Are Species' Geographic Ranges Mainly Determined by Climate?

by

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Abstract

Aim

It is commonly asserted that climate presents the primary constraint on species’ geographic distributions, and therefore, that species' ranges shift in response to changing climate given their specific climatic tolerances. However, supporting evidence is surprisingly inconsistent. Alternatively, spatially structured processes (e.g., dispersal) could more strongly determine species’ geographic distributions. Is climate the primary determinant of species’ geographic distributions, or might non-climatic, spatial processes constitute a stronger influence, such that the effect of climate is indirect? This study tests a number of predictions made by each of these hypotheses, during a single period of time.

Location

Contiguous United States and southern Canada.

Methods

We used 19 species of passerine birds whose distributions fall entirely within the area sampled by the North American Breeding Bird Survey from 1990-2000. We related these distributions to the mean breeding season climate, geographic locations and neighbourhood effects. Two spatial scales were addressed to assess the geographic location of species’ ranges and species' distributions within ranges.

Results

On average, geographic coordinates and a model representing neighbourhood occupancy outperform a simple climatic model. After controlling for geographic coordinates, species occupancy is poorly related to climate. A neighbourhood model on average accounts for the majority of variance captured by geographic coordinates within ranges, and more for the continental placement of ranges. Spatially explicit variables are more important than macroclimatic variables in a predictive model of species occupancy on average.

Main Conclusions

The geographic distributions of wide-spread North American passerine birds appear not to be primarily determined by climate. Our results are consistent with the hypothesis that localized spatial processes such as dispersal are stronger determinants of both continental range placement and within-range distributions of North American birds.

Résumé

Objectif

Il est communément affirmé que le climat est la principale contrainte aux répartitions géographiques des espèces et que les répartitions géographiques d'espèces changent en réponse aux changements climatiques, compte tenu de leurs tolérances climatiques spécifiques. Pourtant, l’évidence appuyant cette idée est assez mixte. D'autres hypothèses postulent que des processus spatialement structurés comme la dispersion contraignent plus fortement les répartitions des espèces. Il y a de l'évidence conséquente avec des hypothèses climatiques ainsi que des hypothèses spatialement structurées, mais peut-on distinguer leurs effets sur les répartitions des espèces? Cette étude teste des prédictions qui découlent de ces hypothèses générales.

Emplacement

Les États-Unis contigus et le sud du Canada.

Méthodes

Nous avons utilisé 19 espèces d'oiseaux passériformes dont les répartitions géographiques se situent entièrement dans la zone échantillonnée par le North American Breeding Bird Survey de 1990 à 2000. Nous avons relié ces répartitions au climat moyen durant la saison de reproduction, aux coordonnées géographiques, ainsi qu'à l’occupation du voisinage par des individus conspécifiques. Nous avons utilisé deux échelles spatiales pour évaluer la localisation continentale des répartitions ainsi que l’occupation des sites à l'intérieur des répartitions continentales.

Résultats

En moyenne, les coordonnées géographiques et un modèle basé sur l’occupation du voisinage surpassent un modèle climatique simple. Après avoir tenu compte des coordonnées géographiques, les répartitions des espèces sont peu liées au climat. Un modèle de paysage capture la majorité de la variance géographique à l'intérieur des répartitions, et plus pour le placement continental des répartitions. Les variables spatiales sont plus importantes, en moyenne, que les variables macroclimatiques dans un modèle prédictif d'occupation des espèces.

Principales conclusions

Les répartitions géographiques des oiseaux passereaux nord-américains à grande diffusion ne semblent pas être principalement déterminées par le climat. Nos résultats sont conséquents avec l'hypothèse selon laquelle des processus spatiaux localisés tels que la dispersion déterminent principalement les répartitions continentales des espèces, ainsi que les distributions à l'intérieur des répartitions.

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Introduction:

With a changing climate, many ecologists in recent years have been interested in asking the question of how will species respond. This question is motivated by the underlying hypothesis, and common belief, that species have specific environmental tolerances and that these tolerances are the primary constraint structuring geographic ranges in space (e.g., Araújo *et al*., 2013; Coristine & Kerr, 2015). Important predictions from this hypothesis (hereafter: “climatically-constrained hypothesis”) are that: 1) geographic variation in the presence or absence of a species will be strongly correlated with climate, 2) when climate changes, species’ ranges should shift spatially to remain within the same climatic envelope, and 3) species’ ranges should expand to fill areas that are climatically tolerated. Failure to remain within that envelope is assumed to be detrimental to the survival of the species (e.g., the notion of "climatic debt": Devictor *et al*., 2012). Much of the current literature appears to support the climatically-constrained hypothesis, in that ecological responses to climatic change are often in the direction one would predict. However, there remain numerous inconsistencies.

Species occurrence is generally correlated with climate (Jeffree & Jeffree, 1996; Parmesan, 1996). Climatic envelopes are therefore often used as a primary means of predicting a species’ potential geographic distribution under climate change (Pearson *et al*., 2002) or in spatially disjunct areas (Wasof *et al*. 2015). Although bioclimatic envelope modeling may be a useful starting point for predictions of species’ distributions (Pearson & Dawson, 2003; Araújo & Peterson, 2012), these models often account for relatively small amounts of variation in predicting species occurrences (Mitikka *et al*., 2008; Watling *et al*., 2013).

Many studies have reported poleward and elevational shifts in species’ geographic ranges over recent decades (Parmesan *et al*., 1999; Parmesan & Yohe, 2003; Root *et al*., 2003; Hickling *et al*., 2006;

Chen *et al*., 2011; La Sorte & Jetz, 2012; Kerr *et al*., 2015; Mason *et al*., 2015). However, these same studies also report that significant numbers of species moved in the opposite direction (towards the equator) or remained static through time (Parmesan & Yohe, 2003; Root *et al*., 2003; Kerr *et al*., 2015; Mason *et al*., 2015). Historically, species did not necessarily track climate change during the late Pleistocene warming (Williams & Jackson, 2007). Recent studies have concluded that the range shifts of passerine birds in recent decades did not track changing climate (Currie & Venne, 2016; Taheri et al. 2016)

Species ranges are predicted to shift or expand to fill climatically suitable habitat (e.g., Leroux *et al*., 2013, Fig.1), however the evidence that they actually do so is surprisingly mixed. Species distributions are often surrounded by climatically suitable habitat that is unoccupied (Svenning & Skov, 2004; Boucher-Lalonde *et al*., 2012), contrary to what one would expect if species' distributions were strictly limited by climate. Species introduced into new continents have been found to occupy ranges of climatic conditions different from those occupied in their native ranges (Rödder & Lötters, 2009). Furthermore, the range of climatic conditions that a species can tolerate in laboratory studies can differ greatly from the macroclimatic conditions that the species' range actually occupies (Sunday *et al*., 2012; Araújo *et al*., 2013).

Do observed correlations between ranges or species' distributions and climate necessarily mean that climate is the main determinant for species' geographic distributions? Previous studies suggest that species' distributions may be spatially structured for non-climatic reasons. The correlation between species' occurrence and their apparent climatic niche has been attributed to the strong spatial autocorrelation in the climatic gradient occupied by a species (Beale *et al*., 2008; Chapman, 2010). Similarly, autocorrelation can account for much of the spatial variation in species' abundances (Bahn &

McGill, 2007). Residual spatial structure has long been observed in species distribution models (Lichstein *et al*., 2002; Bahn *et al*., 2006), a large proportion of which may be attributed to the spatial autocorrelation of environmental variables (Legendre, 1993; Lichstein *et al*., 2002; Bahn *et al*., 2006; and see: Diniz-Filho *et al*., 2003). In addition, after accounting for environmental variables, remaining spatial structure has been observed and attributed to endogenous effects such as dispersal (Bahn *et al*., 2006).

Here we ask: are species' geographic distributions primarily structured by climate (as hypothesized by much of the climate change literature), or might their spatial structure be primarily due to other, non-climatic processes, such that correlations with climate are indirect? Observed inconsistencies may reflect spatial autocorrelation of non-climatic variables that affect habitat suitability. Alternatively, the inconsistencies may be due to spatially structured dynamic processes such as local colonization, extinction and dispersal (e.g., Dias, 1996; Hanski, 1998), where species' geographic distributions may be determined primarily through dispersal limitations, as opposed to climatic tolerances (e.g., Dias, 1996; Hanski, 1998; Hubbell, 2001; Svenning & Skov, 2007). Current climate change literature hypothesizes that species' ranges must shift to remain within the climatic conditions occupied in the recent past, but are those climatic conditions the primary determinant/constraint on a species' geographic distribution, or might the apparent climatic influences be indirect?

More specifically, we test the hypothesis that climate is the primary determinant of species' geographic distributions for North American passerine birds, versus being primarily determined by other factors that are more spatially structured, as evidenced by occupation of neighbouring sites (e.g., dispersal or land cover). We test a number of predictions made by these hypotheses (Table 1) at two spatial scales. Specifically, if species' geographic distributions are primarily determined by climate, then climate should 1) be a stronger predictor of geographic distributions than spatial structure, 2) show correlations with climatic variables that are consistent with a direct affect on species occupancy, and 3) have a decay of spatial autocorrelation similar to that of a species' occupancy (i.e., resemble the spatial structure of their primary determinant). We examined entire species' ranges, as opposed to latitudinal extremes. We use four techniques to test these predictions: 1) multiple regressions and partitioning of variance, 2) structural equation models, 3) spatial decay of autocorrelation and 4) random forest models to assess the relative contributions of each hypothesized influence.

Methods:

Species Data:

To examine species' ranges, we used the species occurrence records in the North American Breeding Bird Survey (BBS) for 19 North American passerine birds sampled between the years of 1990-2000. To arrive at these species, we began with all passerines in the BBS. We excluded species whose ranges (as recorded by NatureServe; http://www.natureserve.org/) extended beyond the area sampled in the BBS. We also eliminated species that occupied fewer than 70 routes between 1990-2000. This left 19 species in our analysis (Table A.1). The time period was chosen to be short enough so that climate change would be minimal, but long enough to average over year-to-year variations in site occupancy and species detection.

We included all BBS routes that were recorded as good quality (i.e., reliably sampled). Only routes that were actively sampled every year from 1990-2000 were included. Routes were also eliminated if they were not within 200km of at least one other BBS route (without which neighbourhood models could not be calculated, see below; Figure A.1). This constraint eliminated <6% of routes for any given species. We considered a species to be present at a given BBS route if it was observed at least once between 1990-2000; it was otherwise considered absent. We used this long period to minimize failures to detect species presence on a route. We also computed species abundance on each route, summed over the study period (where statistically feasible; see Appendix B). Spatial variation in total abundance should be less sensitive to false absences (i.e., failures to detect an individual that was present).

We examined species ranges over two spatial extents for each species. The first extent ("Hemi-Continental" extent) incorporates all BBS routes continent-wide that were not disqualified above. These data include absences outside a species' range. The data therefore mainly address the placement of species' ranges across southern Canada and the contiguous United States. The second extent ("Within-Range" extent) includes the BBS routes within species' ranges (i.e., within a minimum convex polygon around the routes occupied by a given species). The within-range extent for a given species was determined by the outermost occupied routes over the study period. These data address how specific sites are occupied within species' ranges.

Climate Data:

Temperature and precipitation were obtained from the WorldClim database (Hijmans *et al.*, 2005) at a resolution of 30 arc-seconds (~1km^2). We estimated the mean breading season temperature and precipitation by averaging over the WorldClim May - July monthly means (climate normals from 1950-2000). We used climate normals on the assumption that species' ranges respond to long-term average climatic conditions. Currie and Venne (2017), using the same set of species, found that species' ranges did not track fluctuations in climate over the period 1979-2010. Further, the spatial variation across the United States in mean breeding season temperature and precipitation from 1990 to 2000 (obtained from the PRISM Climate Group) is very strongly correlated with the climate normals (r=0.99 and 0.96, respectively). Climate values were extracted at the starting point for every BBS route.

Regression Models:

To compare the explanatory power of climate and of spatial structure (as measured by a purely spatial address: geographical coordinates), simple generalized linear models were constructed. We modeled presence/absence as a function of climate, geographic coordinates, and the proportion of neighbouring routes that are occupied by conspecifics, using regression with a logit link and a binomial error term. A simple climatic model was composed of second order polynomials of mean breeding season temperature and precipitation and their interaction, following Boucher-Lalonde *et al*. (2014), who showed that a model consisting of Gaussian functions of temperature and precipitation explain nearly as much deviance as more complex models.

Similarly, we fitted a simple spatial model of presence/absence as a second order polynomial function of the latitude and longitude of the starting point of each BBS route, and the latitude X longitude interaction. Second order polynomials were included in both climatic and spatial models to allow for the peaked relationship commonly associated with these variables. The statistical explanatory power of our climatic and spatial models was compared using Nagelkerke pseudo R^2 values.

To compare the effects of climate and geographic coordinates, for each species we first fitted models of presence/absence as a function of geographic coordinates and climate (full model, F). We then fitted models as a function of geographic coordinates alone (G), and of climate alone (C). We partitioned variances as follows, where C, G and F represent the pseudo R^2 for models above.

$F - C = X_G$ (i.e., the unique contribution of geographic coordinates) [1]

$F - G = X_C$ (i.e., the unique contribution of climate) [2]

$F - (X_G + X_C) = X_{S \cap G}$ (i.e., the contribution of the collinear variance) [3]

Structural Equation Modelling:

Given that geographic coordinates may have both a direct effect on species' distributions (e.g., through dispersal) and an indirect effect (through the spatial structure of climate), we used structural equation models to test hypothesized directional causal links. Structural equation modelling allows one to test and reject hypothesized causal links among variables. Because species' distributions were polynomial functions of geographic coordinates and climate, the latter two were included as composite variables in the structural models, following Grace & Bollen (2008). Structural equation models were constructed using the “Lavaan” package in R (Rosseel, 2012).

We hypothesized four possible models predicting the causal relationships between geographic coordinates, climate and presence/absence (Figure 1). For each species, models were either retained or rejected based on chi-square test of model fit (integrated in Lavaan). As model A in Figure 1 is a fully saturated model (i.e., 0 degrees of freedom) a chi-square test of model fit could not be calculated. Model A was retained by default if all simpler models were rejected. Indirect effects on the dependent variable are calculated as the product of the two involved paths (Rosseel, 2012).

Neighbourhood Models:

To test for regional, spatially structured processes (e.g., short-distance dispersal, colonization and extinction), we constructed a simple “neighbourhood model” representing occupation of neighbouring routes by conspecifics. Here, we hypothesize that the probability of occurrence on a BBS route is a function of the proportion of neighbouring routes occupied by conspecifics within a given neighbourhood. We defined a neighbourhood as a 200 km buffer around each BBS route, given that residual autocorrelation in bird ranges has been previously found over similar distances (Bahn & McGill, 2007). The proportion of occupied neighbouring routes was calculated for each BBS route, for each of the 19 species.

Spatial Autocorrelation:

Correlograms of Moran’s I for temperature, precipitation and presence/absence (see Appendix C regarding Moran’s I correction on binomial variables, as integrated by Chapman (2010)) were constructed to compare the rates of spatial decay of spatial autocorrelation of the variables. Macroclimatic variables show very regular gradients across the continent. Their autocorrelation would therefore be expected to decay slowly over very long distances. Autocorrelation in species presence/absence caused by short-distance dispersal, or by non-climatic variations in habitat quality, would be expected to decrease as a function of distance much more quickly. If species’ geographic distributions are structured primarily by one of these processes, we would expect the autocorrelation in species’ distributions to show spatial autocorrelation similar to the driving process. We therefore compared the decay rates of spatial autocorrelation (over distance) for presence/absence, temperature and precipitation.

Correlograms were calculated for each environmental descriptor, for each species using the “Spdep” package in R (Bivand & Piras, 2015). We then averaged among species to summarize the general trend for each variable.

Random Forest Regression:

To further compare our spatial, climatic and neighbourhood models in a way that is less dependent upon functional form, we computed a random forest analysis. Random forest modeling has been recently used in species distribution modeling and predicting extinction risks (Cutler *et al*., 2007; Bland *et al*., 2015; Di Marco *et al*., 2015). Random forest modelling is a machine learning technique with many characteristics that make it appropriate for comparing the predictive performance among our climatic, spatial and neighbourhood models, including limited assumptions about data distributions, high classification stability, and the ability to cope with collinear predictors and nonlinear responses (Murray *et al*., 2014; Di Marco *et al*., 2015). Random forests use a cross validated bootstrap procedure to reduce errors and biases among correlated variables (Cutler *et al*., 2007). Variable importance was addressed as a decrease in accuracy as a function of node impurity (the measure of the goodness of a split in the regression tree) using the package "randomForest" in R (Liaw & Wiener, 2002). For both spatial scales, variable importance was measured for all independent spatial and climatic variables.

Results:

Multiple regression, variance partitioning - On average, we found that a model consisting solely of geographic coordinates outperforms the simple climatic model. Geographic coordinates are a better predictor of presence/absence than climate for 68% of species (Wilcoxon signed rank test, $p = 0.020$; Figure 2A) at the within-range scale, and 84% (Wilcoxon signed rank test, $p = 5.3 \times 10^{-5}$; Figure 2B) at the hemi-continental scale.

Partitioning the variances of our geographic coordinates and climatic models showed that the proportion of variance that is related to climate, independently of geographic coordinates, is small: 9% and 4% for the within-range and hemi-continental scales, respectively (Figure 3). The variance related to geographic coordinates, independently of climate, was largest (16.3%) at the within-range scale.

Particularly at the hemi-continental scale, much of the variance in presence/absence is related to the collinearity between climate and geographic coordinates (57.7%).

Neighbourhood - Our neighbourhood model performs similarly to climate at the within-range scale (Wilcoxon signed rank test, p = 0.18; Figure 2A). However, geographical coordinates capture more variance than the neighbourhood model for 74% of species (Wilcoxon signed rank test, p = 0.029; Figure 2a) at the within-range scale. At the hemi-continental scale, neighbourhood processes outperformed climate for 95% (Wilcoxon signed rank test, $p = 3.8 \times 10^{-5}$) of species and outperformed our model of geographic coordinates for 68% (Wilcoxon signed rank test, p = 0.040) of species (Figure 2B).

Structural equation modeling - We created four hypothetical structural equation models (Figure 1), hypothesizing the relative causal relationship among climate, geographical coordinates and presence/absence. We found that, for nearly all species, the retained model included a direct effect of geographical coordinates on presence/absence, with climate mostly having an independent effect at the hemi-continental scale (Figure 4A). Within ranges, a model with no effect of climate, direct or indirect (model C), was retained for 47% of species. At the hemi-continental scale, a model where climate indirectly/partially affects presence/absence (model A) was retained for 79% of species, but the link from geographic coordinates to presence/absence was stronger than the link from climate for every species. On average, for the retained model of each species, the total effect of geographic coordinates on species' occupancy was stronger than that of climate at both spatial scales (Figure 4B).

Spatial autocorrelation - The pattern of spatial autocorrelation is inconsistent with the hypothesis that climate is the major driver of geographic distribution within ranges. Not surprisingly, the spatial autocorrelation of macroclimate (temperature and precipitation) decays slowly with distance, both over the continent as a whole (Figure 5B) and within species' ranges (Figure 5A). If occupancy of a route were mainly determined by macroclimate, then one would expect the spatial decay of presence/absence to resemble that of climate. We found that the spatial autocorrelation of presence/absence does decay with distance in parallel to that of the climatic variables at the hemi-continental scale, but with significantly lower spatial autocorrelation. At the within-range scale, autocorrelation of presence/absence is much lower than that of climate, and it decays spatially much more quickly. This suggests that other, less spatially structured processes shape most of the geographic variation of presence/absence within ranges.

Random forest – To compare further among the individual variables used in our analyses, we examined the relative importance of each independent variable in predicting the presence/absence of a given BBS route. A random forest test of variable importance found spatially explicit variables capture more variance in species' presence/absence on average than climatic variables (Figure 6). The proportion of neighbouring routes occupied by conspecifics was found to be the most important predictor for the geographic distribution of a species on average, followed by longitude and temperature at both, the within-range (Figure 6A) and hemi-continental (Figure 6B) scales.

Discussion:

In this study we tested several predictions of the hypotheses that species' geographic distributions are primarily determined by A) climate, or alternatively, B) non-climatic, spatially structured factors, as reflected in the spatial configuration of species' presence/absence. A summary of the results are outlined in table 1. On average we find that spatial models outperform climatic models.

The locations of species’ ranges on continents are very strongly spatially structured (Figures 2B and 5B). Most of the variance in presence/absence is spatially structured in a way that correlates with climate (62%; Figure 3), but very little variance (4%) is related to climate in a way that is not collinear with spatial coordinates. Quite a bit more of the variance is spatially structured in a way that does not correlate with climate (14%; Figure 3). Thus, spatially structured factors or processes that are unrelated to climate (e.g., land cover, or metapopulation dynamics) could be responsible for as much as 95% (Figure 3) of the statistical relationship between the location of species’ ranges and climate. For most species (79%) climate and geographic coordinates both appear to influence the continental placement of species’ ranges (Figure 4A, model A). However, on average, the path coefficient from climate to presence/absence is much weaker than the path coefficients (total effect) from geographic coordinates to presence/absence (Figure 4B; Appendix B, Table B.6). A strong correlation between climate and geographic coordinates, and the similarities in decaying autocorrelation (Figure 5B), suggests that continental range placements are structured by climate to some degree, but a large, non-climatic spatial effect is predominant. Interestingly, neighbourhood occupancy outperforms geographic coordinates for 13 of 19 species (p = 0.040; Figure 2B) in predicting species occurrence. Climatic tolerances may broadly constrain where species’ ranges can occur; however, the realized geographic structure of presence/absence depends much more strongly on the proximity to neighbouring conspecifics (Figures 6B and 2B).

The distribution of occupied sites within ranges is less predictable than the continental placement of the range as a whole (Figure 2). Spatial processes again appear to be more important than climate (Figures 2A, 3 and 6A). For 45% of species, macroclimate does not appear to have any direct effect on spatial distributions within geographic ranges, but for 30% it does appear to have a partial effect (Figure 4A). On average, the path coefficient from climate to presence/absence is still weaker than the total path coefficients from geographic coordinates to presence/absence (Figure 4B; Appendix B, Table B.5). The relatively low, rapidly decaying spatial autocorrelation within ranges (Figure 5A) also suggests that, within ranges, distributions are structured by local processes. Interestingly, although neighbourhood occupancy appears to have an important effect on species' within-range distributions (Figure 6A), it does not stand out as the dominant influence (Figure 2A). Within-range distributions of species appear to be largely influenced by relatively short-distance spatially structured processes (Figure 5A); however it seems likely that local occupancy is determined by a number of factors, some spatially structured, some not.

Why might spatial configuration be a better determinant of species' distributions than environmental characteristics? It has been previously suggested that the appearance of residual spatial autocorrelation in species' distributions may reflect dispersal limitation (Bahn *et al*., 2006; Bahn & McGill, 2007). Hypotheses such as metapopulation theory (Dias, 1996; Hanski, 1998), occupancy – abundance relationships (Holt *et al*., 2002), the unified neutral theory of biodiversity and biogeography (Hubbell, 2001), and historical influences on current ranges (Svenning & Skov, 2007; Williams & Jackson, 2007) all postulate that dispersal, rather than climatic tolerance, primarily structures species' ranges. Local extinction, dispersal, and colonization can also influence species' occupancy within ranges (Hanski 1998). Our neighbourhood model, which predicts occupancy from the proportion of occupied neighbouring BBS routes, can statistically account for some, but not all, of the spatial effect for within range distributions (Figure 2A). If we had had a gridded dataset with uniform coverage (e.g., Desrochers *et al*., 2016), as opposed to arbitrarily arranged BBS routes, we might have observed a stronger signal of neighbourhood processes. Across the continental United States and southern Canada, our neighbourhood model predicted the location of ranges better than either climate or geographic coordinates (Figure 2B). It is not surprising that the proportion of occupied neighbours is a good predictor of species occupancy at the continental scale, because large parts of the continent contain unoccupied routes surrounded by other unoccupied routes. Although this may lead to high R^2 values, conceptually this reflects the fact that long-distance colonization is rare.

It is also possible that neighbourhood occupancy is simply a measure of suitable habitat in the neighbourhood, and that species occupy a given location as a function of the total amount of available habitat in the landscape (cf. Fahrig 2013). Within the spatial extent of a given habitat, a species' distribution may be predicted fairly well by the occupancy of neighbouring conspecifics simply due to a spatially cohesive structure. In fact, by this theory, one could interpret the results of figures 4 and 5 to suggest that within-range species' occupancy could be primarily determined by habitat availability, while at range edges (hemi-continental scale) may be largely determined by climate. However, there is considerable year-to-year turnover in site occupancy. On average, sites met by the criteria of this study were occupied only 65.7% of the time from 1990-2000, indicating relatively frequent local colonization and extinctions. Assuming that site suitability does not vary greatly from year to year, neighbourhood effects must largely reflect aspects of dispersal. Further, previous studies have found spatial configuration to outperform habitat models (e.g., Bahn & McGill, 2007; Desrocher *et al*., 2016). In addition, when underlying environmental (exogenous) variables have been accounted for, remaining spatial autocorrelation has been attributed to endogenous effects (e.g., dispersal; Bahn *et al*., 2006), concurrent with our findings illustrated in figure 3 regarding residual variance unexplained by climate. Although it is unclear to what degree exogenous variables may be captured by neighbourhood occupancy, it seems likely that a large proportion could be attributed to metapopulation processes such as short-distance dispersal, colonization and extinction.

The concept of “niche” modeling implies that species’ geographic ranges respond principally to local environmental conditions. Our study suggests, in contrast, that dispersal-related processes could be responsible for much of the spatial structure of species’ geographic distributions. A large part of a species’ realized niche may simply reflect a pattern of presence/absence structured by dispersal, which is then superimposed upon spatially autocorrelated environmental surfaces. To the extent that dispersal structures geographic ranges, rather than climate, niche models should make poor predictions of species’ distributions when climatic variables change.

Thus, accounting for the spatial structure of species’ distributions could potentially largely improve climatic predictions of species' ranges (Hanski, 1998; Bahn & McGill, 2007). When we combined our neighbourhood variable (“proportion of occupied neighbouring routes”) to our simple climatic model, the explanatory power of the model increased substantially (Figure 7). Accounting for the spatial configuration within a climatic model appears to increase the predictability to a level similar to that of geographic coordinates. This is unsurprising given that our neighbourhood model was found to account for most (87%; Figure 2A) of the spatial effect in geographic coordinates within ranges, and outperformed geographic coordinates at the hemi-continental scale (Figure 2B).

Although this study suggests that spatial processes may be more important in determining species’ distributions within range and hemi-continental extents, climate undoubtedly still plays an important role over continental extents. Climate has long been suggested to be a major constraint, restricting species to appropriate biomes or biogeographic provinces (Wallace, 1876), and defining provinces to a considerable extent (Stephenson 1990). However, within these biogeographic regions, climate may be less of a determining factor on a species’ geographic location. Species may be able, in principle, to persist in any part of their biogeographic region to which they can disperse. Movements within provinces may in some cases correlate with changes in climate and resemble shifts in a climatic niche.

Caveats:

For our analyses, we created very simple models to account for the most general trends while including the fewest variables. The models that best describe species' geographic distributions do vary among species to some extent. It is not clear to what extent these differences reflect biological differences among species (e.g., differences in physiological tolerance), versus statistical biases arising from the irregular spatial and temporal sampling in the BBS data. For example, we calculated our neighbourhood variable as the proportion of occupied neighbouring routes within 200 km of a given route. We included all BBS routes with at least one occupied neighbour. The density of sampled routes is quite variable across the continent: some routes have just one neighbour (particularly in less populated western areas), while others have many neighbours. Consequently, the error of the estimated proportions is variable and spatially uneven.

Our models assume that geographical coordinates determine climate and not the reverse. Climate can potentially lead to ranges that are spatially structured; however climate does not mechanistically determine latitudes and longitudes. If climate changed on a route, the route's geographical coordinates would not change; in contrast, if a route were moved geographically, it would likely have a different climate.

Further, we retained our SEM model A as a default if all simpler models were rejected. The fact that a statistical test does not reject a model does not necessary mean that model is true. It is possible that none of the proposed models fit the data well; however for the purposes of this comparative study we assumed they were the only possible solutions.

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Table 1. Predictions of the hypotheses that the geographic distributions of North American passerine birds are primarily determined by: A) each species' climatic tolerances, and B) spatial proximity of any given location to other occupied locations.

Test	A) Climatic hypothesis predictions	B) Spatial hypothesis predictions (including GC and NE)	Results
Generalized linear models: P/A = f(climate, geographic coordinates)	- P/A is most strongly related to climate. - After controlling for climate, P/A is unrelated to GC.	- P/A is most strongly related to GC and NE. - After controlling for GC, P/A is unrelated to climate.	- P/A is more strongly related to GC than to climate for most species. - After controlling for GC, P/A is only weakly related to climate at either spatial scale.
Structural equation models that include GC, climate and P/A	- GC directly influence climate, which directly influences P/A. - GC do not directly influence P/A.	- GC directly influence climate, which indirectly influence P/A. - GC directly influence P/A.	- GC directly influences P/A. - Climate has little or partial influence on P/A.
Spatial autocorrelation	- The spatial decay for P/A and for climate is similar.	- The spatial decay for P/A occurs over a shorter distance than climate.	- Within species' ranges, the spatial decay for P/A occurs over a shorter distance than climate. - Spatial decay resembles climate at broader scales.
Neighbourhood processes: P/A = f(proportion of occupied neighbouring routes)	- P/A is more strongly related to climate.	- P/A is more strongly related to NE.	- P/A is more strongly related to NE than to climate for most species.
Random Forest regression	- Climatic variables are most important in predicting P/A.	- Spatially explicit variables are most important in predicting P/A.	- Spatially explicit variables, especially were more important in predicting P/A for most species.

P/A denotes presence/absence, GC denotes geographic coordinates, and NE represents neighbourhood effects.

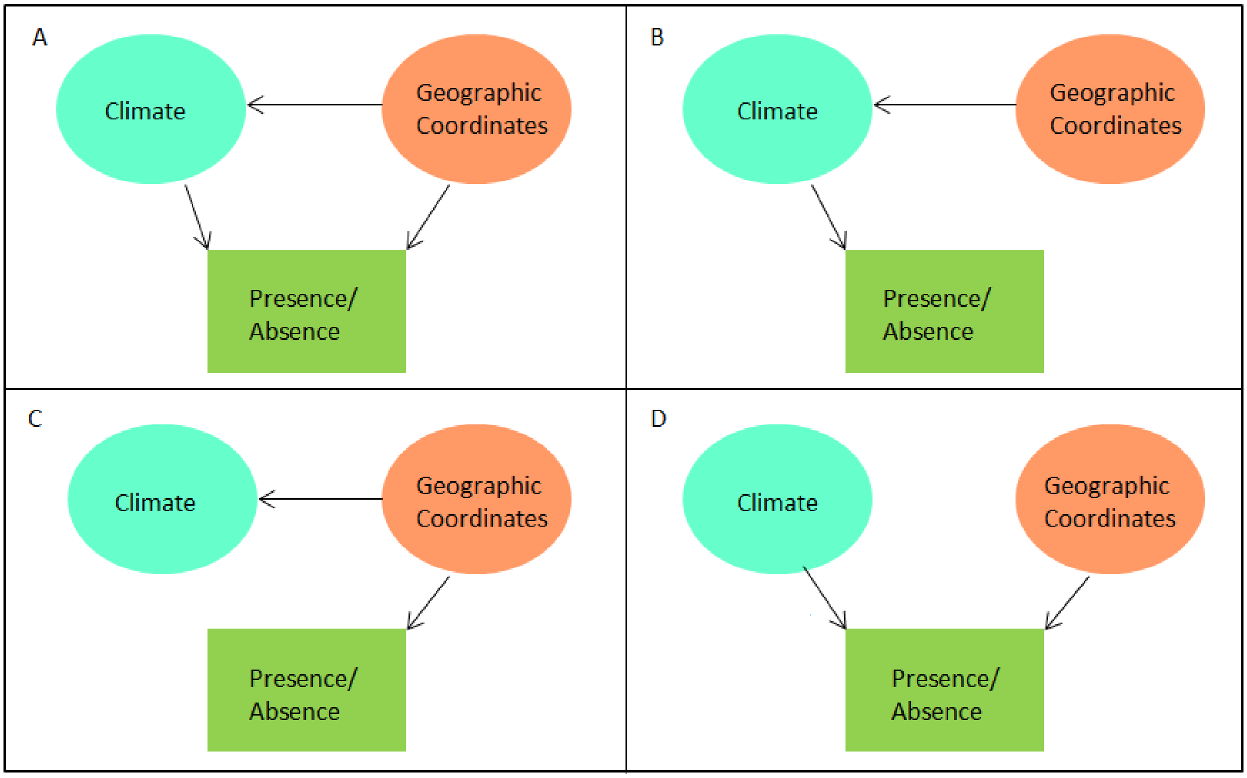


Figure 1. Four (A-D) possible causal models of the relationships among climate (cyan), geographic coordinates (orange) and presence/absence (green). Ovals represent composite variables and rectangles represent simple variables.

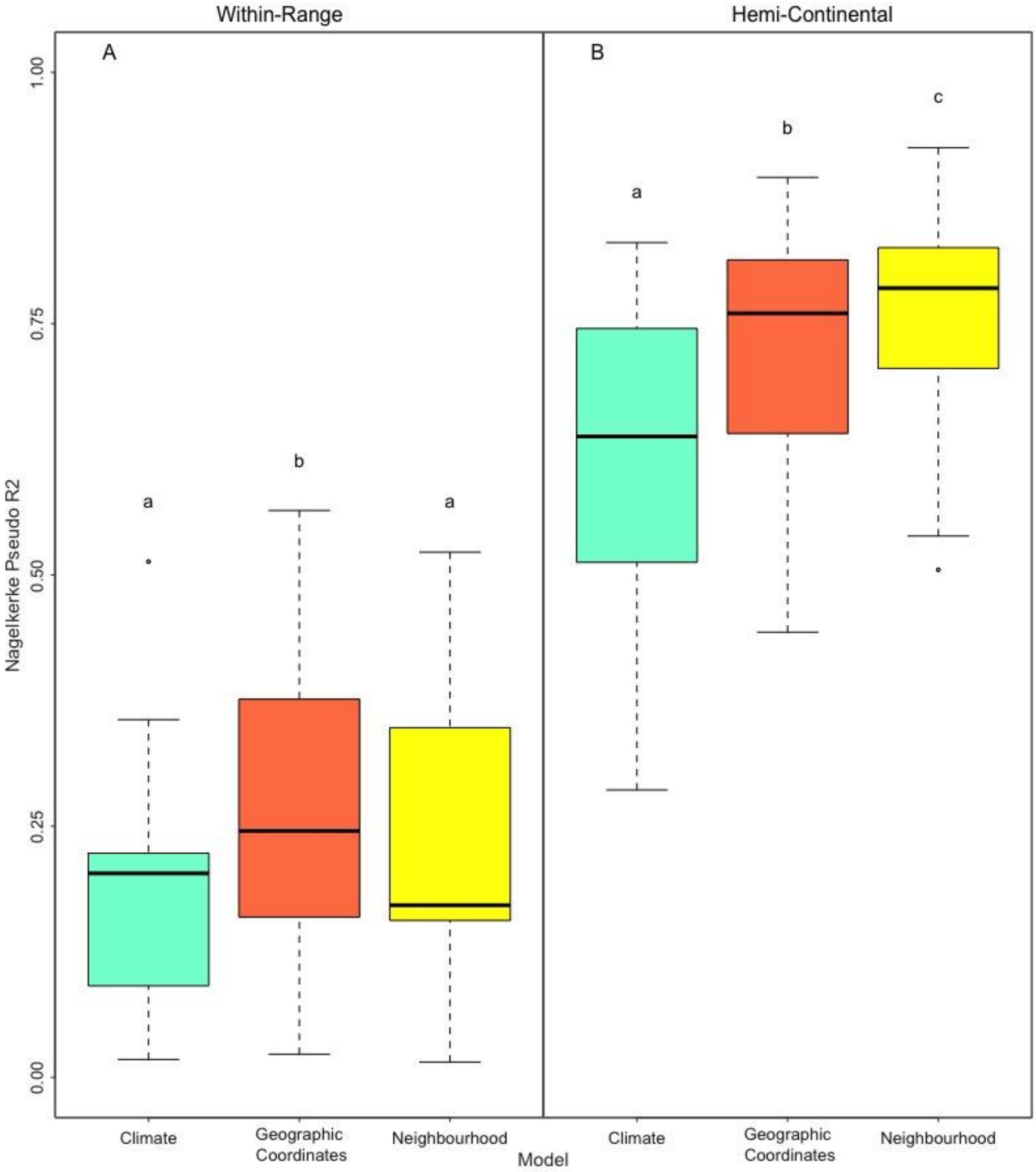
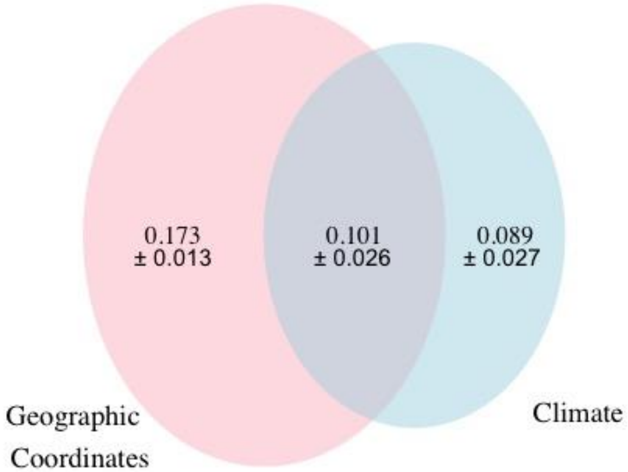

Within-Range
Hemi-Continental
A
B
Nagelkerke Pseudo R2
1.00
0.75
0.50
0.25
0.00
a
b
a
a
b
c
Climate
Geographic Coordinates
Neighbourhood
Climate
Geographic Coordinates
Neighbourhood
Model

Figure 2. Boxplots representing the distribution of Nagelkerke's pseudo R^2 among 19 species of North American passerine birds for three simple models. The "Climate" model (cyan) is a logistic regression of presence/absence as a quadratic function of temperature and precipitation, and their interaction, using sites only within each species' geographic range (A), or across the continental United States and southern Canada (B). The "Geographic Coordinates" model (orange) is a logistic regression of presence/absence as a quadratic function of latitude and longitude, and their interaction, using sites within each species' geographic range (A) and entirely across the continental United States and southern Canada (B). The "Neighbourhood" model (yellow) is a logistic regression of presence/absence as a function of the proportion of occupied sites within a 200 km buffer, using sites only within each species' geographic range (A), or across the continental United States and southern Canada (B). The heavy horizontal lines in the boxes represent medians. A Wilcoxon signed rank test was performed for both within-range and hemi-continental scales. Different lower-case letters (a-c) are assigned to indicate a significant difference ($p<0.05$) of the medians for each panel.

Within-Range



Hemi-Continental

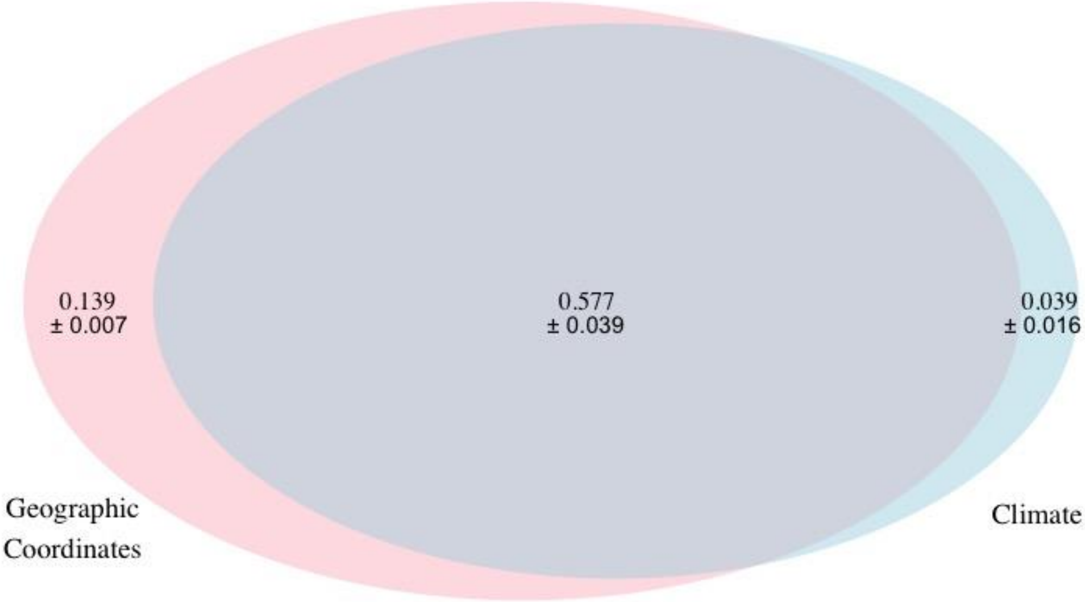


Figure 3. Venn Diagram representing the partitioned variances (average Nagelkerke pseudo R^2 ± standard error) between our simple climatic model and geographic coordinates among 19 species of North American passerine birds. The “Climate” model (blue) is a logistic regression of presence/absence as a quadratic function of temperature and precipitation, and their interaction. The “Geographic Coordinates” model (red) is a logistic regression of presence/absence as a quadratic function of latitude and longitude, and their interaction. Results are presented using sites within each species’ geographic range (top) and entirely across the continental United States and southern Canada (bottom).

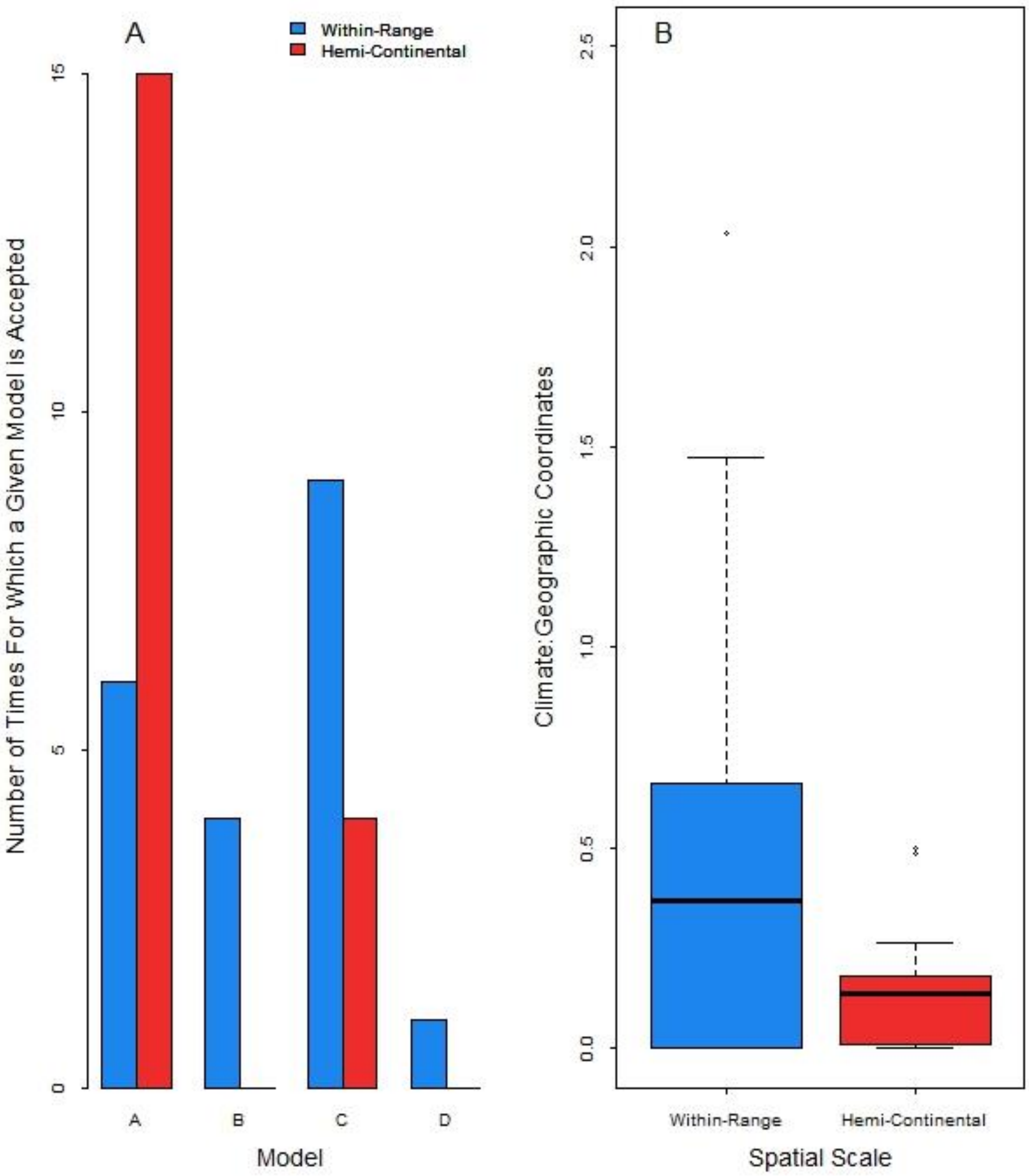

A
Within-Range
Hemi-Continental
Number of Times For Which a Given Model is Accepted
0
5
10
15
A
B
C
D
Model
B
Climate:Geographic Coordinates
0.0
0.5
1.0
1.5
2.0
2.5
Within-Range
Hemi-Continental
Spatial Scale

Figure 4. A) A histogram representing the number of species for which each of the four hypothesized structural equation models are retained (i.e., Chi-square p >0.05), for each of the within-range (blue) and hemi-continental (red) extents (n = 20 and 19 for the within-range and hemi-continental extents respectively). The models are shown in Figure 1. Model A includes direct effects of both geographic coordinates and climate on the presence/absence of North American passerine birds, with an indirect effect of geographic coordinates acting through climate. In model B, only climate directly affects presence/absence. In model C, only geographic coordinates directly affect presence/absence. Model D represents direct effects of both geographic coordinates and climate, with no effect of geographic coordinates on climate. B) Boxplots representing the ratio of the total effects of climate and geographic coordinates on the occupancy of 19 North American passerine birds, as measured by the path coefficients of the retained models (A) in Figure 1, for each of the within-range (blue) and hemi-continental (red) extents (n=19). The total effects of climate and geographic coordinates were averaged among models in cases where multiple models were retained. The heavy horizontal lines in the boxes represent medians.

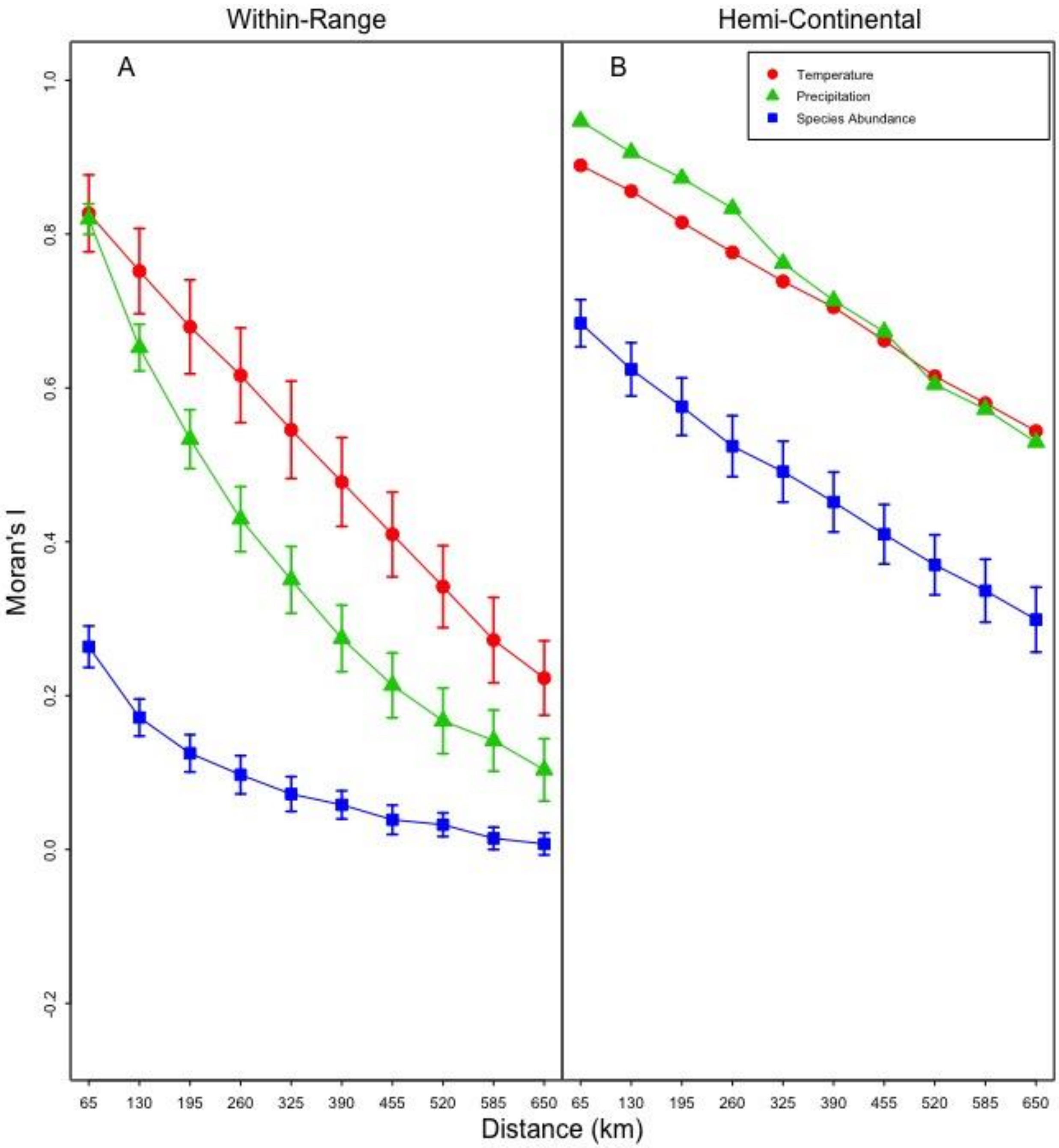

Within-Range
Hemi-Continental
A
B
Temperature
Precipitation
Species Abundance
Moran's I
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
65
130
195
260
325
390
455
520
585
650
Distance (km)

Figure 5. Correlogram of Moran’s I, representing the decay of spatial autocorrelation (+/- standard error) over distance (km) for presence/absence (square), temperature (circle) and precipitation (triangle), averaged over 19 North American passerine bird species. Panel (A) shows results for sites located within a species’ geographic range; panel (B) shows results using sites across the continental United States and southern Canada.

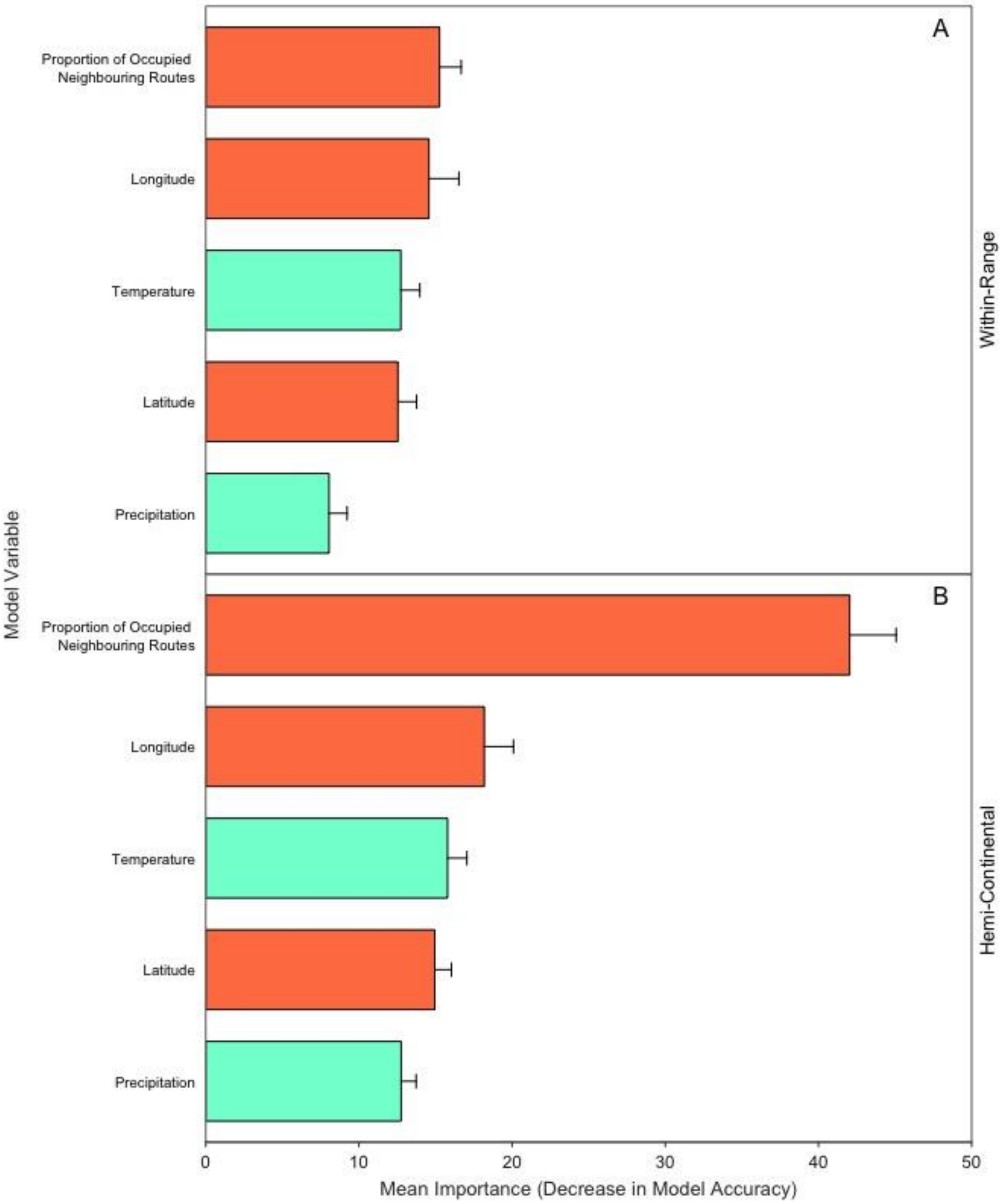
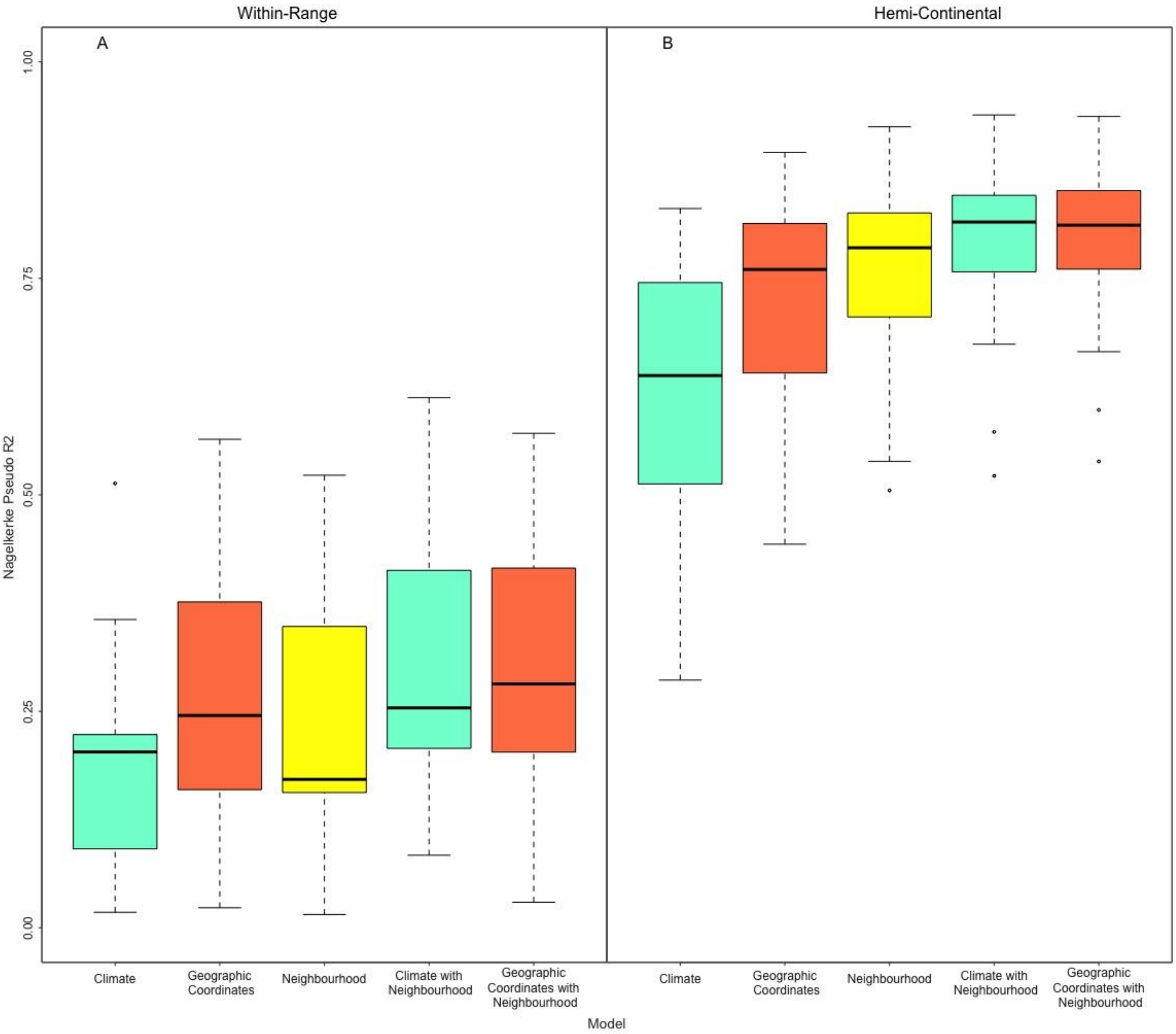
A
B
Within-Range
Hemi-Continental
Model Variable
Proportion of Occupied Neighbouring Routes
Longitude
Temperature
Latitude
Precipitation
Proportion of Occupied Neighbouring Routes
Longitude
Temperature
Latitude
Precipitation
0
10
20
30
40
50
Mean Importance (Decrease in Model Accuracy)

Figure 6. A bar plot representing the decrease in model accuracy (+ standard error) as a measure of variable importance over all nine variables examined, averaged over 19 North American passerine bird species. Panel (A) shows results for sites located within a species' geographic range; panel (B) shows results using sites across the continental United States and southern Canada. Spatially structured variables are represented in orange, climatic variables are represented in cyan.



Within-Range
Hemi-Continental
A
B
Nagelkerke Pseudo R2
1.00
0.75
0.50
0.25
0.00
Climate
Geographic Coordinates
Neighbourhood
Climate with Neighbourhood
Geographic Coordinates with Neighbourhood
Climate
Geographic Coordinates
Neighbourhood
Climate with Neighbourhood
Geographic Coordinates with Neighbourhood
Model

Figure 7. Boxplots representing the distribution of Nagelkerke's pseudo R^2 among 19 species of North American passerine birds for five simple models. The "Climate" and "Geographic Coordinates" models are a logistic regression of presence/absence as a quadratic function of temperature and precipitation, and their interaction ("Climate" model), and longitude and latitude, and their interaction ("Geographic Coordinates" model). The "Neighbourhood" model (yellow) is a logistic regression of presence/absence as a function of the proportion of occupied sites within a 200 km buffer. The "Climate with Neighbourhood" and "Geographic Coordinates with Neighbourhood" models are the respective "Climate" and "Geographic Coordinates" models with the addition of the simple neighbourhood variable of the proportion of occupied neighbouring sites. The analysis was completed using sites located within each species' geographic range (A), or across the continental United States and southern Canada (B), that were found to have at least one other site within 200km. Climatic models are presented in cyan and spatial models are presented in orange.

Appendix A: Supplementary Data Information

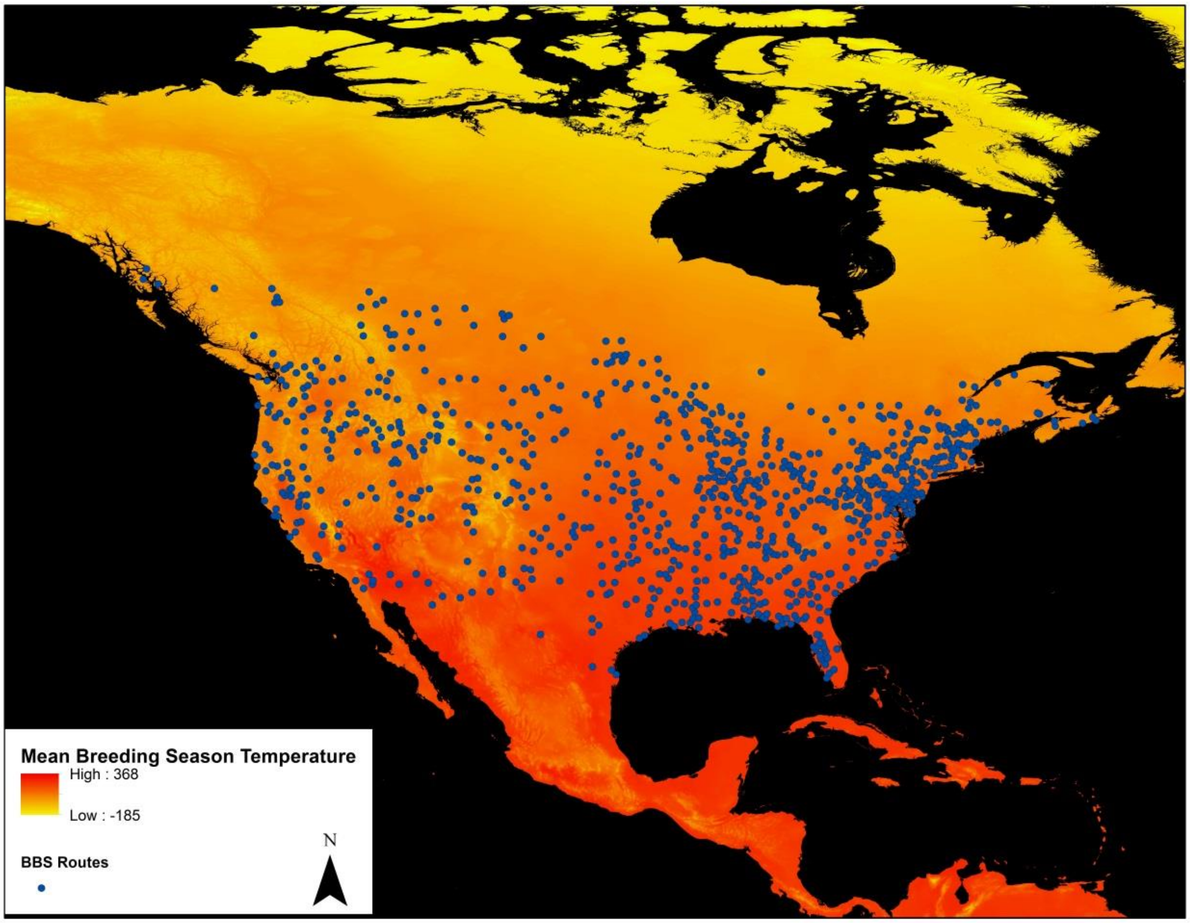


Figure A.1. Distribution of sampled North American Breeding Bird Survey routes for the years 1990-2000, plotted over the mean breeding season temperature for North America.

Table A.1. List of North American breeding bird species included in the study (n=19).

Species Name	**English Common Name**
Contopus virens	Eastern Wood-Pewee
Empidonax virescens	Acadian Flycatcher
Empidonax traillii	Willow Flycatcher
Corvus ossifragus	Fish Crow
Nucifraga columbiana	Clark's Nutcracker
Spizella pusilla	Field Sparrow
Pipilo erythrophthalmus	Eastern Towhee
Spiza americana	Dickcissel
Calamospiza melanocorys	Lark Bunting
Piranga olivacea	Scarlet Tanager
Protonotaria citrea	Prothonotary Warbler
Helmitheros vermivorum	Worm-eating Warbler
Vermivora chrysoptera	Golden-winged Warbler
Oreoscoptes montanus	Sage Thrasher
Toxostoma rufum	Brown Thrasher
Sitta pusilla	Brown-headed Nuthatch
Baeolophus bicolor	Tufted Titmouse
Poecile carolinensis	Carolina Chickadee
Hylocichla mustelina	Wood Thrush

Appendix B: Species-specific Results

Table B.1. Nagelkerke's pseudo R^2 values are presented for 19 species of North American passerine birds for three simple models using sites located within each species' geographic range. The "Climate" model is either a logistic regression of presence/absence, or a zero-inflated negative binomial regression of species abundance, as a quadratic function of temperature and precipitation, and their interaction. The "Space" model is either a logistic regression of presence/absence, or a zero inflated negative binomial regression of species abundance as a quadratic function of latitude and longitude, and their interaction. The "Neighbourhood" model is a logistic regression of presence/absence as a function of the proportion of occupied sites within a 200 km buffer.

	Presence/Absence			**Abundance**	
	Climate	**Geographic Coordinates**	**Neighbourhood**	**Climate**	**Geographic Coordinates**
Eastern Wood-Pewee	0.23	0.30	0.16	0.20	0.25
Acadian Flycatcher	0.07	0.26	0.24	0.14	0.29
Willow Flycatcher	0.06	0.13	0.16	0.14	0.21
Fish Crow	0.10	0.13	0.17	0.23	0.29
Clark's Nutcracker	0.22	0.07	0.05	0.24	0.12
Field Sparrow	0.40	0.40	0.36	0.32	0.31
Eastern Towhee	0.22	0.44	0.39	0.28	0.49
Dickcissel	0.12	0.48	0.52	0.27	0.58
Lark Bunting	0.47	0.45	0.48	0.61	0.54
Scarlet Tanager	0.23	0.24	0.30	0.31	0.31
Prothonotary Warbler	0.18	0.14	0.17	0.30	0.29
Worm-eating Warbler	0.06	0.04	0.02	0.18	0.17
Golden-winged Warbler	0.05	0.20	0.17	0.17	0.36
Sage Thrasher	0.16	0.06	0.03	0.39	0.32
Brown Thrasher	0.23	0.25	0.16	0.36	0.39
Brown-headed Nuthatch	0.17	0.21	0.14	0.26	0.35
Tufted Titmouse	0.31	0.41	0.40	0.24	0.39
Carolina Chickadee	0.21	0.35	0.28	0.19	0.36
Wood Thrush	0.02	0.39	0.33	0.13	0.42

Table B.2. Nagelkerke's pseudo R^2 values are presented for 19 species of North American passerine birds for three simple models using sites located across the continental United States and southern Canada. The "Climate" model is either a logistic regression of presence/absence, or a zero-inflated negative binomial regression of species abundance, as a quadratic function of temperature and precipitation, and their interaction. The "Space" model is either a logistic regression of presence/absence, or a zero inflated negative binomial regression of species abundance as a quadratic function of latitude and longitude, and their interaction. The "Neighbourhood" model is a logistic regression of presence/absence as a function of the proportion of occupied sites within a 200 km buffer.

	Presence/Absence			**Abundance**	
	Climate	**Geographic Coordinates**	**Neighbourhood**	**Climate**	**Geographic Coordinates**
Eastern Wood-Pewee	0.83	0.87	0.85	0.64	0.68
Acadian Flycatcher	0.58	0.76	0.78	0.44	0.58
Willow Flycatcher	0.29	0.46	0.51	0.29	0.41
Fish Crow	0.50	0.67	0.82	0.37	0.49
Clark's Nutcracker	0.62	0.62	0.56	0.39	0.40
Field Sparrow	0.77	0.77	0.78	0.60	0.60
Eastern Towhee	0.73	0.83	0.82	0.60	0.70
Dickcissel	0.49	0.70	0.77	0.41	0.60
Lark Bunting	0.61	0.78	0.80	0.39	0.46
Scarlet Tanager	0.71	0.76	0.79	0.58	0.63
Prothonotary Warbler	0.53	0.52	0.65	0.39	0.42
Worm-eating Warbler	0.35	0.54	0.54	0.31	0.41
Golden-winged Warbler	0.41	0.44	0.74	0.31	0.41
Sage Thrasher	0.64	0.71	0.67	0.37	0.42
Brown Thrasher	0.76	0.80	0.79	0.65	0.68
Brown-headed Nuthatch	0.66	0.78	0.84	0.43	0.54
Tufted Titmouse	0.78	0.88	0.89	0.62	0.71
Carolina Chickadee	0.78	0.90	0.93	0.58	0.69
Wood Thrush	0.68	0.83	0.83	0.54	0.70

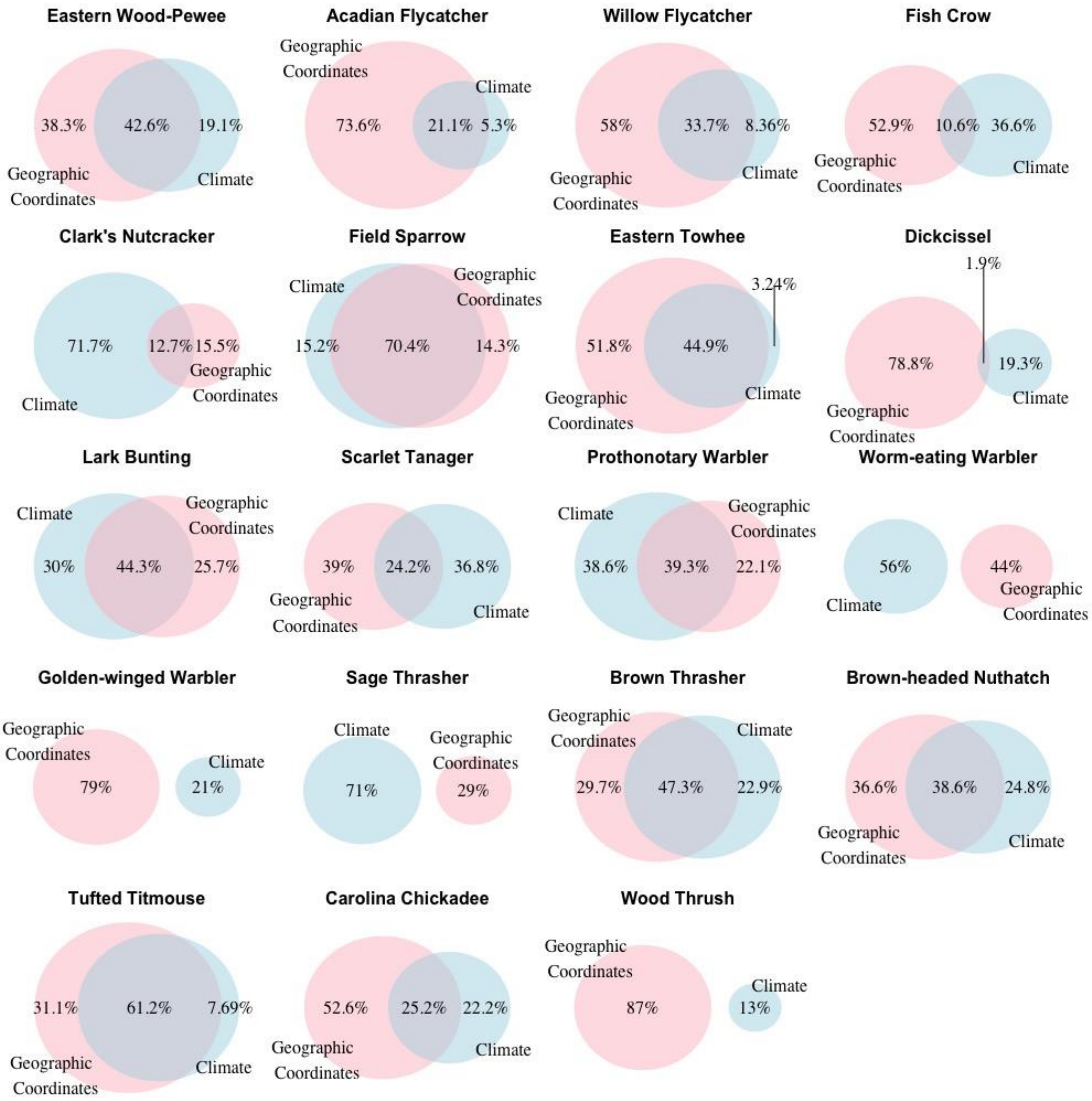
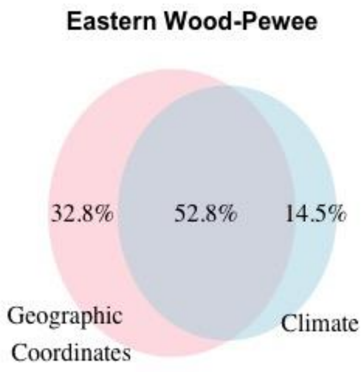
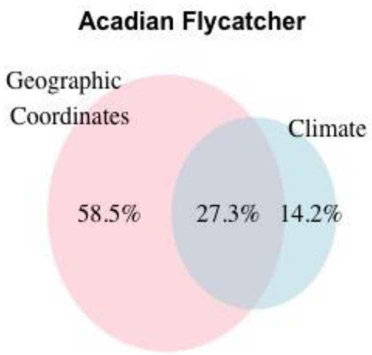
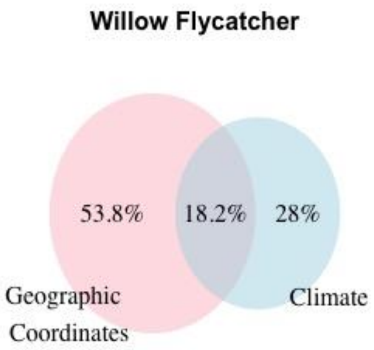
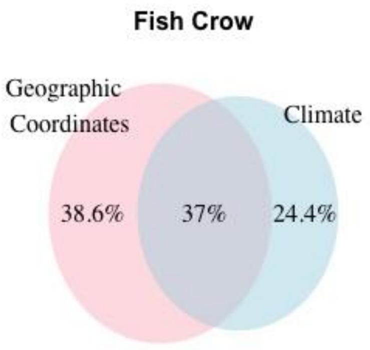

Eastern Wood-Pewee
38.3%
42.6%
19.1%
Geographic Coordinates
Climate
Acadian Flycatcher
Geographic Coordinates
Climate
73.6%
21.1%
5.3%
Willow Flycatcher
58%
33.7%
8.36%
Geographic Coordinates
Climate
Fish Crow
52.9%
10.6%
36.6%
Geographic Coordinates
Climate
Clark's Nutcracker
71.7%
12.7%
15.5%
Geographic Coordinates
Climate
Field Sparrow
Climate
Geographic Coordinates
15.2%
70.4%
14.3%
Eastern Towhee
3.24%
51.8%
44.9%
Geographic Coordinates
Climate
Dickcissel
1.9%
78.8%
19.3%
Geographic Coordinates
Climate
Lark Bunting
Climate
Geographic Coordinates
30%
44.3%
25.7%
Scarlet Tanager
39%
24.2%
36.8%
Geographic Coordinates
Climate
Prothonotary Warbler
Climate
Geographic Coordinates
38.6%
39.3%
22.1%
Worm-eating Warbler
56%
44%
Climate
Geographic Coordinates
Golden-winged Warbler
Geographic Coordinates
79%
Climate
21%
Sage Thrasher
Climate
71%
Geographic Coordinates
29%
Brown Thrasher
Geographic Coordinates
Climate
29.7%
47.3%
22.9%
Brown-headed Nuthatch
36.6%
38.6%
24.8%
Geographic Coordinates
Climate
Tufted Titmouse
31.1%
61.2%
7.69%
Geographic Coordinates
Climate
Carolina Chickadee
52.6%
25.2%
22.2%
Geographic Coordinates
Climate
Wood Thrush
Geographic Coordinates
87%
Climate
13%

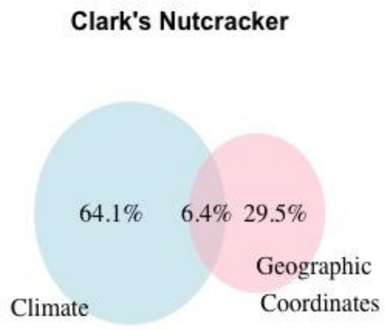
Figure B.1. Venn diagrams representing the partitioned variances of Nagelkerke pseudo R^2 between our simple climatic model and geographic coordinates among 19 species of North American passerine birds. The “Climate” model (blue) is a logistic regression of presence/absence as a quadratic function of temperature and precipitation, and their interaction. The “Geographic Coordinates” model (red) is a logistic regression of presence/absence as a quadratic function of latitude and longitude, and their interaction. The largest proportion of independently explained variance is represented from left to right for each diagram. Results are presented as a percentage of total variance explained using sites located within each species’ geographic range.

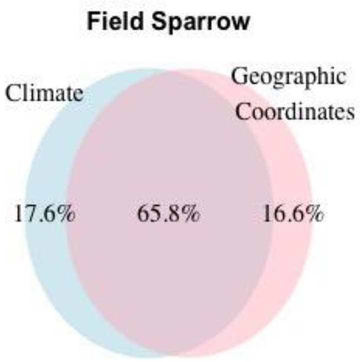

Eastern Wood-Pewee

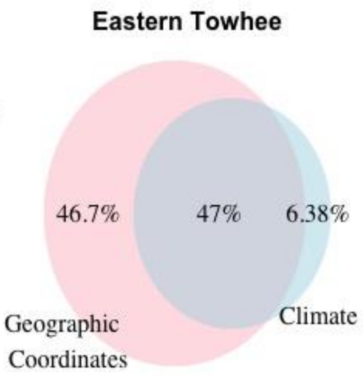

Acadian Flycatcher

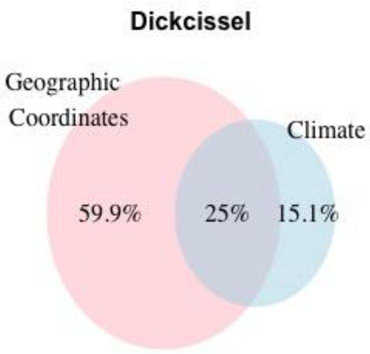

Willow Flycatcher

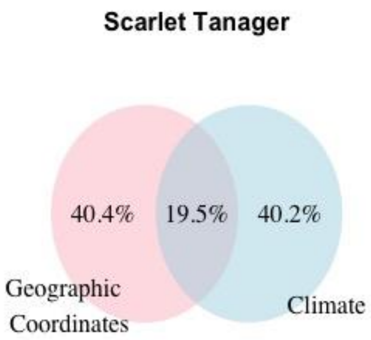

Fish Crow

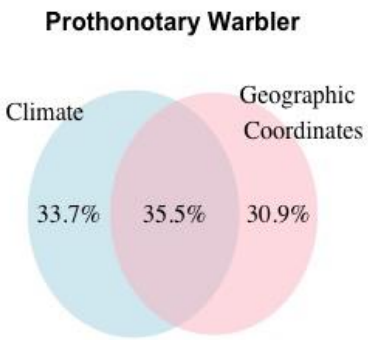

Clark's Nutcracker

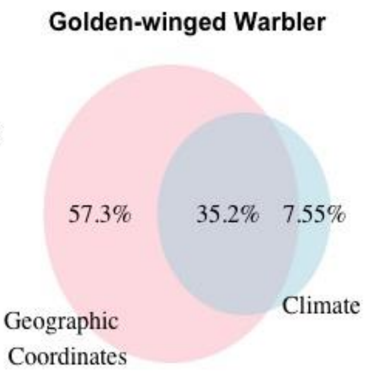

Field Sparrow

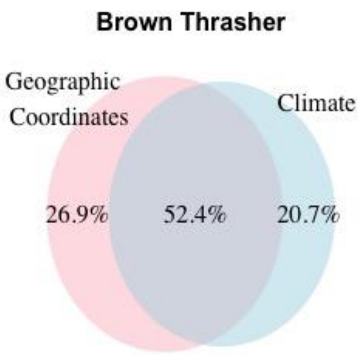

Eastern Towhee

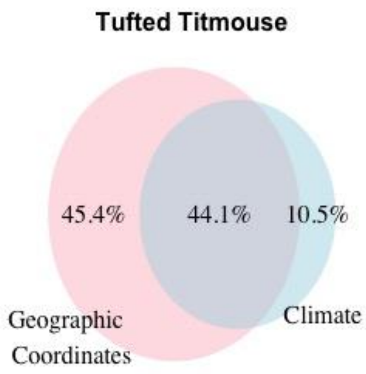

Dickcissel

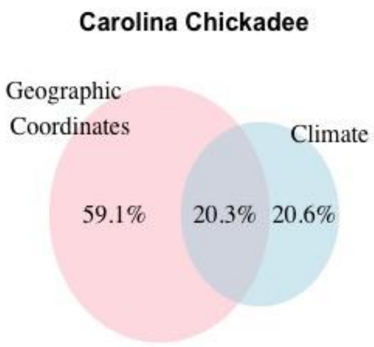

Scarlet Tanager


Prothonotary Warbler


Golden-winged Warbler


Brown Thrasher


Tufted Titmouse


Carolina Chickadee

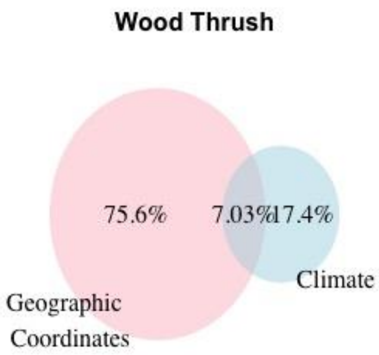
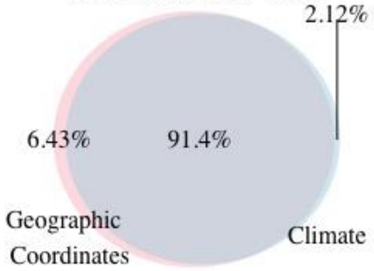
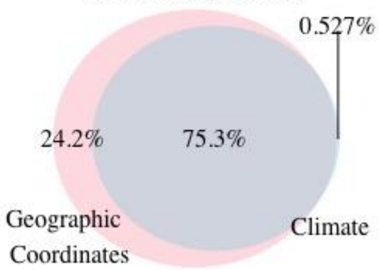

Wood Thrush

Figure B.2. Venn diagrams representing the partitioned variances of Nagelkerke pseudo R^2 between our simple climatic model and geographic coordinates among 15 species of North American passerine birds. The “Climate” model (blue) is a zero-inflated negative binomial regression of species abundance as a quadratic function of temperature and precipitation, and their interaction. The “Geographic Coordinates” model (red) is a zero-inflated negative binomial regression of species abundance as a quadratic function of latitude and longitude, and their interaction. The largest proportion of independently explained variance is represented from left to right for each diagram. Results are presented as a percentage of total variance explained using sites located within each species’ geographic range.

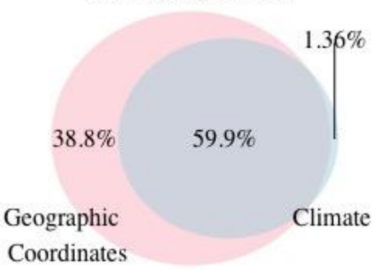
Eastern Wood-Pewee



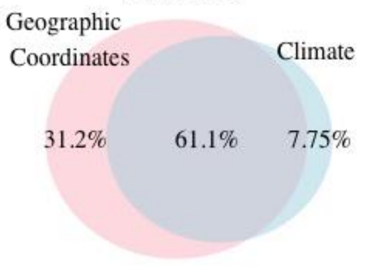
Acadian Flycatcher



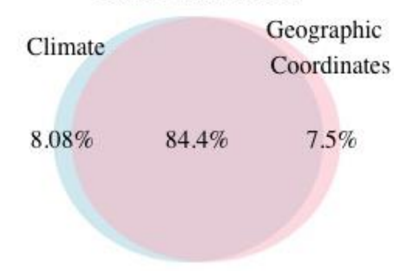
Willow Flycatcher



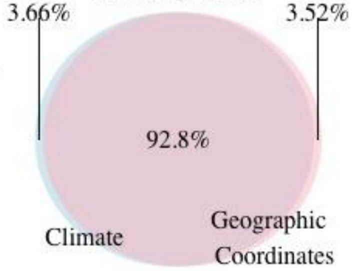
Fish Crow



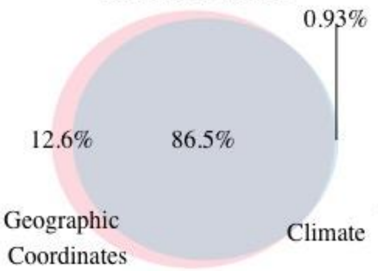
Clark's Nutcracker



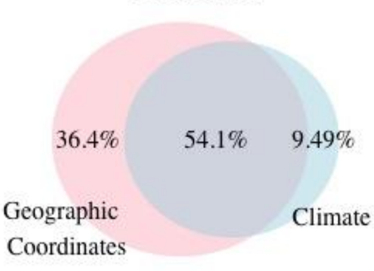
Field Sparrow



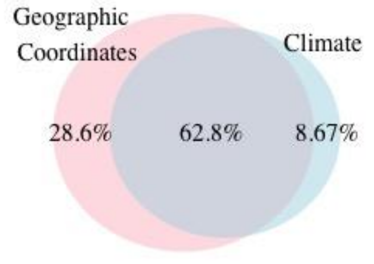
Eastern Towhee



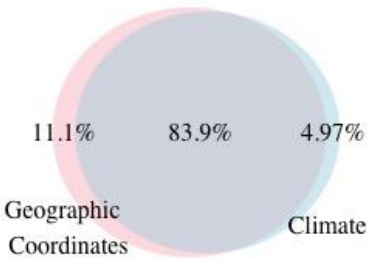
Dickcissel



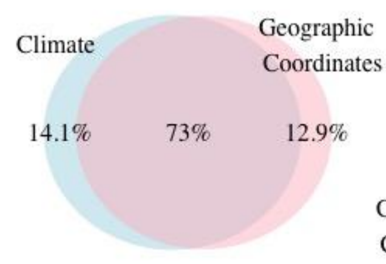
Lark Bunting



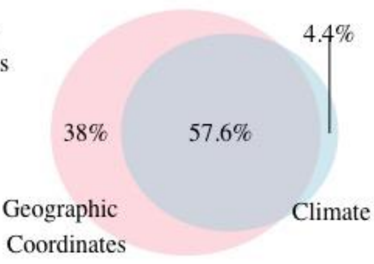
Scarlet Tanager



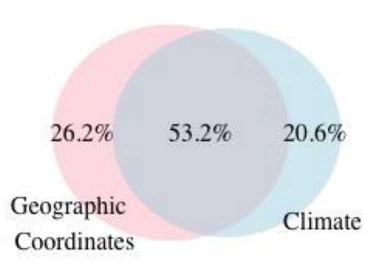
Prothonotary Warbler



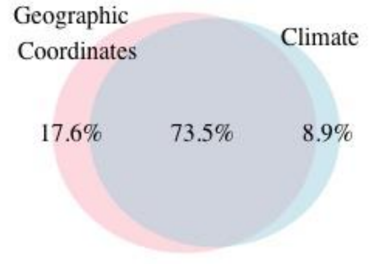
Worm-eating Warbler



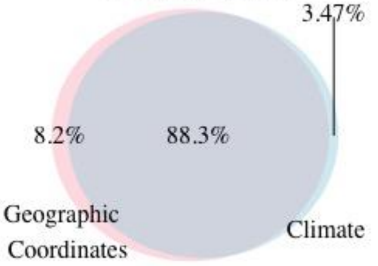
Golden-winged Warbler



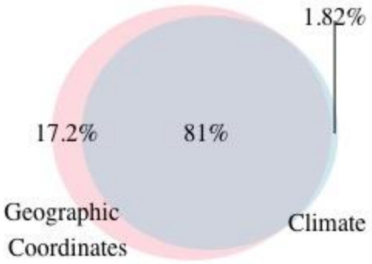
Sage Thrasher



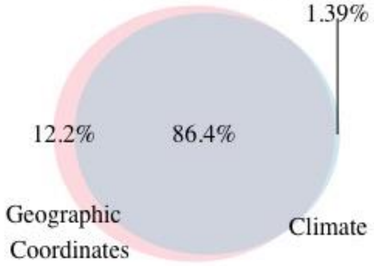
Brown Thrasher



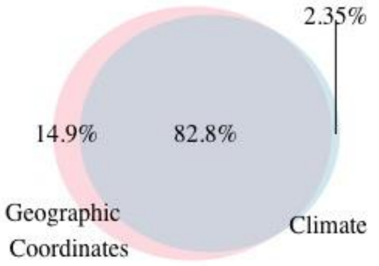
Brown-headed Nuthatch



Tufted Titmouse



Carolina Chickadee



Wood Thrush

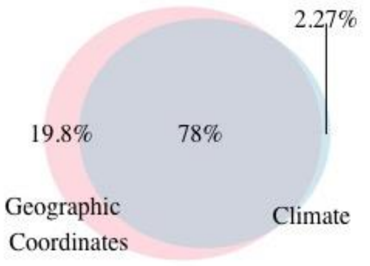


Figure B.3. Venn diagrams representing the partitioned variances of Nagelkerke pseudo R^2 between our simple climatic model and geographic coordinates among 19 species of North American passerine birds. The “Climate” model (blue) is a logistic regression of presence/absence as a quadratic function of temperature and precipitation, and their interaction. The “Geographic Coordinates” model (red) is a logistic regression of presence/absence as a quadratic function of latitude and longitude, and their interaction. The largest proportion of independently explained variance is represented from left to right for each diagram. Results are presented as a percentage of total variance explained using sites located across the continental United States and southern Canada.

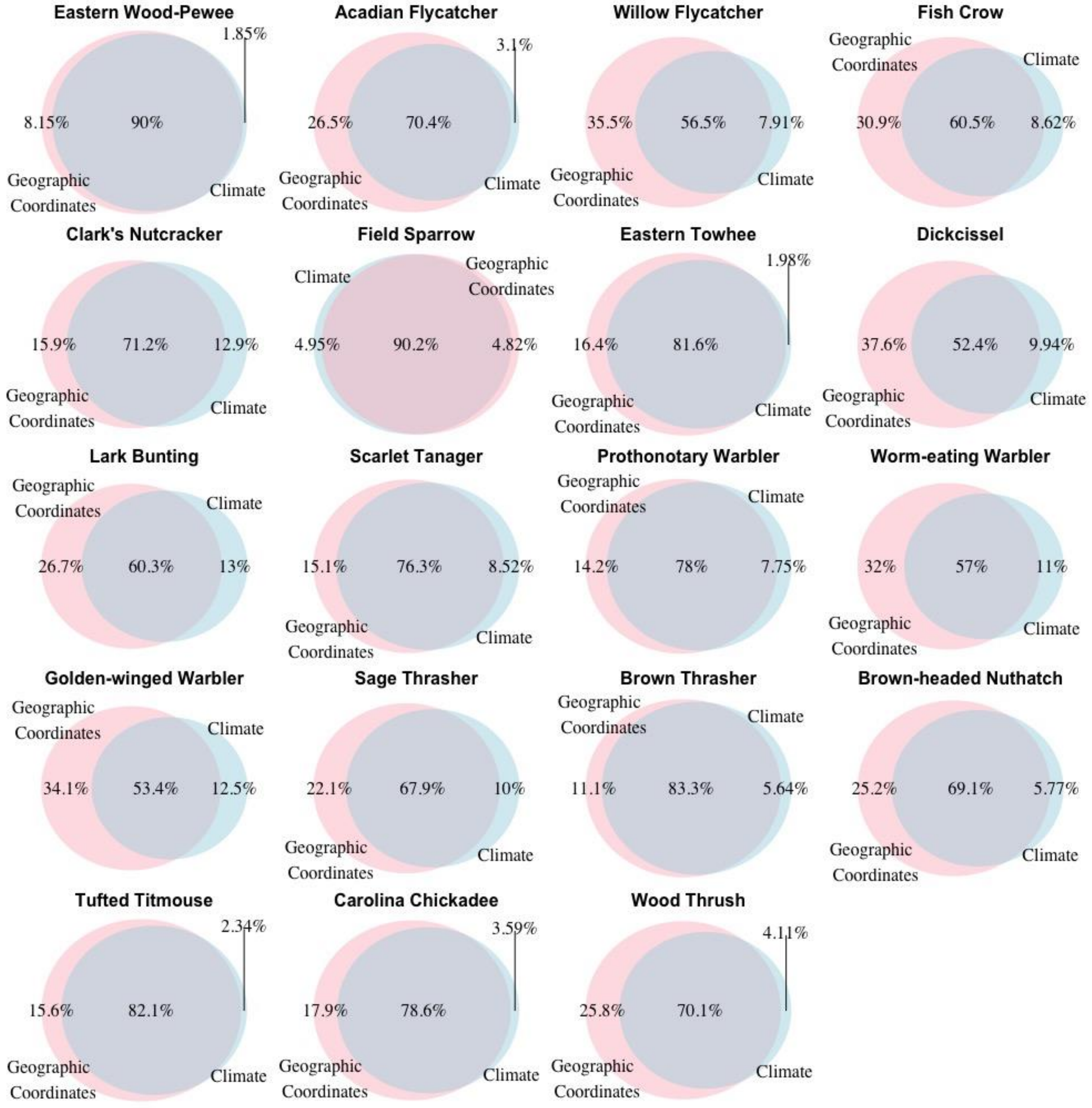

Eastern Wood-Pewee
8.15%
90%
1.85%
Geographic Coordinates
Climate
Acadian Flycatcher
26.5%
70.4%
3.1%
Geographic Coordinates
Climate
Willow Flycatcher
35.5%
56.5%
7.91%
Geographic Coordinates
Climate
Fish Crow
Geographic Coordinates
Climate
30.9%
60.5%
8.62%
Clark's Nutcracker
15.9%
71.2%
12.9%
Geographic Coordinates
Climate
Field Sparrow
Climate
Geographic Coordinates
4.95%
90.2%
4.82%
Eastern Towhee
16.4%
81.6%
1.98%
Geographic Coordinates
Climate
Dickcissel
37.6%
52.4%
9.94%
Geographic Coordinates
Climate
Lark Bunting
Geographic Coordinates
Climate
26.7%
60.3%
13%
Scarlet Tanager
15.1%
76.3%
8.52%
Geographic Coordinates
Climate
Prothonotary Warbler
Geographic Coordinates
Climate
14.2%
78%
7.75%
Worm-eating Warbler
32%
57%
11%
Geographic Coordinates
Climate
Golden-winged Warbler
Geographic Coordinates
Climate
34.1%
53.4%
12.5%
Sage Thrasher
22.1%
67.9%
10%
Geographic Coordinates
Climate
Brown Thrasher
Geographic Coordinates
Climate
11.1%
83.3%
5.64%
Brown-headed Nuthatch
25.2%
69.1%
5.77%
Geographic Coordinates
Climate
Tufted Titmouse
15.6%
82.1%
2.34%
Geographic Coordinates
Climate
Carolina Chickadee
17.9%
78.6%
3.59%
Geographic Coordinates
Climate
Wood Thrush
25.8%
70.1%
4.11%
Geographic Coordinates
Climate

Figure B.4. Venn diagrams representing the partitioned variances of Nagelkerke pseudo R^2 between our simple climatic model and geographic coordinates among 19 species of North American passerine birds. The “Climate” model (blue) is a zero-inflated negative binomial regression of species abundance as a quadratic function of temperature and precipitation, and their interaction. The “Geographic Coordinates” model (red) is a zero-inflated negative binomial regression of species abundance as a quadratic function of latitude and longitude, and their interaction. The largest proportion of independently explained variance is represented from left to right for each diagram. Results are presented as a percentage of total variance explained using sites located across the continental United States and southern Canada.

Table B.3. Path coefficients for Model A (Figure 1) are presented for the relationships among climate, geographic coordinates and presence/absence for each of the 19 North American passerine birds. Results are presented for each species using sites located within each species' geographic range.

	Geographic Coordinates -> Climate	**Climate -> Presence/Absence**	**Geographic Coordinates -> Presence/Absence**
Eastern Wood-Pewee	0.473	0.071	0.427
Acadian Flycatcher	0.221	-0.001	0.567
Willow Flycatcher	0.538	-0.005	0.510
Fish Crow	0.488	0.114	0.475
Clark's Nutcracker	0.735	0.362	0.255
Field Sparrow	0.852	0.251	0.292
Eastern Towhee	0.261	0.025	0.471
Dickcissel	0.073	0.038	0.509
Lark Bunting	0.580	0.144	0.407
Scarlet Tanager	0.640	0.213	0.369
Prothonotary Warbler	0.984	0.513	0.088
Worm-eating Warbler	0.437	0.211	0.418
Golden-winged Warbler	0.076	0.028	0.560
Sage Thrasher	0.922	0.478	0.116
Brown Thrasher	0.669	0.167	0.374
Brown-headed Nuthatch	0.807	0.081	0.489
Tufted Titmouse	0.526	0.081	0.461
Carolina Chickadee	0.376	0.107	0.435
Wood Thrush	0.023	-0.004	0.536

Table B.4. Path coefficients for Model A (Figure 1) are presented for the relationships among climate, geographic coordinates and presence/absence for each of the 19 North American passerine birds. Results are presented for each species using sites located across the continental United States and southern Canada.

	Geographic Coordinates -> Climate	**Climate -> Presence/Absence**	**Geographic Coordinates -> Presence/Absence**
Eastern Wood-Pewee	0.587	0.034	0.462
Acadian Flycatcher	0.248	0.000	0.528
Willow Flycatcher	0.430	-0.017	0.505
Fish Crow	0.209	0.018	0.568
Clark's Nutcracker	0.193	0.001	0.585
Field Sparrow	0.862	0.110	0.423
Eastern Towhee	0.798	0.061	0.453
Dickcissel	0.304	0.076	0.438
Lark Bunting	0.087	0.004	0.548
Scarlet Tanager	0.680	0.065	0.512
Prothonotary Warbler	0.485	0.037	0.521
Worm-eating Warbler	0.119	0.003	0.572
Golden-winged Warbler	0.289	0.029	0.500
Sage Thrasher	0.272	0.002	0.569
Brown Thrasher	0.822	0.117	0.429
Brown-headed Nuthatch	0.568	0.003	0.554
Tufted Titmouse	0.392	0.029	0.504
Carolina Chickadee	0.268	0.013	0.537
Wood Thrush	0.334	0.016	0.533

Table B.5. Path coefficients for Model B (Figure 1) are presented for the relationships among climate, geographic coordinates and presence/absence for each of the 19 North American passerine birds. Results are presented for each species using sites located within each species' geographic range.

	Geographic Coordinates -> Climate	**Climate -> Presence/Absence**	**p-value (Chi-square)**
Eastern Wood-Pewee	0.484	0.250	0.000
Acadian Flycatcher	0.241	0.195	0.000
Willow Flycatcher	0.543	0.232	0.000
Fish Crow	0.504	0.258	0.002
Clark's Nutcracker	0.780	0.425	0.253
Field Sparrow	0.886	0.443	0.000
Eastern Towhee	0.303	0.287	0.000
Dickcissel	0.198	0.246	0.000
Lark Bunting	0.813	0.312	0.001
Scarlet Tanager	0.723	0.375	0.000
Prothonotary Warbler	0.985	0.574	0.689
Worm-eating Warbler	0.453	0.252	0.109
Golden-winged Warbler	0.088	0.042	0.004
Sage Thrasher	0.942	0.516	0.697
Brown Thrasher	0.678	0.285	0.000
Brown-headed Nuthatch	0.818	0.438	0.040
Tufted Titmouse	0.539	0.263	0.000
Carolina Chickadee	0.388	0.158	0.000
Wood Thrush	0.028	0.018	0.000

Table B.6. Path coefficients for Model B (Figure 1) are presented for the relationships among climate, geographic coordinates and presence/absence for each of the 19 North American passerine birds. Results are presented for each species using sites located across the continental United States and southern Canada.

	Geographic Coordinates -> Climate	**Climate -> Presence/Absence**	**p-value (Chi-square)**
Eastern Wood-Pewee	0.606	0.061	0.000
Acadian Flycatcher	0.257	0.030	0.000
Willow Flycatcher	0.457	0.096	0.000
Fish Crow	0.213	0.024	0.000
Clark's Nutcracker	0.193	0.001	0.000
Field Sparrow	0.910	0.270	0.000
Eastern Towhee	0.823	0.292	0.000
Dickcissel	0.330	0.158	0.000
Lark Bunting	0.089	0.004	0.000
Scarlet Tanager	0.694	0.102	0.000
Prothonotary Warbler	0.491	0.049	0.000
Worm-eating Warbler	0.119	0.003	0.000
Golden-winged Warbler	0.292	0.030	0.000
Sage Thrasher	0.273	0.002	0.000
Brown Thrasher	0.840	0.228	0.000
Brown-headed Nuthatch	0.568	0.003	0.000
Tufted Titmouse	0.406	0.062	0.000
Carolina Chickadee	0.269	0.014	0.000
Wood Thrush	0.338	0.026	0.000

Table B.7. Path coefficients for Model C (Figure 1) are presented for the relationships among climate, geographic coordinates and presence/absence for each of the 19 North American passerine birds. Results are presented for each species using sites located within each species' geographic range.

	Geographic Coordinates -> Climate	**Geographic Coordinates -> Presence/Absence**	**p-value (Chi-square)**
Eastern Wood-Pewee	0.473	0.498	0.084
Acadian Flycatcher	0.221	0.566	0.972
Willow Flycatcher	0.538	0.505	0.886
Fish Crow	0.488	0.589	0.150
Clark's Nutcracker	0.735	0.617	0.000
Field Sparrow	0.852	0.544	0.000
Eastern Towhee	0.261	0.496	0.224
Dickcissel	0.073	0.546	0.000
Lark Bunting	0.580	0.550	0.001
Scarlet Tanager	0.640	0.581	0.000
Prothonotary Warbler	0.984	0.601	0.004
Worm-eating Warbler	0.437	0.629	0.002
Golden-winged Warbler	0.076	0.588	0.211
Sage Thrasher	0.922	0.594	0.002
Brown Thrasher	0.669	0.541	0.000
Brown-headed Nuthatch	0.807	0.571	0.685
Tufted Titmouse	0.526	0.542	0.059
Carolina Chickadee	0.376	0.542	0.001
Wood Thrush	0.023	0.532	0.600

Table B.8. Path coefficients for Model C (Figure 1) are presented for the relationships among climate, geographic coordinates and presence/absence for each of the 19 North American passerine birds. Results are presented for each species using sites located across the continental United States and southern Canada.

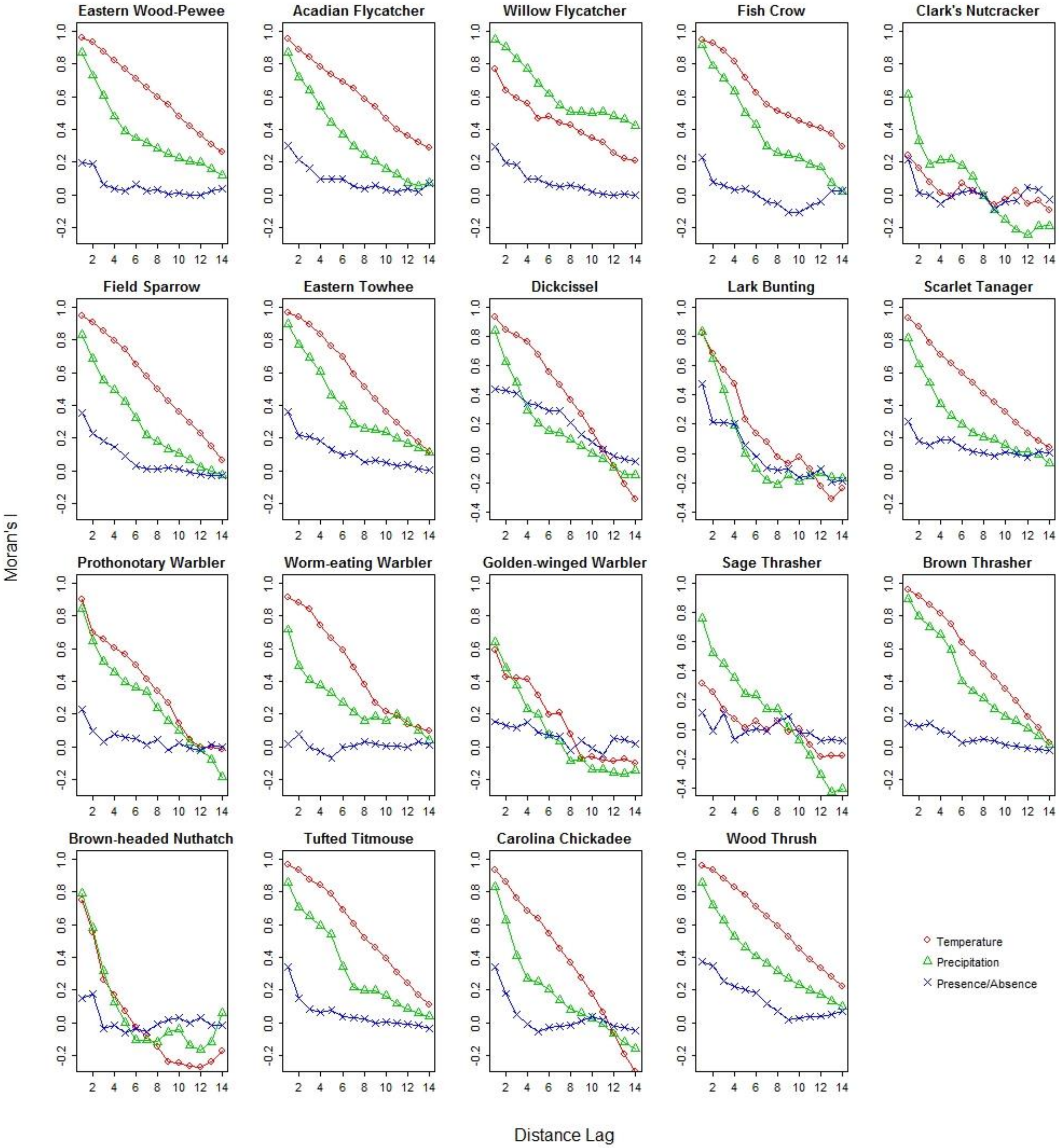
	Geographic Coordinates -> Climate	**Geographic Coordinates -> Presence/Absence**	**p-value (Chi-square)**
Eastern Wood-Pewee	0.587	0.496	0.000
Acadian Flycatcher	0.248	0.528	0.990
Willow Flycatcher	0.430	0.487	0.049
Fish Crow	0.209	0.586	0.001
Clark's Nutcracker	0.193	0.586	0.000
Field Sparrow	0.862	0.533	0.000
Eastern Towhee	0.798	0.514	0.006
Dickcissel	0.304	0.514	0.000
Lark Bunting	0.087	0.552	0.000
Scarlet Tanager	0.680	0.577	0.000
Prothonotary Warbler	0.485	0.558	0.000
Worm-eating Warbler	0.119	0.575	0.062
Golden-winged Warbler	0.289	0.529	0.000
Sage Thrasher	0.272	0.571	0.007
Brown Thrasher	0.822	0.546	0.000
Brown-headed Nuthatch	0.568	0.556	0.135
Tufted Titmouse	0.392	0.532	0.000
Carolina Chickadee	0.268	0.549	0.000
Wood Thrush	0.334	0.549	0.003

Table. B.9. Path coefficients for Model D (Figure 1) are presented for the relationships among climate, geographic coordinates and presence/absence for each of the 19 North American passerine birds. Results are presented for each species using sites located within each species' geographic range.

	Climate -> Presence/Absence	**Geographic Coordinates -> Presence/Absence**	**p-value (Chi-square)**
Eastern Wood-Pewee	0.445	0.557	0.000
Acadian Flycatcher	0.282	0.532	0.000
Willow Flycatcher	0.277	0.384	0.000
Fish Crow	0.329	0.408	0.000
Clark's Nutcracker	0.531	0.296	0.000
Field Sparrow	0.668	0.631	0.000
Eastern Towhee	0.477	0.733	0.000
Dickcissel	0.397	0.687	0.000
Lark Bunting	0.753	0.758	0.000
Scarlet Tanager	0.623	0.520	0.000
Prothonotary Warbler	0.476	0.431	0.000
Worm-eating Warbler	0.284	0.221	0.000
Golden-winged Warbler	0.267	0.548	0.050
Sage Thrasher	0.432	0.267	0.000
Brown Thrasher	0.461	0.519	0.000
Brown-headed Nuthatch	0.419	0.441	0.000
Tufted Titmouse	0.551	0.683	0.000
Carolina Chickadee	0.473	0.661	0.000
Wood Thrush	0.148	0.646	0.000

Table B.10. Path coefficients for Model D (Figure 1) are presented for the relationships among climate, geographic coordinates and presence/absence for each of the 19 North American passerine birds. Results are presented for each species using sites located across the continental United States and southern Canada.

	Climate -> Presence/Absence	**Geographic Coordinates -> Presence/Absence**	**p-value (Chi-square)**
Eastern Wood-Pewee	0.855	0.860	0.000
Acadian Flycatcher	0.917	0.977	0.000
Willow Flycatcher	0.606	0.793	0.000
Fish Crow	0.888	0.978	0.000
Clark's Nutcracker	0.880	0.890	0.000
Field Sparrow	0.865	0.876	0.000
Eastern Towhee	0.866	0.914	0.000
Dickcissel	0.850	0.955	0.000
Lark Bunting	0.839	0.897	0.000
Scarlet Tanager	0.912	0.900	0.000
Prothonotary Warbler	0.935	0.919	0.000
Worm-eating Warbler	0.863	0.826	0.000
Golden-winged Warbler	0.758	0.792	0.000
Sage Thrasher	0.922	0.945	0.000
Brown Thrasher	0.859	0.863	0.000
Brown-headed Nuthatch	0.905	0.884	0.000
Tufted Titmouse	0.868	0.904	0.000
Carolina Chickadee	0.938	0.980	0.000
Wood Thrush	0.835	0.853	0.000



Eastern Wood-Pewee
Acadian Flycatcher
Willow Flycatcher
Fish Crow
Clark's Nutcracker
Field Sparrow
Eastern Towhee
Dickcissel
Lark Bunting
Scarlet Tanager
Prothonotary Warbler
Worm-eating Warbler
Golden-winged Warbler
Sage Thrasher
Brown Thrasher
Brown-headed Nuthatch
Tufted Titmouse
Carolina Chickadee
Wood Thrush
Moran's I
Distance Lag
2 4 6 8 10 12 14
-0.4 -0.2 0.0 0.2 0.4 0.6 0.8 1.0
◇ Temperature
△ Precipitation
× Presence/Absence

Figure B.5. Correlograms of Moran's I representing the decay of spatial autocorrelation over distance for presence/absence (cross), temperature (circle) and precipitation (triangle), for each of the 19 North American passerine bird species. Results are presented for sites located within each species' geographic range. Distance lags are a measure of distance threshold corresponding to the generation of neighbours around a given point (i.e., first generation are neighbours closest to a given route, second generation are neighbours closest to first generation etc.).

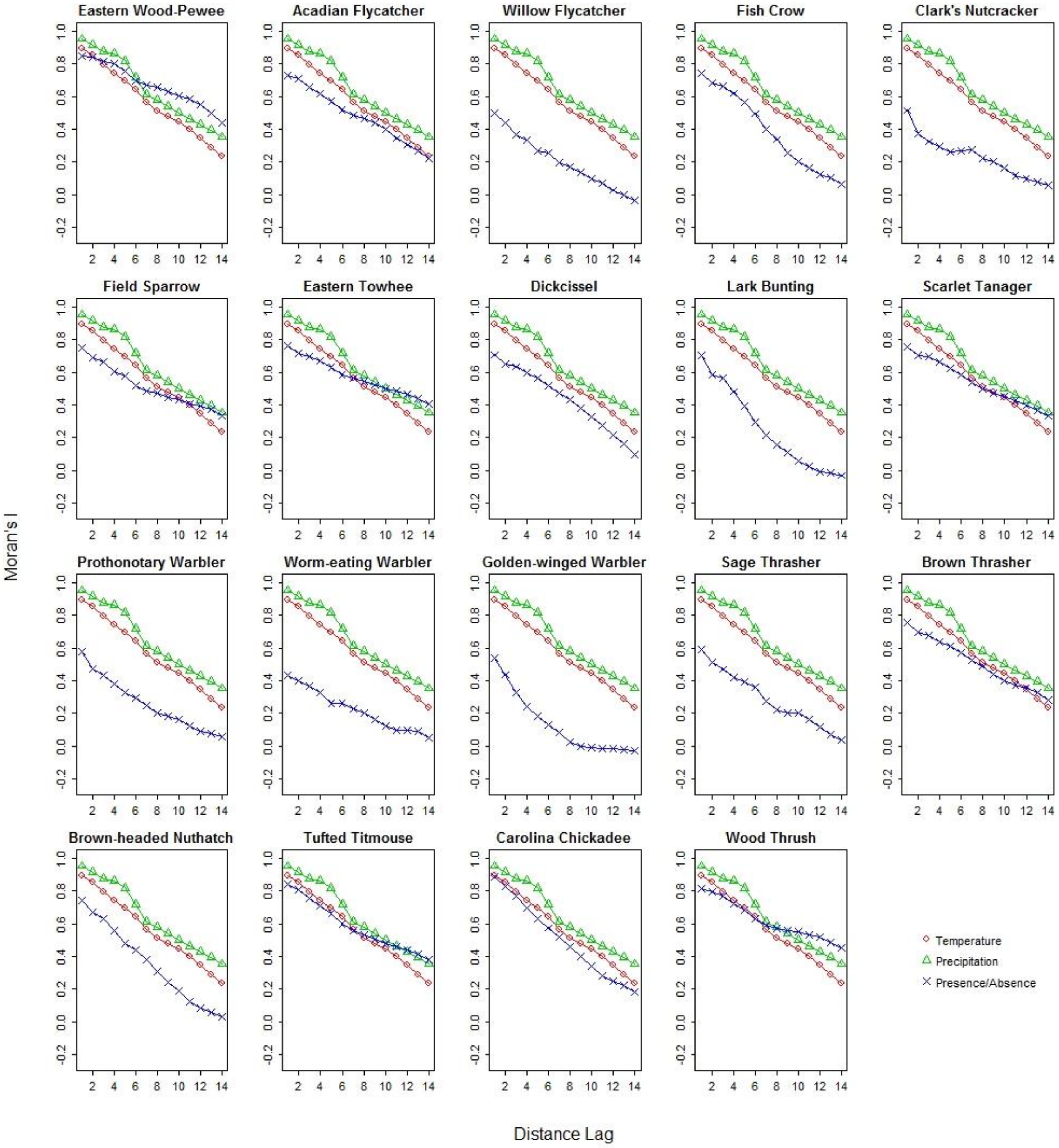

Eastern Wood-Pewee
Acadian Flycatcher
Willow Flycatcher
Fish Crow
Clark's Nutcracker
Field Sparrow
Eastern Towhee
Dickcissel
Lark Bunting
Scarlet Tanager
Prothonotary Warbler
Worm-eating Warbler
Golden-winged Warbler
Sage Thrasher
Brown Thrasher
Brown-headed Nuthatch
Tufted Titmouse
Carolina Chickadee
Wood Thrush
Moran's I
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
2
4
6
8
10
12
14
Distance Lag
◇ Temperature
△ Precipitation
× Presence/Absence

Figure B.6. Correlograms of Moran’s I representing the decay of spatial autocorrelation over distance for presence/absence (cross), temperature (circle) and precipitation (triangle), for each of the 19 North American passerine bird species. Results are presented for sites located across the continental United States and southern Canada. Distance lags are a measure of distance threshold corresponding to the generation of neighbours around a given point (i.e., first generation are neighbours closest to a given route, second generation are neighbours closest to first generation etc.).


Eastern Wood-Pewee
Acadian Flycatcher
Willow Flycatcher
Fish Crow
Clark's Nutcracker
Field Sparrow
Eastern Towhee
Dickcissel
Lark Bunting
Scarlet Tanager
Prothonotary Warbler
Worm-eating Warbler
Golden-winged Warbler
Sage Thrasher
Brown Thrasher
Brown-headed Nuthatch
Tufted Titmouse
Carolina Chickadee
Wood Thrush
Longitude
Latitude
Precipitation
Temperature
Proportion of Occupied Neighbouring Routes
Climatic Variable
Spatially Explicit Variable
Mean Importance (Decrease in Model Accuracy)

Figure B.7. Bar plots representing the decrease in model accuracy as a measure of variable importance over all nine variables examined, for each of the 19 North American passerine bird species. Results are presented using sites located within each species' geographic range. Spatially structured variables are represented in orange, climatic variables are represented in cyan.


Eastern Wood-Pewee
Acadian Flycatcher
Willow Flycatcher
Fish Crow
Clark's Nutcracker
Field Sparrow
Eastern Towhee
Dickcissel
Lark Bunting
Scarlet Tanager
Prothonotary Warbler
Worm-eating Warbler
Golden-winged Warbler
Sage Thrasher
Brown Thrasher
Brown-headed Nuthatch
Tufted Titmouse
Carolina Chickadee
Wood Thrush
Longitude
Latitude
Precipitation
Temperature
Proportion of Occupied Neighbouring Routes
0 10 20 30 40 50
0 10 20 30 40 50 60
0 5 10 15 20 25 30
0 10 20 30 40
0 20 40 60 80
Climatic Variable
Spatially Explicit Variable
Mean Importance (Decrease in Model Accuracy)

Figure B.8. Bar plots representing the decrease in model accuracy as a measure of variable importance over all nine variables examined, for each of the 19 North American passerine bird species. Results are presented using sites located across the continental United States and southern Canada. Spatially structured variables are represented in orange, climatic variables are represented in cyan.

Appendix C: Correction for Moran’s I on Binomial Variables

Due to the fact that Moran’s I is highest when prevalence is 0.5, Chapman (2010) corrected Moran’s I values for presence/absence to account for potentially erroneous representations of spatial autocorrelation. The model $I = b_0 + b_1 X (\text{prevalence} - 0.5)^2$ was fit by regression and the residuals were extracted as a measure of local autocorrelation. Following this method, here, prevalence was calculated for each spatial lag of 65 km, for every BBS route, for each of the 19 species, and was incorporated to calculate corrected Moran’s I values (Figure C.1). The results were considered negligible from those illustrated in Figure 5.

To further address any potential errors stemming from calculating Moran’s I with binary variables, we also produced the analysis for species abundance (Figure C.2). Within-range, the decay of spatial autocorrelation of abundance performs similarly to that of presence/absence (Figure 5a), indicating that abundance may also be driven by more regionalized processes (e.g., short-distance dispersal), as opposed to macroclimate. At the hemi-continental scale, the spatial decay of autocorrelation differs greatly from that observed with presence/absence (Figure 5b). It is unsurprising that species abundance at the hemi-continental scale resembles the spatial decay within species’ ranges as abundance is much more sensitive to regional processes than is presence/absence. Conceptually, this observation reflects the notion that species’ abundances may depend primarily on local colonization and extinction at both spatial scales.

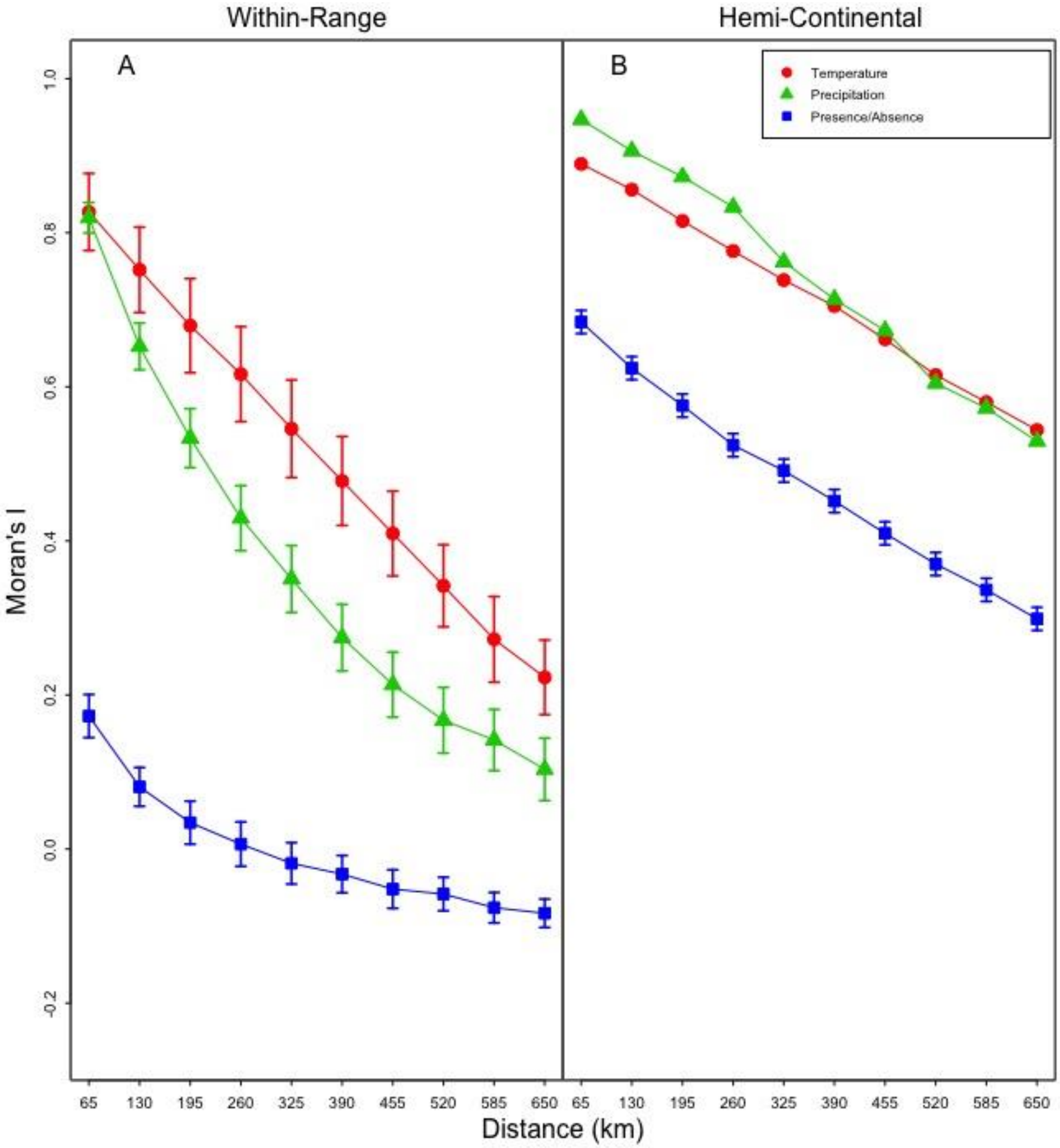

Within-Range
Hemi-Continental
A
B
Temperature
Precipitation
Presence/Absence
Moran's I
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
65
130
195
260
325
390
455
520
585
650
Distance (km)

Figure C.1. Correlogram of corrected Moran's I (following Chapman (2010)), representing the decay of spatial autocorrelation (+/- standard error) over distance (km) for presence/absence (square), temperature (circle) and precipitation (triangle), averaged over 19 North American passerine bird species. Panel (A) shows results for sites located within a species' geographic range; panel (B) shows results using sites across the continental United States and southern Canada.

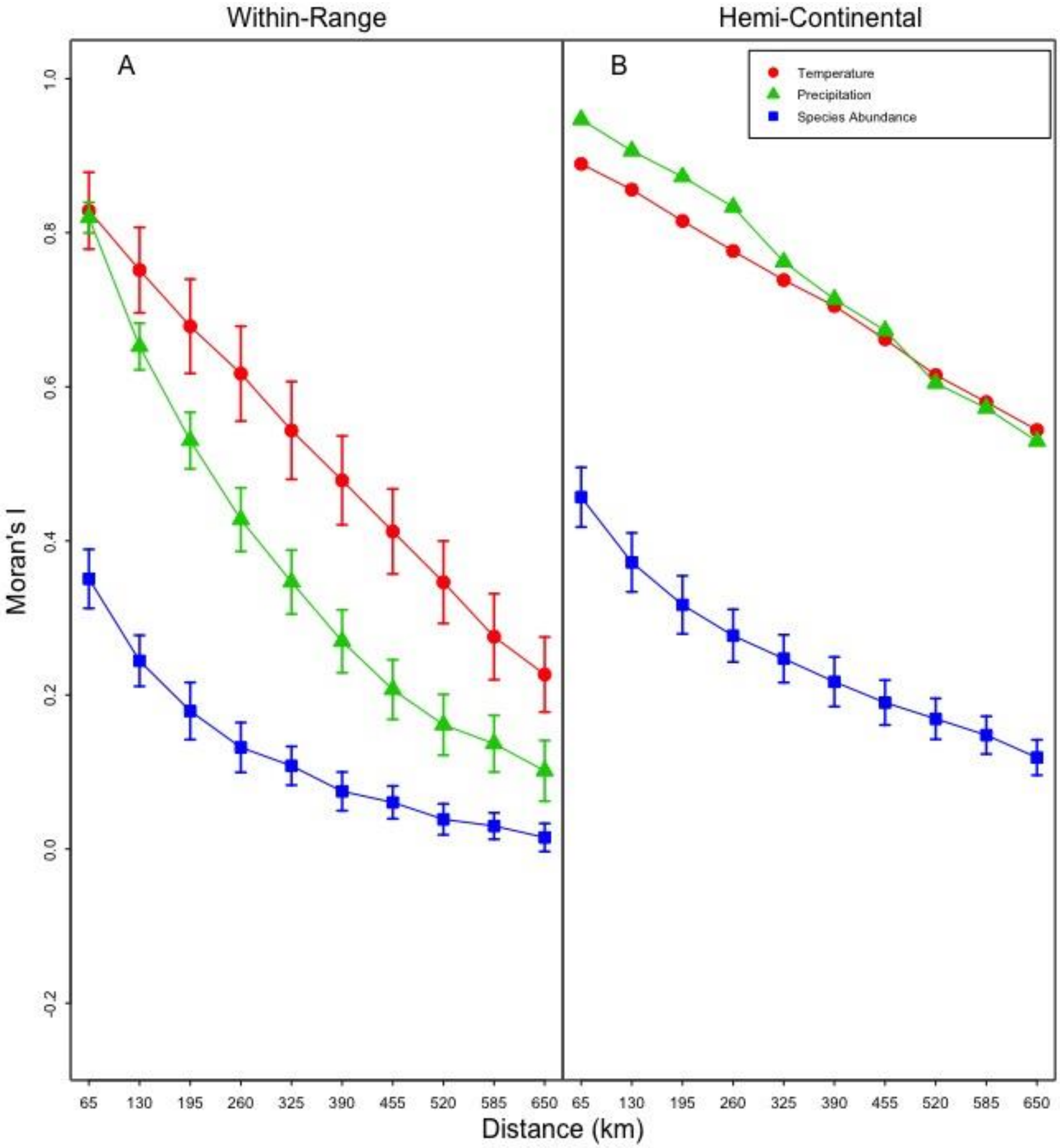

Within-Range
Hemi-Continental
A
B
Temperature
Precipitation
Species Abundance
Moran's I
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
65
130
195
260
325
390
455
520
585
650
Distance (km)

Figure C.2. Correlogram of Moran's I, representing the decay of spatial autocorrelation (+/- standard error) over distance (km) for species abundance (square), temperature (circle) and precipitation (triangle), averaged over 19 North American passerine bird species. Panel (A) shows results for sites located within a species' geographic range; panel (B) shows results using sites across the continental United States and southern Canada.