Evaluating ecological uniqueness over broad spatial extents using species distribution modelling

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Abstract: Aim: 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 investigate how LCBD indices can be used to predict ecological uniqueness over broad spatial extents using species distribution modelling and citizen science data.

Location: North America.

Time period: 2000s.

Major taxa studied: Parulidae.

Methods: 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 examined the site-wise difference using direct comparison, a spatial autocorrelation test, and generalized linear regression. We also investigated the relationship between LCBD values and species richness in different regions and at various spatial extents and the effect of the proportion of rare species on the relationship.

Results: Our results showed that the relationship between richness and LCBD values varies according to the region and the spatial extent at which it is applied. It is also affected by the proportion of rare species in the community. Species distribution models provided highly correlated estimates with observed data, although spatially autocorrelated.

Main conclusions: Sites identified as unique over broad spatial extents may vary according to the regional richness, total extent size, and the proportion of rare species. 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.

Keywords:
beta diversity
ecological uniqueness
local contributions to beta diversity
species distribution modelling
broad spatial scale
eBird

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Introduction

Beta diversity, defined as the variation in species composition among sites in a geographic region of interest (Legendre, Borcard, and Peres-Neto 2005), is an essential measure to describe the organization of biodiversity through space. Total beta diversity within a community can be partitioned into local contributions to beta diversity (LCBD) (Legendre and De Cáceres 2013), which allows the identification of sites with exceptional species composition, hence unique biodiversity. Such a method, focusing on specific sites, is useful for both community ecology and conservation biology, as it highlights areas that are most important for their research or conservation values. For example, sites with unique community composition often differ from those with high species richness, possibly as they harbour rare species or help maintain beta diversity (da Silva, Hernández, and Heino 2018; Heino et al. 2017; Landeiro et al. 2018). Hence, focusing on unique community composition may prove useful as a complementary approach to species richness (Heino and Grönroos 2017; da Silva, Hernández, and Heino 2018; Yao et al. 2021; Dubois, Proulx, and Pellerin 2020). However, the use of LCBD indices is currently limited in two ways. First, LBCD indices are typically used on data collected over local or regional scales with relatively few sites, for example on fish communities at intervals along a river or stream (Legendre and De Cáceres 2013). Second, LCBD calculation methods require complete information on community composition, such as a community composition matrix Y; thus, they are inappropriate for partially sampled sites (e.g., where data for some species is missing or uncertain) and cannot directly provide assessments for unsampled ones. Accordingly, the method is of limited use to identify areas with exceptional biodiversity in regions with sparse sampling. However, predictive approaches are increasingly common given the recent development of computational methods, which often uncover novel ecological insights from existing data (Poisot et al. 2019), including in unsampled or lesser-known locations, as well as larger spatial scales. Thus, biodiversity modelling can fill in knowledge gaps and needs to be better integrated with conservation decisions (Pollock et al. 2020).

Species distribution models (SDMs) (Guisan and Thuiller 2005) can bring a new perspective to LCBD studies by filling in gaps and performing analyses on much broader scales. In a community matrix Y, such as required for LCBD calculation, ecological communities are abstracted as assemblages of species present at different sites. Viewing communities as such opens the perspective of predicting community composition from predictions of individual species, which is the aim of SDMs, thus allowing calculating LCBD values. At their core, SDMs aim at predicting the distribution of a species based on information about where the species was previously reported, matched with environmental data at those locations, and then make predictions at other (unsampled) locations based on their respective environmental conditions. Community-level modelling from SDMs is not an especially novel idea (Ferrier et al. 2002; Ferrier and Guisan 2006), but it is increasingly relevant with the advent of large-scale, massive, and open data sources on species occurrences, often contributed by citizens, such as GBIF and eBird (Sullivan et al. 2009).

Many approaches allow going from single-species SDMs to a whole community, although these have not been explicitly evaluated for ecological uniqueness and LCBD indices. The simplest approach is stacked distribution models (S-SDMs) (Ferrier and Guisan 2006; Guisan and Rahbek 2011). Single species SDMs are first performed separately, then combined to form a community prediction on which community-level analyses can be applied. On the other hand, joint species distribution models (JSDMs) (Pollock et al. 2014) try to improve species distribution predictions by incorporating species co-occurrence into the models. However, these models do not always improve community-level predictions compared to S-SDMs (Norberg et al. 2019; Zurell et al. 2020). S-SDMs also tend to overestimate species richness (Dubuis et al. 2011; D'Amen et al. 2015; Zurell et al. 2020), which could result from thresholding the probabilities into presence-absence data before stacking the species distributions (Calabrese et al. 2014). Summing the occurrence probabilities without applying a threshold is, therefore, another alternative (Calabrese et al. 2014). However, this may limit some analyses as it does not return species identities for every site (Zurell et al. 2020), as is required with LCBD calculations. Spatially explicit species assemblage modelling (SESAM) (Guisan and Rahbek 2011), hierarchical modelling of species communities (HMSC) (Ovaskainen et al. 2017), and Bayesian networks (BN) (Staniczenko et al. 2017) are other alternatives that could yield better community predictions than S-SDMs. However, they add methodological and computational overload, impeding their use for broad spatial extents, and are often validated against extensive work on species richness. By comparison, ecological uniqueness and LCBD indices have rarely been used in predictive frameworks. Therefore, S-SDMs may prove an appropriate first step to establish some baselines, especially given that calculating LCBD values on SDM predictions will raise some important issues, such as calculating the uniqueness scores on much bigger community matrices and broader scales than what is typically done.

The total number of sites will increase (1) because of the spatially continuous nature of the predictions, as there will be more sites in the region of interest than the number of sampled sites, and (2) because of the larger spatial extent allowed for the SDM predictions. A high number of SDM-predicted sites with a large extent opens up the possibility of capturing a lot of variability of habitats and community composition, but also many very similar ones. This could change the way that exceptional sites contribute to the overall variance in the large-scale community. LCBD scores have typically been used at local or regional scales with relatively few sites (Legendre and De Cáceres 2013; da Silva and Hernández 2014; Heino et al. 2017; Heino and Grönroos 2017). Some studies did use the measure over broader, near-continental extents (Yang et al. 2015; Poisot et al. 2017; Taranu, Pinel-Alloul, and Legendre 2020), but the total number of sites in these studies was relatively small. Recent studies also investigated LCBD and beta diversity on sites distributed in contiguous grids or as pixels, hence uniform sampling intervals and no spatial gaps, but these did not cover large extents and a high number of sites (Tan et al. 2017, 2019; Legendre and Condit 2019; D'Antraccoli et al. 2020). Two recent studies have, however, adopted promising predictive approaches on regional extents. First, Niskanen et al. (2017) predicted LCBD values of plant communities (and three other diversity measures) on a continuous scale and a high number of sites (> 25,000) using Boosted Regression Trees (BRTs). However, they modelled the diversity measures directly after calculating them on a smaller number of sampled sites. They obtained lower predictive accuracy for LCBD than for the other diversity measures, highlighting the challenge to predict the measure. Second, Vasconcelos, Nascimento, and Prado (2018) used ecological niche models (ENMs) to predict anurans ecological niches according to actual and forecasted environmental conditions, then calculated the LCBD values on the predictions to identify biodiversity hotspots. Using this approach, predicted LCBD values are calculated in a closer way to the original formulation based on community composition. This development of predictive approaches is exciting, especially as it could be pushed a step further to continental extents, a higher number of sites, and more species occurrences using SDMs and massive data sources. Still, it should be accompanied by an investigation of the determinant of ecological uniqueness in such conditions.

Measuring ecological uniqueness from LCBD indices over broad spatial extents and spatially continuous data also raises the question of which sites will be identified as exceptional and for what reason. The method intends that sites should stand out and receive a high LCBD score whenever they display an exceptional community composition, be it a unique assemblage of species that may have a high conservation value or a richer or poorer community than most in the region (Legendre and De Cáceres 2013). Both the original study and many of the later empirical ones have shown a negative relationship between LCBD scores and species richness (Legendre and De Cáceres 2013; da Silva and Hernández 2014; Heino et al. 2017; Heino and Grönroos 2017), although other studies observed both negative and positive relationships at different sites (Kong et al. 2017) or quadrats (Yao et al. 2021). Some studies showed that the direction of the relationship is related to the percentage of rare species in the community (da Silva, Hernández, and Heino 2018; Yao et al. 2021). The LCBD-richness relationship and the effect of the proportion of rare species should therefore be investigated over broad spatial extents, as beta diversity and species rarity are both concepts that depend on scale. For instance, total beta diversity increases with spatial extent (Barton et al. 2013) and is strongly dependent on scale, notably because of higher environmental heterogeneity and sampling of different local species pool (Heino et al. 2015), which could potentially add some variation to the relationship.

Here, we examine whether the LCBD method can assess ecological uniqueness over broad spatial extents based on predictions of species distributions and evaluate whether this reveals novel ecological insights regarding the identification of exceptional biodiversity areas. We first predicted species distributions on continental scales using extended occurrence data from eBird and Bayesian additive regression trees (BARTs). We then quantified uniqueness with the local contributions to beta diversity measure for both predicted and observed data. Next, we examined the site-wise difference using direct comparison, a spatial autocorrelation test, and generalized linear regression. We then investigated the relationship between uniqueness and species richness for different regions and scales and according to the proportion of rare species.

2

Methods

2.1. Occurrence data We used occurrence data from eBird (Sullivan et al. 2009) downloaded through the eBird Basic Data set from June 2019 (eBird Basic Dataset 2019). We restricted our analyses to the New World warbler family (*Parulidae*) in North America (Canada, United States, Mexico) using the *R* package `auk` (Strimas-Mackey, Miller, and Hochachka 2018) to extract and process bird sightings records from the eBird database. eBird is a semi-structured citizen science data set, meaning that observations are reported as checklists of species detected in an observation run (Johnston et al. 2020). Observers can explicitly specify that their checklist contains all species they could detect and identify during a sampling event, in which case it is labelled as a “complete checklist.” Using complete checklists instead of regular checklists allows researchers to infer non-detections in locations where detection efforts did occur, which offers performance gains in species distribution models (Johnston et al. 2020). Therefore, we selected the data from the complete checklists only. Our final data set comprised 62 warbler species and nearly 23 million observations from 9 million checklists. Warblers are a diverse group with many species, are popular among birders given their charismatic aspect, are distributed in diverse areas and present relatively everywhere in North America.

2.2. Environmental data Our environmental data consisted of climatic data from the WorldClim 2.1 database (Fick and Hijmans 2017) and land cover data from the Copernicus Global Land Service (Buchhorn et al. 2019). We restricted these data to a spatial extent comprised between -145.0 and -50.0 degrees of longitude and between 20.0 and 75.0 degrees of latitude (Fig. 1). First, the WorldClim data consists of spatially interpolated monthly climate data for global land areas. We used the standard *bioClim* variables from WorldClim 2.1, which represent annual trends, ranges, and extremes of temperature and precipitation, but selected only 8 out of the 19 ones to avoid redundancy (bio1, bio2, bio5, bio6, bio12, bio13, bio14, bio15). We downloaded the data at a resolution of 10 arcminutes (around 18 km² at the equator), the coarsest resolution available, using the *Julia* package `SimpleSDMLayers.jl` (Dansereau and Poisot 2021). The coarse resolution should mitigate potential imprecision in the eBird data regarding the extent of the sampled areas in each observation checklist. Moreover, some studies have argued that coarser resolutions lead to less overestimation of species richness and better identification of bird biodiversity hotspots given the patchiness of observation data (Hurlbert and Jetz 2007). We acknowledge that using an arcminutes-based resolution means that the surface area of our pixels will not be equal depending on the latitude. Second, the Copernicus data is a set of variables representing ten land cover classes (e.g., crops, trees, urban areas) and measured as a percentage of land cover. The data is only available at a finer resolution of 100 m, which we downloaded directly from the website. We coarsened it to the same ten arcminute resolution as the WorldClim data by averaging the pixels' cover fraction values with `GDAL` (GDAL/OGR contributors 2021). We first selected the ten land cover variables but later removed two (moss and snow) from our predictive models. Their cover fraction was 0% on all sites with warbler observations; hence they did not provide any predictive value to our SDM models.

2.3. Species distribution models We converted the occurrence data to a presence-absence format compatible with community analyses. We considered every pixel from our ten arcminutes environmental layers as a site. We then verified, for each species, if there was a single observation in every site. Finally, we recorded the outcome as a binary value: present (1) if a species was ever recorded in a site and absent (0) if it was not. Complete checklists help ensure that these zeros represent non-detections, rather than the species not being reported; hence we considered them as absence data, similar to Johnston et al. (2020), although we recognize that there subsists a doubt about this.

We predicted species distribution data on continuous scales from our presence-absence data using Bayesian Additive Regression Trees (BARTs) (Chipman, George, and McCulloch 2010), a classification and regression trees method recently suggested for species distribution modelling (Carlson 2020). BARTs are sum-of-trees models, conceptually similar to Boosted Regression Trees and Random Forest, but following a Bayesian paradigm: trees are constrained as weak learners by priors regarding structure and nodes (Chipman, George, and McCulloch 2010; Carlson 2020). Then, fitting and inference is made through an iterative Bayesian backfitting MCMC algorithm generating a posterior distribution of predicted classification probabilities (Chipman, George, and McCulloch 2010; Carlson 2020). We used the package `embarcadero` (Carlson 2020) in *R* to compute the BART models. First, we performed BARTs separately for all species and estimated the probability of occurrence for all the sites in the pseudo-rectangular spatial units of 10 arcminutes in the region of interest. We then converted the results to a binary outcome according to the threshold that maximized the True Skill Statistic (TSS) for each species, as suggested by Carlson (2020).

2.4. Quantification of ecological uniqueness We used the method of Legendre and De Cáceres (2013) to quantify compositional uniqueness from overall beta diversity for both the observed and predicted data. First, we assembled the presence-absence data by site to form two site-by-species community matrices, one from observed data, called Y (39,091 sites by 62 species), and one from predicted data, called $\hat{Y}$ (99,609 sites by 62 species). Next, we measured species richness per site as the sum of the presences in each row, i.e., the number of species present. Finally, we removed the sites without any species from the predicted community matrix $\hat{Y}$, for a new total of 92,117 sites (this was not necessary for the observed community matrix Y, as it was, by design, only composed of sites with at least one species present). We applied the Hellinger transformation to both matrices, as recommended by Legendre and De Cáceres (2013) for presence-absence data. We then measured total beta diversity as the variance of the community matrices and calculated the local contributions to beta diversity (LCBD), which quantify how much a specific site (a row in each matrix) contributes to the overall variance in the community (Legendre and De Cáceres 2013). High LCBD values indicate a unique community composition, while low values indicate a more common species set. Measuring beta diversity as the variance of the community matrices offers a critical advantage in computations in this case, as alternative approaches based on sites' pairwise dissimilarity would require a much higher number of calculations given the high number of sites in our study. We note that our LCBD values, which add up to 1 because the raw LCBD values are divided by the total sum-of-squares of the data matrix, were very low given the high number of sites in both Y and $\hat{Y}$. However, the relative difference between the scores in one set matters more than the absolute value to differentiate their uniqueness.

2.5. Comparison of observed and predicted values We performed three verification to compare the species richness and uniqueness estimates obtained from our predicted species distributions to those obtained with the occurrence data from eBird. First, we performed a direct comparison by subtracting the richness and LCBD estimates obtained from Y (the observed data) from the estimates obtained from $\hat{Y}$ (the predicted data). To do so, we used the richness estimates as-is but modified the LCBD values to achieve a non-biased comparison, given that the original values are calculated for the same sites but on sets of different lengths. Therefore, we recomputed the LCBD scores only for the sites for which we had occurrences in both Y and $\hat{Y}$, which mostly corresponded to the sites in Y, minus a few sites where the SDMs predict no species occurrence. We then plotted the richness and LCBD differences to examine their spatial distributions. Second, we performed the modified t test from Clifford, Richardson, and Hemon (1989) to assess the correlation between the observed and predicted estimates and test for spatial autocorrelation. We performed the test separately for the richness and the LCBD estimates. We used the `modified.ttest` function from the package `SpatialPack` (Vallejos, Osorio, and Bevilacqua 2020) in *R*. Third, we performed Generalized Linear Models between the observed and predicted estimates and plotted the deviance residuals to examine their spatial distribution. We used a negative binomial regression with a log link function using the package `MASS` (Venables and Ripley 2002) in *R* for the richness estimates as our values shown overdispersion (Fletcher and Fortin 2018). We used a beta regression with a logit link function using the package `betareg` (Cribari-Neto and Zeileis 2010) for the LCBD values as they vary between 0 and 1, similar to Heino and Grönroos (2017) and Yao et al. (2021).

2.6. Investigation of regional and scaling variation We recalculated LCBD values on various subregions at different locations and scales to investigate possible regional and scaling effects. First, we selected two subregions of equivalent sizes (20.0 longitude degrees by 10.0 latitude degrees) with contrasting richness profiles to verify if the relationship between species richness and LCBD values was similar. We selected a Northeast subregion (longitude between -80.0 and -60.0, latitude between 40.0 and 50.0), mostly species-rich, and a Southwest subregion (longitude between -120.0 and 100.0, latitude between 30.0 and 40.0), mostly species-poor (for both the observed and predicted data). Fig. 4 shows the coordinates and spatial extents of both subregions. Second, we recalculated the LCBD indices at three different extents, starting with a focus on the Northeast subregion and progressively extending the extent to encompass the Southwest subregion (Fig. 5). These are conceptually similar to the spatial windows of Barton et al. (2013), which allow one to study the variation of beta diversity according to spatial extent. We did these two verifications with both the observed and predicted data but only illustrate the results with the predicted data as both were qualitatively similar.

2.7. Proportion of rare species We investigated the effect of the proportion of rare species in the community on the direction of the relationship between species richness and LCBD values in our Northeast and Southwest subregions. Following De Cáceres et al. (2012) and Yao et al. (2021), we classified species as rare when they occurred in less than 40% of the sites in each subregion. We calculated the proportion of rare species for every site. We then grouped the sites for both subregions depending on whether they were part of an ascending or a descending portion in the LCBD-richness relationship. Given that the relationship sometimes displays a curvilinear form with a positive quadratic term (Heino and Grönroos 2017; Tan et al. 2019), we separated the ascending and descending portions based on the species richness at the site with the lowest LCBD value (we used the median richness if there were multiple sites with the lowest LCBD value), which corresponds to the inflection point of the relationships shown on Fig. 4. For example, the lowest LCBD value was 7.032e-5 in the Northeast subregion and the median richness (as there were multiple sites with this LCBD value) was 23. All the sites with more than 23 species were assigned to the ascending portion, and all the sites with 23 species or fewer were assigned to the descending portion. In the Southwest subregion, the lowest LCBD value and its corresponding (median) richness were 6.035e-5 and 12, respectively. We then mapped the ascending and descending groups to view their spatial distribution. We also examined the distribution of the rare species proportions in both groups using a density plot. Similar to our previous verification, we performed this analysis with both observed and predicted data but once again only illustrate the results with the predicted data as both were qualitatively similar.

2.8. Software We used *Julia v1.6.1* (Bezanson et al. 2017) for most of the project and *R v4.0.2* (R Core Team 2020) for some specific steps. We used the *Julia* package `SimpleSDMLayers.jl` (Dansereau and Poisot 2021) as the basic framework for our analyses, to download the WorldClim 2.1 data, and to map our results through the package's integration of `Plots.jl`. We also used `StatsPlots.jl` to produce the density plots in our rare species analysis. We used the *R* packages `auk` (Strimas-Mackey, Miller, and Hochachka 2018) to extract and manipulate eBird data, `embarcadero` (Carlson 2020) to perform the BART models, `vegan` (Oksanen et al. 2019) to perform the Hellinger transformations, `SpatialPack` to perform the modified t test, as well as `MASS` (Venables and Ripley 2002) and `betareg` (Cribari-Neto and Zeileis 2010) to perform the negative binomial and beta regressions, respectively. We used `GDAL` to coarsen the Copernicus land cover data. All the scripts used for the analyses are available at `https://github.com/gabrieldansereau/betadiversity-hotspots`.

3

Results

3.1. Species distribution models generate relevant community predictions Species richness from observation data (Fig. 1a) was higher on the East Coast and lower on the West Coast, with many unsampled patches in the North, Midwest, and Southwest. Richness results from SDM data (Fig. 1b) displayed higher richness on the East Coast and sites

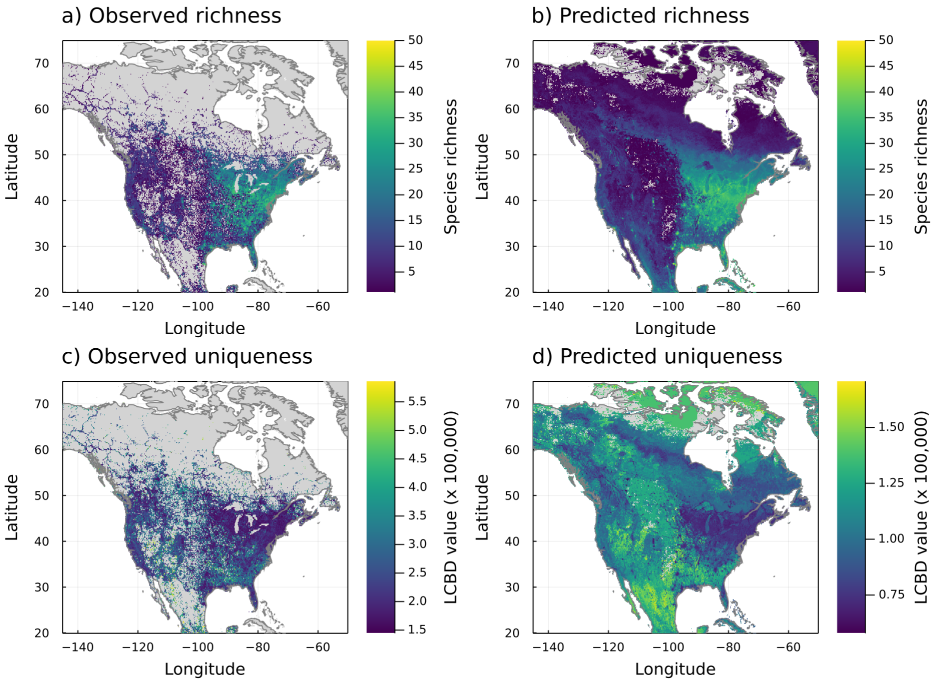


Figure 1 Comparison of species richness and LCBD scores from observed and predicted warbler occurrences in North America. Values were calculated for sites representing ten arcminute pixels. We measured species richness after converting the occurrence data from eBird (a) and the SDM predictions from our 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). LCBD values ranged between 1.444e-5 and 5.860e-5 for observation data and between 5.788e-6 and 1.706e-5 for SDM data. The total beta diversity was 0.608 for the observation data and 0.775 for the SDM data. Areas in light grey (not on the colour scale) represent mainland sites with environmental data but without any warbler species present.

with few or no species up north and in the Midwest. There was no clear latitudinal gradient in richness but rather an East-West one. Landmarks such as the Rockies and croplands in the Midwest (which should be species-poor habitats) were notably visible on the maps, separating the East and West. LCBD scores from observation data (Fig. 1c) were low on the East Coast and higher on the border of sampled sites in the Midwest. They were also higher in the North and in the South, where observations were sparser. Results from SDM predictions were similar (Fig. 1d), with lower LCBD values in the East and more unique sites in the Midwest region, Central Mexico, and some Northern regions. There was no clear latitudinal gradient, and the East-West contrast, while present, was less clear than on the richness maps. LCBD values ranged between 1.444e-5 and 5.860e-5 for observation data and between 5.788e-6 and 1.706e-5 for SDM data. The total beta diversity was 0.608 for the observation data and 0.775 for the SDM data.

The modified *t* test of Clifford, Richardson, and Hemon (1989) showed high correlation between the observed and predicted estimates of richness and uniqueness, as well as spatial autocorrelation in the values. For species richness, the correlation coefficient was 0.7802, the *F*-statistic was 20,162, and the p-value was 6.126e-04. For LCBD scores, the correlation coefficient was 0.5207, the *F*-statistic was 40,942, and the p-value was 3.936e-09.

The difference between the observed and predicted estimates (predicted richness - observed richness and predicted LCBD - observed LCBD) showed opposite geographic distributions for species richness and ecological uniqueness (Fig. 2). Predicted richness estimates were higher than observed estimates on the East Coast in particular as well as on the West Coast and in Mexico, but are lower than observed estimates in the Midwest (Fig. 2a). Predicted LCBD estimates, on the other hand, were lower than observed estimates on the East Coast and higher in the Midwest (Fig. 2b). Regression residuals showed similar geographic distributions to their corresponding difference values (Fig. 3).

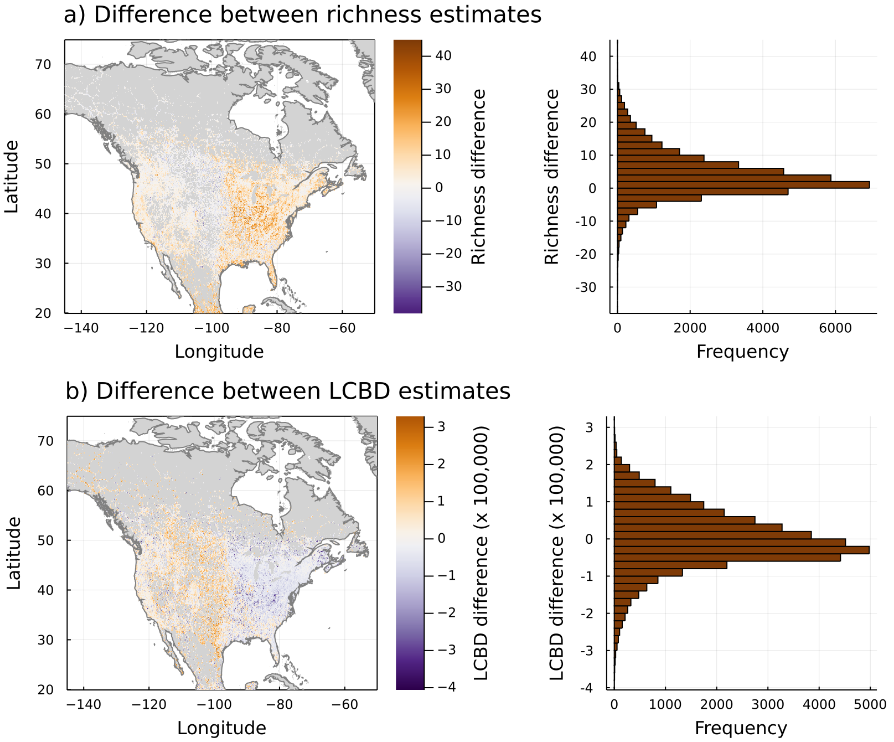


Figure 2 Comparison between observed and predicted estimates of species richness (a) and ecological uniqueness (b). The difference values represent the estimate from the predicted data set minus the estimate from the observed data set. The difference values for richness ranged between -38 and 45 (a). LCBD values were recalculated for the same set of sites with observations in both data sets. Recalculated LCBD ranged between 1.450e-5 and 5.910e-5 for observation data and between 1.117e-5 and 5.132e-5 for SDM data. The difference values for LCBD scores ranged between -4,060e-5 and 3.297e-5 (b)

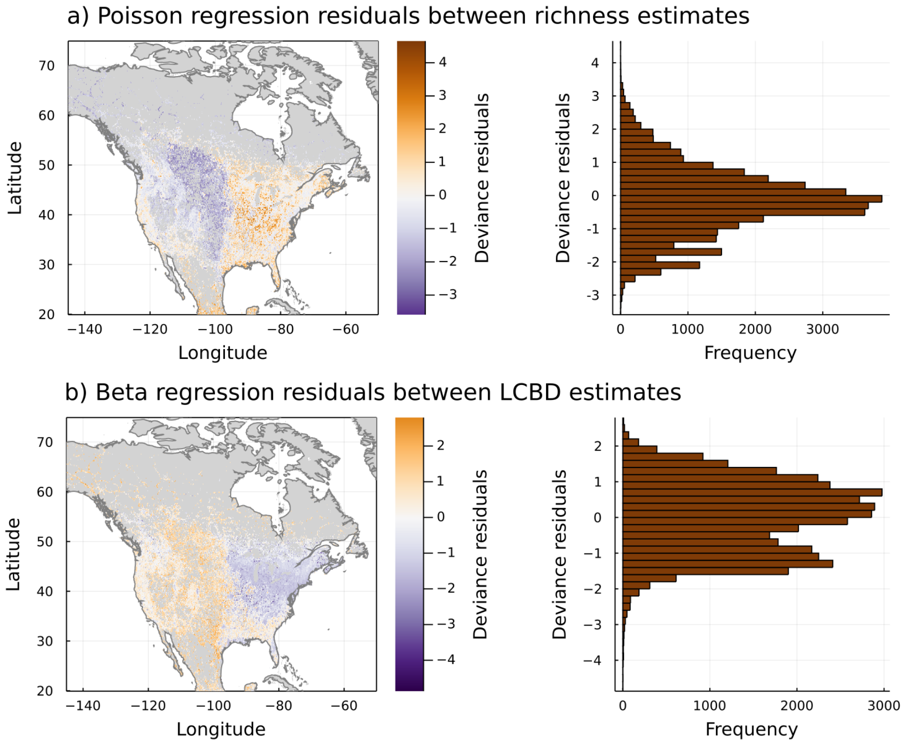
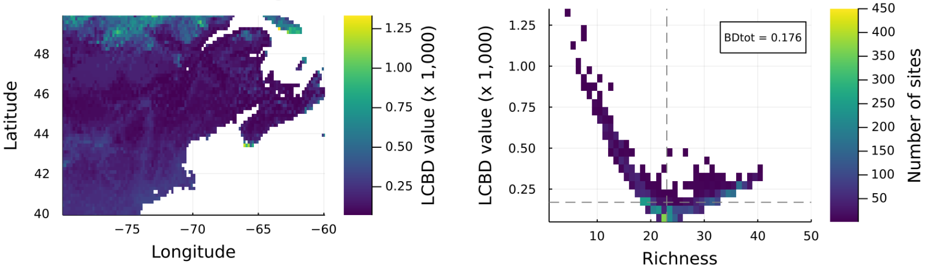


Figure 3 Comparison of the regression residuals between the observed and predicted estimates of species richness (a) and ecological uniqueness (b). The estimate from the predicted data set was used as the dependent variable and the estimate from the observed data set as the independent variable. A negative 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. The deviance residuals for richness ranged between -3,591 and 4,654 (a). LCBD values were recalculated for the same set of sites with observations in both data sets. The deviance residuals for LCBD scores ranged between -4,866 and 2,799 (b).


a) Northeast subregion

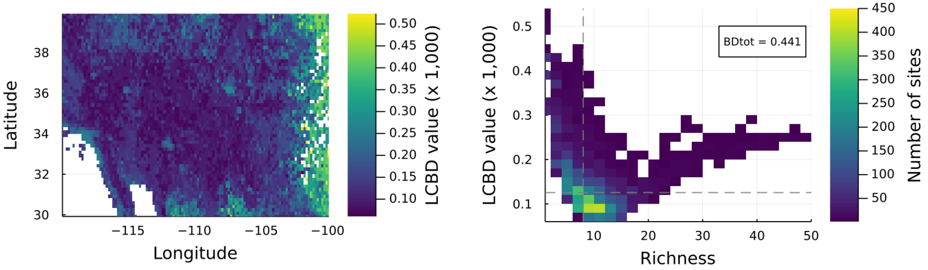

b) Southwest subregion

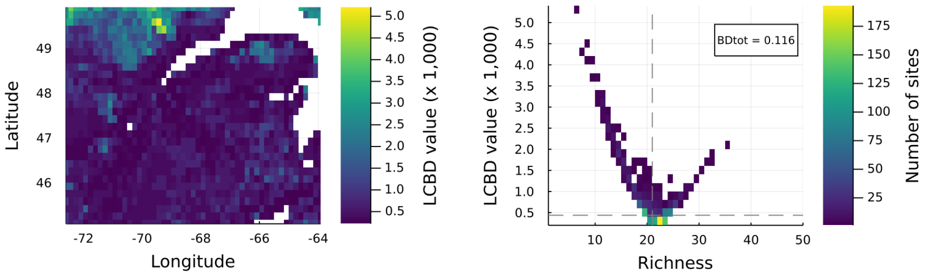
Figure 4 Comparison between a species-rich region (Northeast, a) and a species-poor one (Southwest, b) based on the SDM predictions for warbler species in North America. The richness-LCBD relationship displayed contrasting profiles for the subregions according to their general richness. Total beta diversity was higher in the Southwest subregion than in the Northeast one. The left-side figures represent the LCBD scores for the assembled presence-absence predictions, calculated separately in each region after applying the Hellinger transformation. The right-side figures represent the decreasing relationship between LCBD values and species richness, with the number of sites in the bins of the 2-dimensional histogram. The vertical and horizontal dashed lines respectively represent the median richness and LCBD value in each region. LCBD values ranged between 7.032e-5 and 1.333e-3 for the Northeast subregion and between 6.035e-5 and 5.236e-4 for the Southwest one.

3.2. Uniqueness displays regional variation as two distinct profiles The relationship between LCBD values and species richness displayed contrasting profiles in species-rich and species-poor regions (Fig. 4). In the species-rich northeastern region of our study extent (North America), LCBD scores displayed a mostly decreasing relationship with species richness, with a slightly curvilinear form and increase of values for very rich sites. The sites with the highest LCBD values, i.e., the unique ones in terms of species composition, were the species-poor sites, while the species-rich sites displayed lower LCBD scores. The Southwest subarea showed a different relationship with a much sharper initial decline and a more significant increase as richness reaches 20 species. The sites with the highest LCBD values were the poorest ones in terms of species richness, as in the Northeast region, but the species-rich sites were proportionally more unique in the Southwest region. Total beta diversity was also higher in the Southwest subregion (0.441) than in the Northeast one (0.176), indicating higher compositional differences between the sites. LCBD values ranged between 7.032e-5 and 1.333e-3 for the Northeast subregion and between 6.035e-5 and 5.236e-4 for the Southwest one.

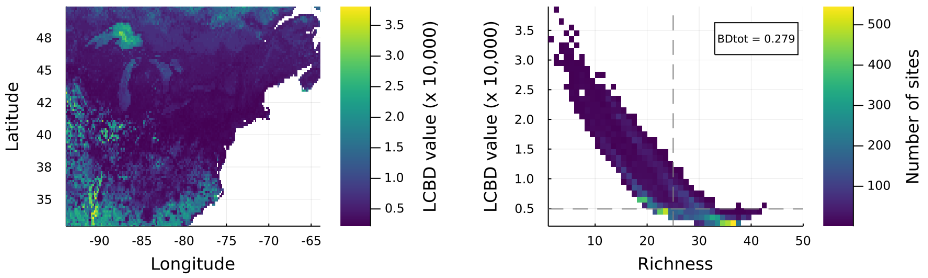
3.3. Uniqueness depends on the scale on which it is measured The LCBD-richness relationship showed important variation when scaling up and changing the region's extent (Fig. 5). For smaller extents, starting with a species-rich region, the relationship is well defined, decreasing, and curvilinear. However, as the extent increases and progressively reaches species-poor regions, the relationship broadens, displays more variance, and loses its curvilinear aspect while keeping a decreasing form. Total beta diversity was higher when increasing the spatial extent, going from 0.116 to 0.279 and 0.682. LCBD values ranged between 2.195e-4 and 5.209e-3 at the finest scale, between 1.478e-4 and 3.500e-3 at the intermediate one, and between 1.179e-05 and 5.218e-05 at the broadest one.

3.4. Uniqueness depends on the proportion of rare species The proportion of rare species differed depending on the classification of sites in the ascending or descending portions of the LCBD-richness relationship (Fig. 6). The proportion of rare species was

a) Regional extent



b) Intermediate extent



c) Continental extent

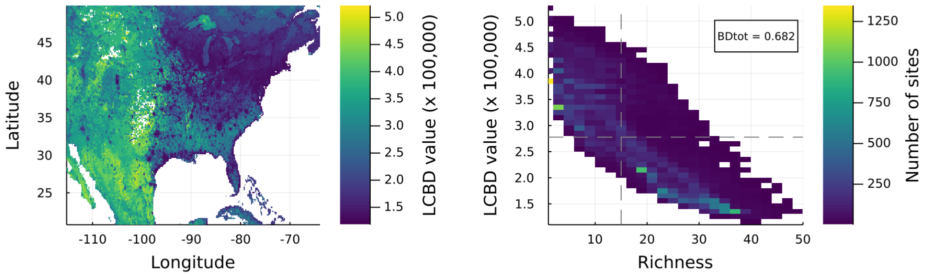
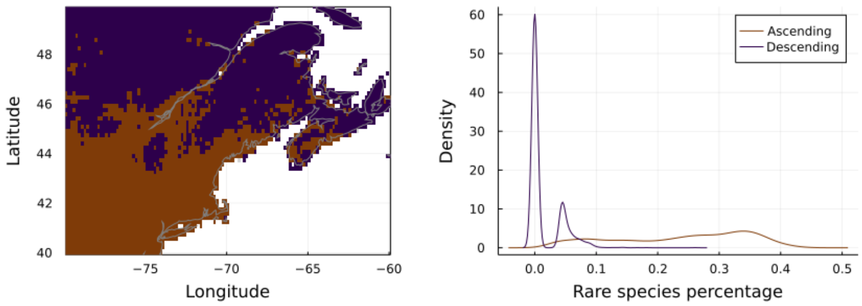


Figure 5 Effect of extent size on the relationship between site richness and LCBD values based on the SDM predictions for warbler species in North America. The relationship progressively broadens and displays more variance when scaling up while total beta diversity increases. The LCBD values were recalculated at each scale based on the sites in this region. LCBD values ranged between 2.195e-4 and 5.209e-3 at the finest scale, between 1.478e-4 and 3.500e-3 at the intermediate one, and between 1.179e-05 and 5.218e-05 at the broadest one. The vertical and horizontal dashed lines respectively represent the median richness and LCBD value in each region.

a) Northeast subregion



b) Southwest subregion

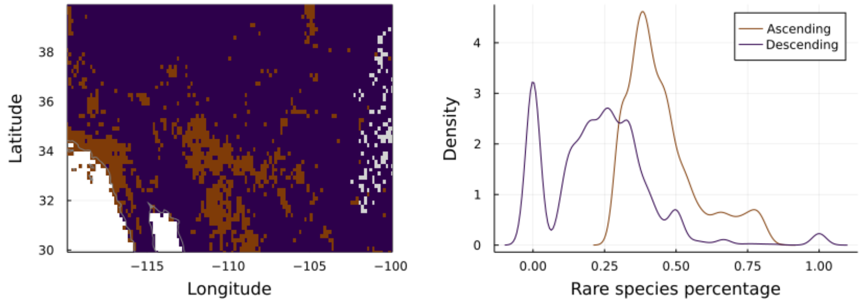


Figure 6 Proportion of rare species in the ascending and descending portions of the LCBD-richness relationship for the Northeast (a) and Southwest (b) subregions. The left side figures show the geographic distribution of the sites from each group. Sites were assigned to the ascending portion if their 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 are density plots of the proportion of rare species in each group. 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.

higher in the sites corresponding to the ascending portions of the relationships shown in Fig. 4 than in the sites corresponding to the descending portions. The classification of the sites in the two portions showed a clear latitudinal gradient in the Northeast subregion, while it was distributed in patches in the Southwest subregion.

4

Discussion

Our results showed a decreasing relationship between species richness and LCBD values on broad spatial extents (Fig. 5c) but also highlighted that the exact form of this relationship varies depending on the region and the spatial extent on which it is measured. Our species-rich Northeast subregion (Fig. 4) showed a decreasing relationship, very similar to previous studies, and slightly curvilinear, as described by Heino and Grönroos (2017) and Tan et al. (2019). This result for warbler species is in line with the original study on fish communities (Legendre and De Cáceres 2013) and with following ones on insect metacommunities (da Silva and Hernández 2014; Heino et al. 2017; Heino and Grönroos 2017), dung beetles (da Silva, Hernández, and Heino 2018; da Silva, Bogoni, and Heino 2020), aquatic beetles (Heino and Alahuhta 2019), stream macroinvertebrates (Sor, Legendre, and Lek 2018), stream diatoms (Vilmi, Karjalainen, and Heino 2017), multi-trophic pelagic food webs (phytoplankton, zooplankton, fish) (Taranu, Pinel-Alloul, and Legendre 2020), temperate forest trees (Tan et al. 2019), mammals (medium-to-large, small, volant) (da Silva, Bogoni, and Heino 2020), wetland birds (de Deus et al. 2020), and a few other phylogenetic groups (plants, lizards, mites, anurans, mesoinvertebrates) (Landeiro et al. 2018). However, it was originally argued that the negative relationship was not general or obligatory (Legendre and De Cáceres 2013). Different LCBD-richness relationships have also been observed, with both positive and negative relationships for different sites or taxonomic groups in some studies (Kong et al. 2017; Teittinen et al. 2017), as well as a negative relationship with the number of common species but a positive relationship with the number of rare species (Qiao et al. 2015). Our results further show that the relationship may depend on the region's richness profile, as the relationship was different in our species-poor Southwest subregion, with a sharper initial decrease. Therefore, the curvilinear form may depend on how big the contrast will be between the region's median richness and its richest ecologically possible sites.

The variation in the LCBD-richness relationship when scaling up and changing the overall study extent showed that the uniqueness patterns highlighted are not necessarily the same depending on the scale on which it is used. The subregions' uniqueness profiles will merge at broad spatial scales, but this can create a new profile with a lot more variation. When too many poor sites are present, rich sites will almost certainly have lower LCBD values. Aggregating too many different sites might then possibly mask some patterns of uniqueness. Total beta diversity, on the other hand, showed the variation expected from previous studies, increasing with spatial extent (Fig. 5) (Barton et al. 2013; Heino et al. 2015). Its value was high at the continental scale (0.628) but lower than what has been observed in some studies (e.g. 0.80 in Sor, Legendre, and Lek (2018)).

Our results confirm that the proportion of rare species in the community may have an effect on the direction of the relationship between species richness and ecological uniqueness. da Silva, Hernández, and Heino (2018) suggested that the proportion of rare and common species in the communities seems to determine if the relationship will be negative, non-significant, or positive. Yao et al. (2021) supported this idea and showed that the relationship was negative when the proportion of rare species was lower and positive when the relationship was high. Our results further show that sites associated with a positive relationship within a curvilinear one tended to have a higher rare species proportion (Fig. 6). This also implies that the proportion of rare species was higher in species-rich sites than in species-poor ones in both our Northeast and Southwest subregions. Further work should attempt to disentangle the effects of the rare species proportion and of the region's richness profile.

Our results showed that SDM models provide richness and uniqueness predictions highly correlated similar to the occurrence data while filling gaps in poorly sampled regions (Fig. 1). However, the results showed spatial autocorrelation and tended to underestimate uniqueness in species-rich regions and overestimate it in species-poor ones (Figs. 2, 3). Overprediction of richness using S-SDMs was reported previously (Dubuis et al. 2011; D'Amen et al. 2015; Zurell et al. 2020). Predictive approaches and spatial structures have been less studied for LCBD values compared to species richness, but some studies did show that LCBD distributions were spatially structured across sampling sites (da Silva, Hernández, and Heino 2018). Our results over broad spatial extents did not concord exactly with those of Heino and Alahuhta (2019), as LCBD scores increased both in the North and South, hence did not strictly increase with latitude, and also showed a clear East-West gradient. Nonetheless, the predictions for regions with sparse sampling are of interest as they allow a quantitative evaluation, however imperfect, for sites where we would otherwise have no information. Our SDMs also offered relevant LCBD predictions using eBird, arguably one of the largest presence-absence data sets available (when using its complete checklist system), and showed the measure's potential on such massive data. These two elements open up new opportunities for LCBD analyses on extended spatial scales, as well as for the diversity of taxons to which this type of analysis can be applied. An interesting way forward would be to test these results using more advanced community assembling techniques than S-SDMs. The use SESAM with probabilistic SDMs, probability ranking, and species richness predictions as macroecological constraints returns high site-level prediction accuracy (Zurell et al. 2020) and would be compatible with presence-absence LCBD calculations. The use of probabilistic stacks rather than binary ones (Calabrese et al. 2014) could also constitute a novel way to calculate LCBD indices.

Both these procedures should reduce the richness deviation we observed, and it would be interesting to verify if this can also be the case with LCBD values. Overall, our distribution results have implications for conservation, as they confirm that species richness and ecological uniqueness measured from LCBD values may conflict and highlight different potential hotspots (Dubois, Proulx, and Pellerin 2020; Yao et al. 2021), thus reinstating the need to protect both with complementary strategies.

This study showed how ecological uniqueness can be measured on broad spatial extents, including for regions with sparse sampling. First, the negative relationship often observed between species richness and local contributions to beta diversity (LCBD) can take different forms depending on the richness profile of the regions on which it is measured. Therefore, species-rich and species-poor regions may display different ways to be unique. Second, the negative relationship is not constant when varying the spatial study extent and may be less clearly defined at broad scales when contrasting regional relationships are present, even creating a new, distinct one. Finally, species distribution models (SDMs) offer a promising way to generate uniqueness predictions on broad spatial extents and could prove useful to identify beta diversity hotspots in unsampled locations on large spatial scales, which could be important targets for conservation purposes.

5

Acknowledgments

We acknowledge that this study was conducted on land within the traditional unceded territory of the Saint Lawrence Iroquoian, Anishinabewaki, Mohawk, Huron-Wendat, and Omàmiwininiwak nations. We have received financial support from the Fonds de recherche du Québec - Nature et technologie (FRQNT) and the Computational Biodiversity Science and Services (BIOS²) NSERC CREATE training program.

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