCBD values  
382 may conflict and highlight different potential hotspots (Dubois, Proulx, and Pellerin 2020; Yao

383 et al. 2021), thus reinstating the need to protect both with complementary strategies.

384 Our predictions for regions with sparse sampling are of interest as they allow a quantitative  
385 evaluation, however imperfect, for sites where we would otherwise have no information. Our  
386 SDMs also offered relevant LCBD predictions using eBird, arguably one of the largest presence-  
387 absence data sets available (when using its complete checklist system), showing the measure's  
388 potential on such massive data. Together, the potential to generate uniqueness predictions in  
389 new locations and through massive data opens new opportunities for LCBD analyses on ex-  
390 tended spatial scales and on a broader diversity of taxons. An interesting way forward would  
391 be to test these results using more advanced community assembling techniques than S-SDMs.  
392 The use of SESAM (Guisan and Rahbek 2011) with probabilistic SDMs, probability ranking,  
393 and species richness predictions as macroecological constraints returns high site-level prediction  
394 accuracy (Zurell et al. 2020) and would be compatible with presence-absence LCBD calcula-  
395 tions. The use of probabilistic stacks rather than binary ones (Calabrese et al. 2014) could also  
396 constitute a novel way to calculate LCBD indices. Both these procedures should reduce the  
397 richness deviation we observed, and it would be interesting to verify if this can also be the case  
398 with LCBD values. An ensemble of SDM algorithms could also be used to capture a broader  
399 range of possible outcomes for the LCBD predictions. However, given the high performance  
400 of BARTs in model comparisons (Konowalik and Nosol 2021; Tytar and Baidashnikov 2021)  
401 and the large extent we covered, we do not believe the changes to the LCBD gradients would be  
402 strong enough to affect our results in a meaningful way.

403 This study showed how ecological uniqueness can be measured over broad spatial extents, in-  
404 cluding for regions with sparse sampling, and how scale changes may affect beta diversity quan-  
405 tification. It is the first study to assess the relevance of local contributions to beta diversity  
406 calculated on the output of species distribution models. It is also the first to compare the re-  
407 lationship between LCBD values and species richness for different regions and spatial extents.  
408 First, our results showed that the negative relationship often observed between species richness  
409 and LCBD scores can take different forms depending on the richness profile of the regions on  
410 which it is measured. Therefore, species-rich and species-poor regions may display different  
411 ways to be unique. Second, the negative relationship was not constant when varying the spatial

412 study extent and may be less clearly defined at broad scales when contrasting regional relation-  
413 ships are present. The broad-scale uniqueness profile might then be completely distinct from  
414 the regional profiles constituting it. Finally, species distribution models offer a promising way  
415 to generate uniqueness predictions on broad spatial extents and could prove useful to identify  
416 beta diversity hotspots in unsampled locations on large spatial scales, which could be important  
417 targets for conservation purposes.

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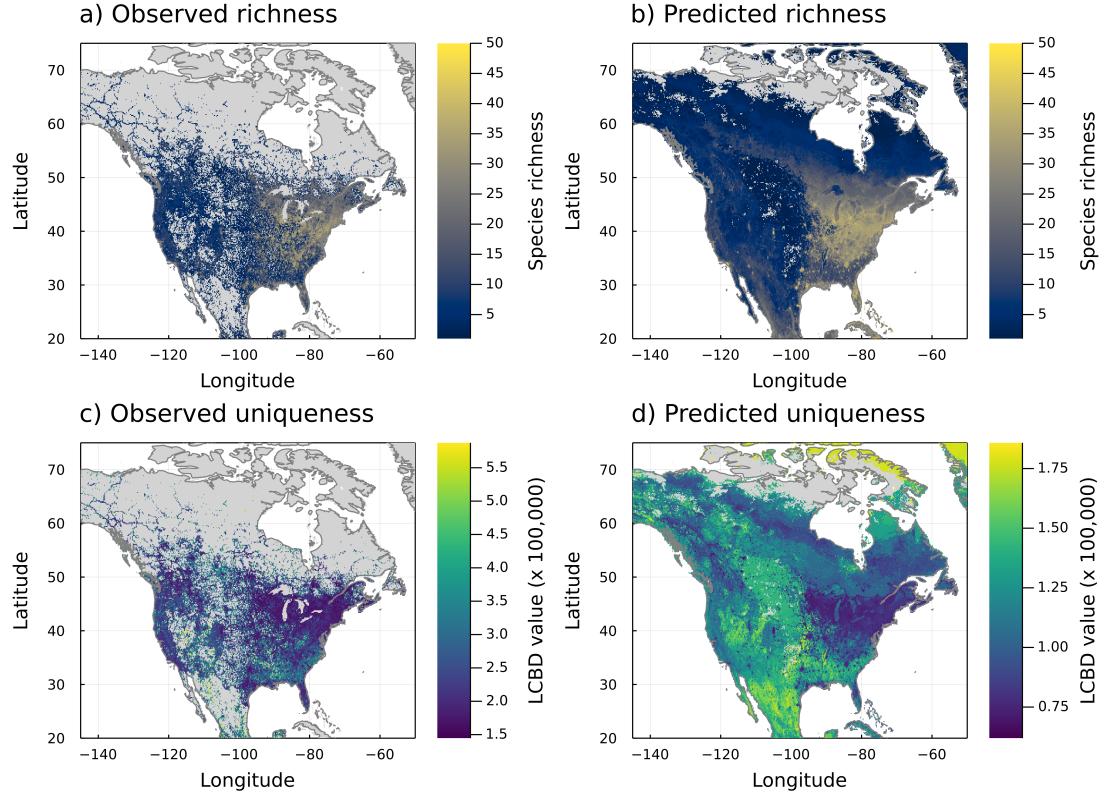


Figure 1: Comparison of species richness and LCBD scores from observed and predicted warbler occurrences in North America. Values were calculated for sites representing ten arcminute pixels. We measured species richness after converting the occurrence data from eBird (a) and the SDM predictions from our single-species BART models (b) to a presence-absence format per species. We applied the Hellinger transformation to the presence-absence data, then calculated the LCBD values from the variance of the community matrices separately for the occurrence data (c) and the SDM predictions (d). Areas in light grey (not on the colour scale) represent mainland sites with environmental data but without any warbler species present.

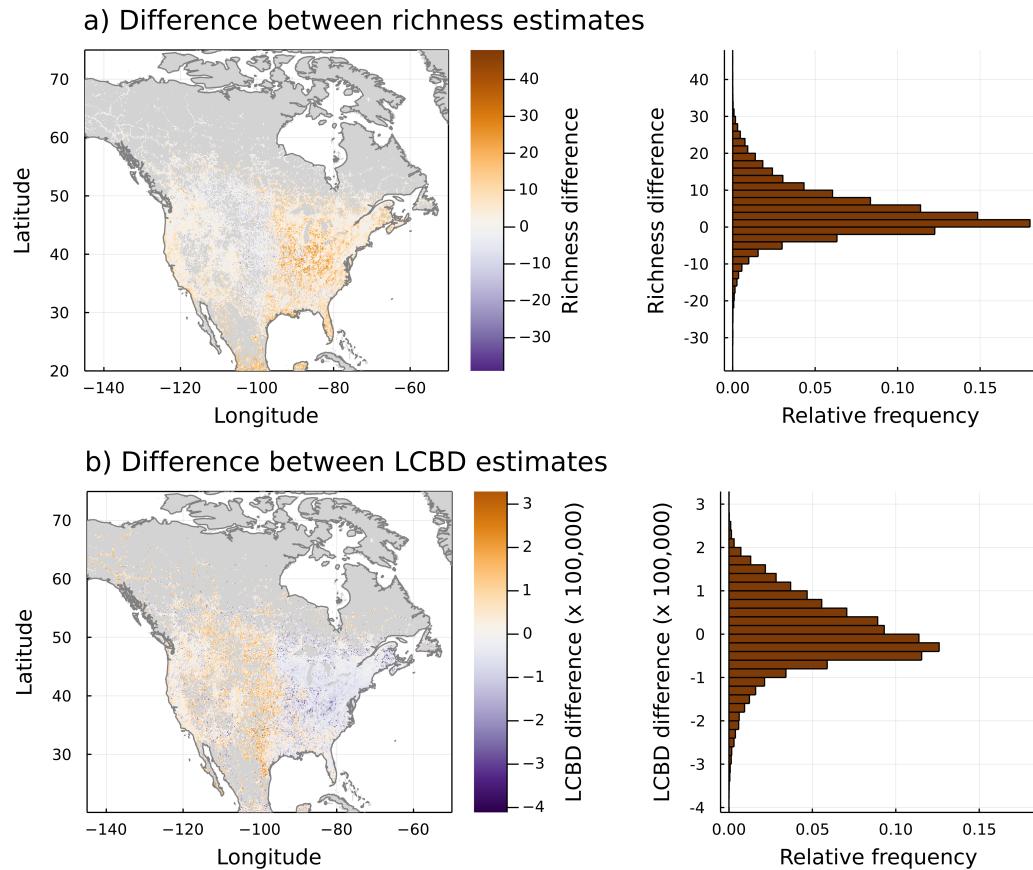


Figure 2: Comparison between observed and predicted estimates of species richness (a) and ecological uniqueness (b). The difference values represent the estimate from the predicted data set minus the estimate from the observed data set. LCBD values were recalculated for the same set of sites with observations in both data sets.

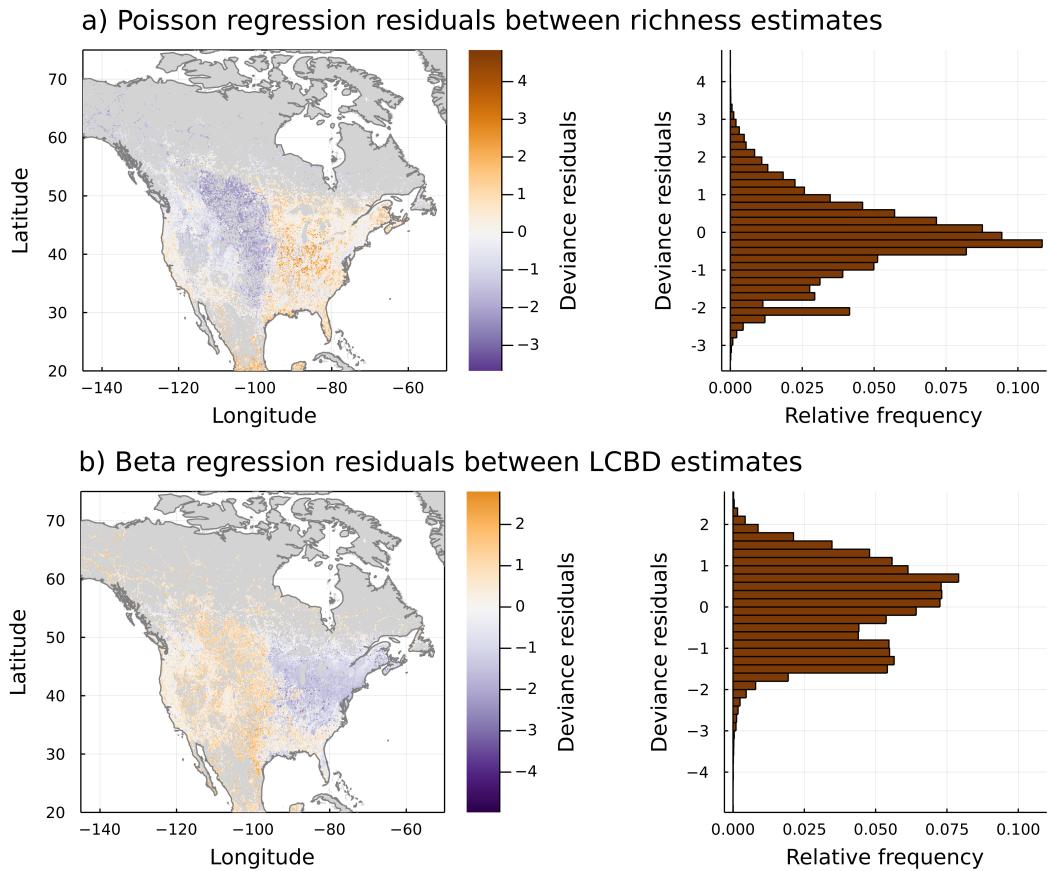


Figure 3: Comparison of the regression residuals between the observed and predicted estimates of species richness (a) and ecological uniqueness (b). The estimate from the predicted data set was used as the dependent variable and the estimate from the observed data set as the independent variable. A negative binomial regression with a log link function was used for species richness, and a beta regression with a logit link function was used for uniqueness. LCBD values were recalculated for the same set of sites with observations in both data sets.

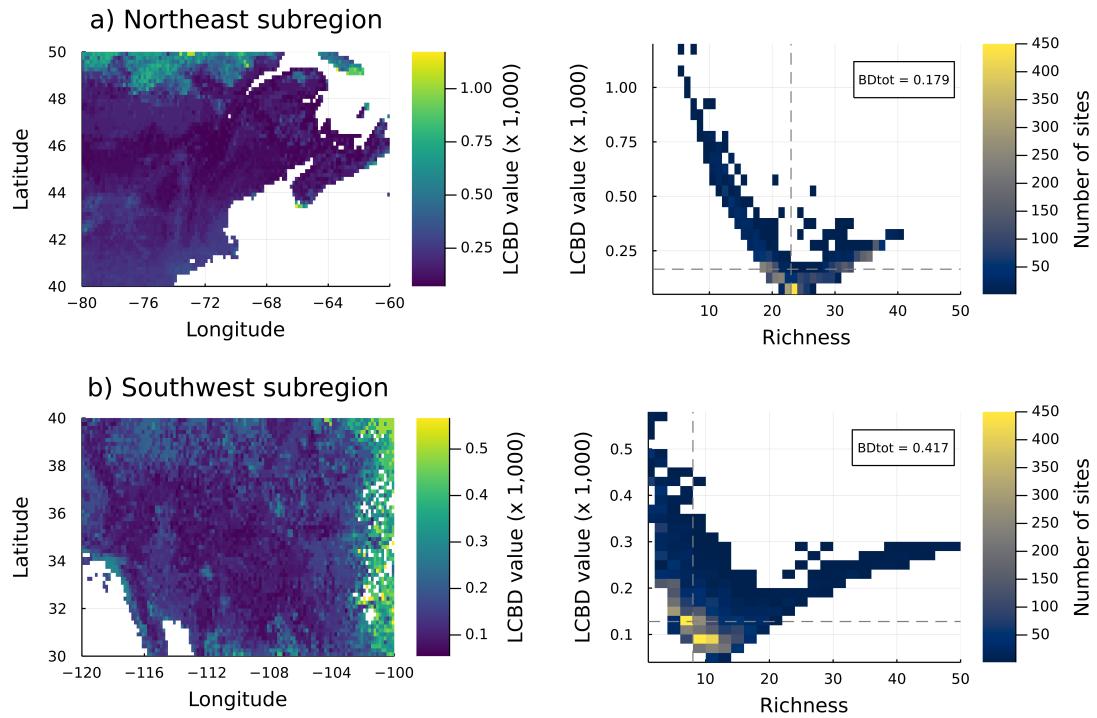


Figure 4: Comparison between a species-rich region (Northeast, a) and a species-poor one (Southwest, b) based on the SDM predictions for warbler species in North America. The left-side figures represent the LCBD scores for the assembled presence-absence predictions, calculated separately in each region. The colour scales are set to the respective range of LCBD scores to highlight the relative change within each region rather than compare the scores between both regions. The right-side 2-dimensional histograms represent the decreasing and slightly curvilinear relationship between LCBD values and species richness. The vertical and horizontal dashed lines respectively represent the median richness and LCBD value in each region, while BDtot represents the total beta diversity.

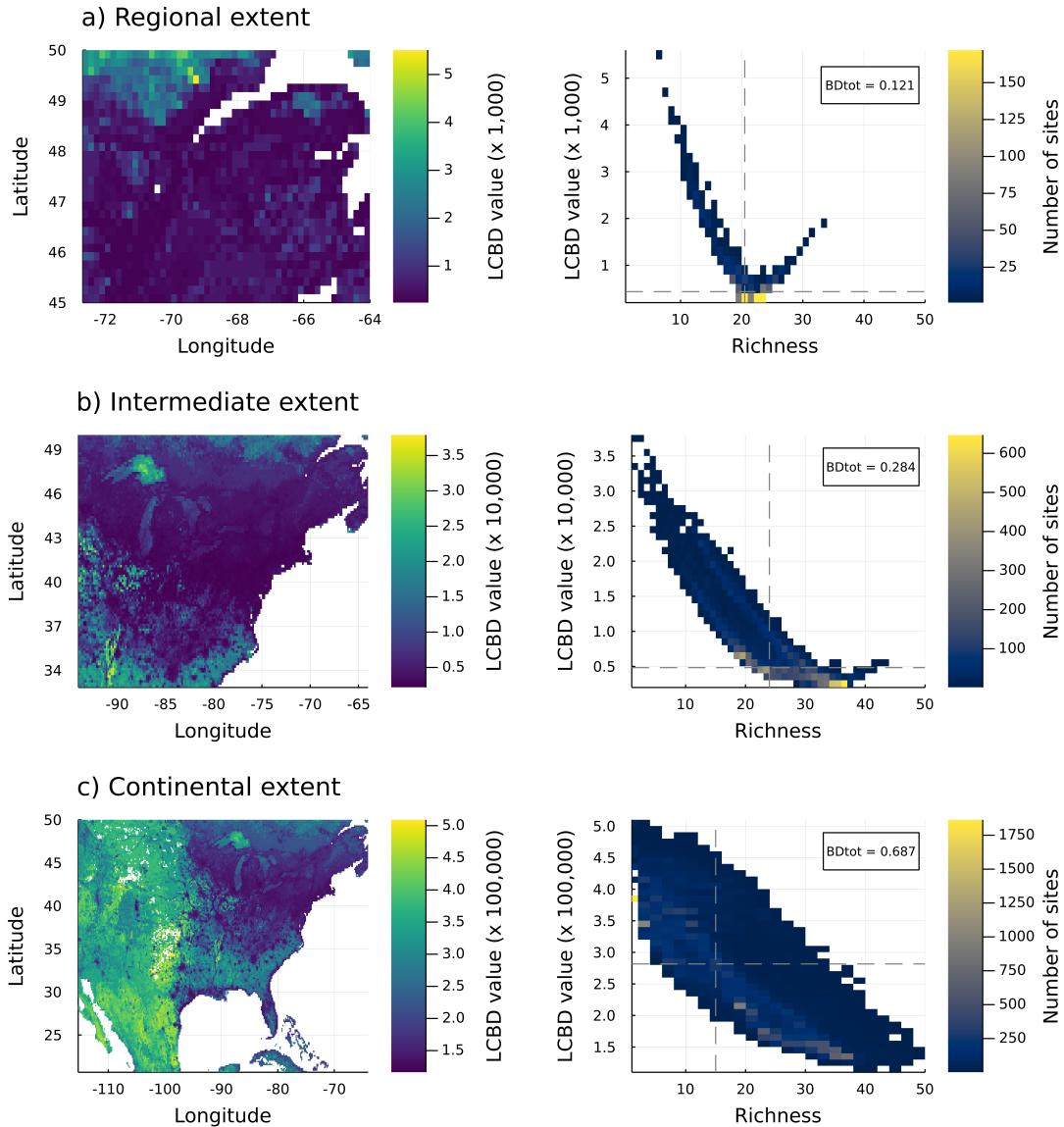


Figure 5: Effect of extent size on the relationship between site richness and LCBD values based on the SDM predictions for warbler species in North America. The relationship progressively broadens and displays more variance when scaling up while total beta diversity increases. The LCBD values were recalculated at each scale based on the sites in this region. The vertical and horizontal dashed lines respectively represent the median richness and LCBD value in each region, while BDtot represents the total beta diversity.

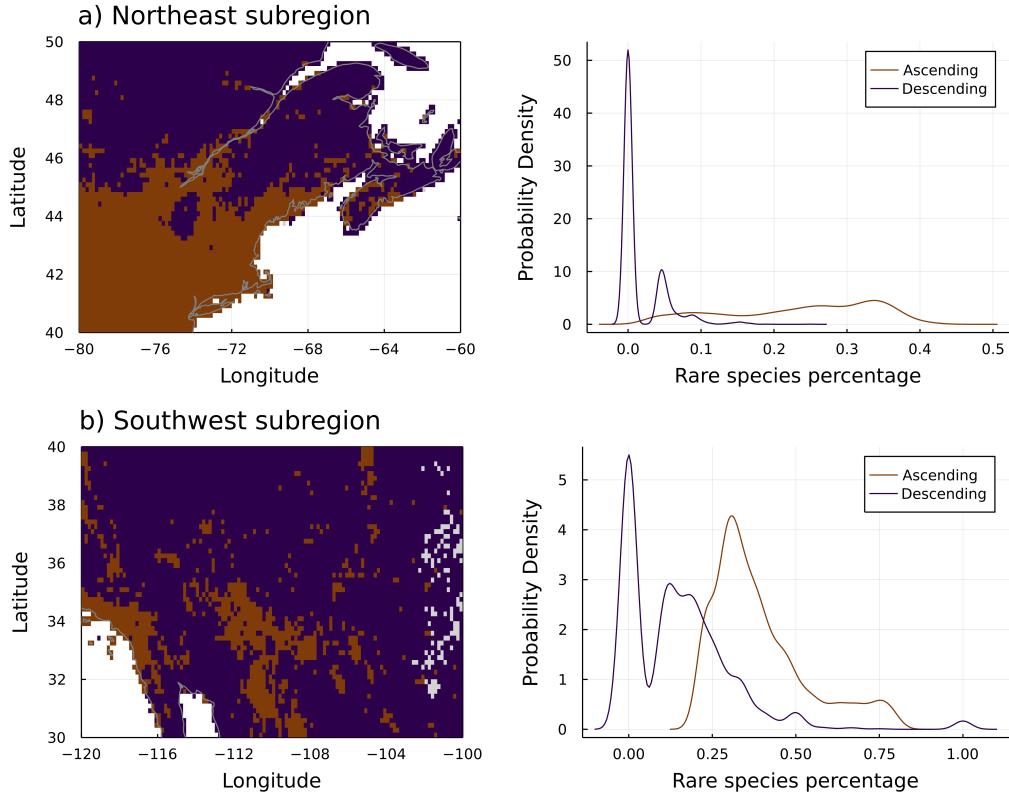


Figure 6: Proportion of rare species in the ascending and descending portions of the LCBD-richness relationship for the Northeast (a) and Southwest (b) subregions. The left side figures show the geographic distribution of the sites from each group. Sites were assigned to the ascending portion if their species richness was higher than the richness of the site with the lowest LCBD value, which corresponds to the inflection point of the right side figures of Fig. 4, and in the descending portion otherwise. The right side figures represent the kernel density estimation of the proportion of rare species in each group. Values on the y-axis are probability densities scaled so that the area under the curve equals one. Similarly, the area under the curve for a given range of values on the x-axis (proportions of rare species) represents the probability of observing a value in that range. Species were classified as rare when they occurred in fewer than 40% of the sites in the subregion. The proportion of rare species was then calculated for every site.