Can species distribution models predict colonizations and extinctions?

By

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Résumé

Objectif

MaxEnt, une technique de modélisation de la distribution des espèces très populaire a été largement utilisée pour relier les distributions géographiques des espèces aux conditions environnementales et pour prédire les changements dans la répartition des espèces en réponse aux changements climatiques. Ici, nous testons sa capacité prédictive dans le temps (plutôt que dans l'espace, comme c'est généralement le cas) en modélisant la colonisation et l'extinction.

Emplacement

États-Unis et sud du Canada.

Période de temps

1979-2009

Principaux taxons étudiés

Vingt et une espèces d'oiseaux passereaux.

Méthodes

Nous avons utilisé MaxEnt pour relier les distributions géographiques des espèces à la variation des conditions environnementales en Amérique du Nord. Nous avons ensuite modélisé la colonisation et l'extinction entre 1979 et 2009 en fonction de l’habitabilité précédente, du changement interannuel de l’habitabilité (tous deux estimées par les modèles MaxEnt) et de l'occupation du voisinage. Nous avons évalué si les effets étaient dans les directions anticipées, nous avons partitionné la déviance expliquée des modèles, et avons comparé la précision des modèles de colonisation et d'extinction à l'AUC des modèles MaxEnt.

Résultats

La colonisation et l'extinction varient en fonction de l’habitabilité précédente, du changement interannuel d’habitabilité et de l'occupation du voisinage, dans les directions attendues. Le changement dans la qualité de l'habitat explique très peu par rapport aux autres prédicteurs. L'occupation du voisinage explique une plus grande part de la déviance dans les modèles de colonisation que dans les modèles d'extinction. L'AUC des modèles MaxEnt est corrélé avec la valeur prédictive des modèles d’extinction, mais pas avec celle des modèles de colonisation.

Principales conclusions

MaxEnt semble capturer un effet réel de l'environnement sur la distribution des espèces puisque l'effet de la qualité de l'habitat est détecté à la fois dans le temps et dans l'espace. Cependant, le changement dans la qualité de l'habitat est un mauvais prédicteur du changement d'occupation. Sur de courtes échelles temporelles, l'occupation du voisinage par des congénères prédit aussi bien les changements d'occupation que les modèles MaxEnt. La capacité des modèles MaxEnt à prédire la variation géographique de l'occupation des espèces donne peu d'indications sur la transférabilité des modèles dans le temps. Ainsi, la valeur prédictive des modèles de distribution d’espèces risque d’être surestimée lorsqu'ils sont évalués spatialement. Dans le futur, les prédictions des réponses des espèces aux changements climatiques devraient faire une distinction entre colonisation et extinction, et reconnaître que les deux processus ne sont pas également bien prédits par les SDM.

Abstract

Aim

MaxEnt, a very popular species distribution modelling technique, has been used extensively to relate species' geographic distributions to environmental variables and to predict changes in species' distributions in response to environmental change. Here, we test its predictive ability through time (rather than through space, as is commonly done) by modeling colonizations and extinctions.

Location

Continental U.S. and southern Canada.

Time period

1979-2009

Major taxa studied

Twenty-one species of passerine birds.

Methods

We used MaxEnt to relate species' geographic distributions to the variation in environmental conditions across North America. We then modelled site-specific colonizations and extinctions between 1979 and 2009 as functions of MaxEnt-estimated previous habitat suitability and inter-annual change in habitat suitability and neighborhood occupancy. We evaluated whether the effects were in the expected direction, we partitioned model's explained deviance, and we compared colonization and extinction model's accuracy to MaxEnt's AUC.

Results

Colonization and extinction probabilities both varied as functions of previous habitat suitability, change in habitat suitability, and neighborhood occupancy, in the expected direction. Change in habitat suitability explained very little deviance compared to other predictors. Neighborhood occupancy accounted for more explained deviance in colonization models than in extinction models. MaxEnt AUC correlates with extinction models' predictive ability, but not with that of colonization models.

Main conclusions

MaxEnt appears to sometime capture a real effect of the environment on species' distributions since a statistical effect of habitat suitability is detected through both time and space. However, change in habitat suitability (which is much smaller through time than through space) is a poor predictor of change in occupancy. Over short time scales, proximity of sites occupied by conspecifics predicts changes in occupancy just as well as MaxEnt. The ability of MaxEnt models to predict spatial variation in occupancy (as measured by AUC) gives little indication of transferability through time. Thus, the predictive value of species distribution models may be overestimated when evaluated through space only. Future prediction of species' responses to climate change should make a distinction between colonization and extinction, recognizing that the two processes are not equally well predicted by SDMs.

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Introduction

Species distribution models (SDMs), also called environmental niche models or bioclimatic envelope models, are the main tool used to predict the movement of species in response to climate change. Based on a Hutchinsonian niche concept, SDMs relate the presence of species to physical characteristics of the environment. SDMs assume that species' responses to environmental variables do not vary through time or space (i.e. the assumption of stationarity) (Pearman et al., 2008; Wiens et al., 2010). SDMs assume further that species are near equilibrium with the environmental variables that drive their distributions (i.e. that suitable habitats are mainly occupied, while unsuitable habitats are unoccupied), and that ranges are not limited by dispersal.

It has been argued that the assumptions of SDMs might not be met under climate change because the distribution of suitable environmental condition is always changing (Yackulic et al., 2015). In fact, recent literature indicates that the extremes of environmental conditions within the geographic range currently occupied by a species only very vaguely reflects the species' tolerances (Araújo et al., 2013; Boucher-Lalonde et al., 2014a; Hargreaves et al., 2014; but see Lee-Yaw et al., 2016). Clearly, species' geographic ranges could potentially be affected by other factors such as biotic interactions (Davis et al., 1998a, 1998b; Svenning & Skov, 2007; Svenning et al., 2014), dispersal (Marsico & Hellmann, 2009), macroevolutionary history (Roy et al., 2009), and stochastic factors (Rosindell et al., 2011). Insofar as non-climatic influences on ranges actually are important, the *realized* geographic distribution of species (on which SDMs are based) may not be a very good indicator of their environmental tolerances, and SDMs may poorly predict species response to climate change (Anderson, 2013). In principle, the *potential* distribution, based on laboratory-measured physiological tolerance, should be a more relevant predictor of the consequences of climate change (Phillips, 2008). However, even the potential climatic niches of species are not necessarily good predictors of their ranges (e.g., reptiles in Fig. 5 in Araújo et al 2013). Yet, for want of a better alternative, environmental niche models have been used to predict changes in the geographic distributions of species in response to climate change (Matthews et al., 2011; Reese & Skagen, 2017) up to several decades in the future (Thomas et al., 2004; Thuiller, 2004).

With over 6000 published applications (Phillips et al., 2017) since it was first proposed, MaxEnt (Phillips et al., 2006), a presence-only modelling technique, stands out as one of the most used (and misused: Yackulic et al., 2013) SDM techniques**.** MaxEnt is applied to important questions in ecology and conservation (Elith et al., 2011), including the potential effect of climate change on the distribution of species (Yates et al., 2010) and the risk of invasion of introduced species (Wang et al., 2007). Its ease of use, its comparatively good performance at describing species' current distributions (Elith et al., 2006) and its ability to use the most widely available type of data (presence only) have probably played a role in its popularity. Like most presence-only models, MaxEnt contrasts the environmental conditions at known occurrence sites to "background" conditions that characterize the conditions available for the species within the study region (Phillips et al., 2006).

The typical way of assessing SDM performance is cross-validation: testing the model on randomly selected, held-out subsets of a dataset. Variations on the cross-validation procedure have been proposed as ways to evaluate model transferability. The procedure generally relies on non-random cross-validation, where the data are divided into training and testing data sets based on geographic region (Wenger & Olden, 2012; Radosavljevic & Anderson, 2014). Even using these methods, due to spatial autocorrelation, dependence between test data and training data is unavoidable and leads to inflated measures of model performance (Bahn & McGill, 2013). Moreover, any spatially structured predictor variable may perform well in an SDM (i.e. show reasonable goodness of fit), irrespective of whether a causal link exists (Bahn & McGill, 2007; Beale, 2008; Chapman, 2010; Fourcade et al., 2017). While these methods can be used to evaluate spatial transferability, they do not test a model's ability to predict temporal variation, and it is unclear to what extent spatial transferability can be used as a surrogate for temporal transferability.

If SDMs capture the causal relationships that determine species' geographic distributions, then the models should predict changes in geographic distributions when the driving variables change (e.g. Kharouba et al., 2009). Furthermore, if SDMs are to be used to *predict* distributional shifts in response to climate change, then a better way of evaluating SDMs would be to test whether *change* in habitat suitability is followed by the predicted *change* in occupancy through time. This is the same as asking whether SDMs can predict colonization and extinction, since changes in the geographical extent of a species can ultimately be described in terms of local colonization and extinction.

Here, we examined the colonization and extinction dynamics of 21 passerine bird species between 1979 and 2009 at sites across their entire breeding ranges, as documented in the North American Breeding Bird Survey (BBS) (Pardieck et al., 2017). We related these colonizations and extinctions to environmental changes. First, we tested whether the ability of a MaxEnt model to describe spatial variation in occupancy is a good indication of its ability to predict temporal variation in occupancy. Then, we tested the predictions that 1) changes in habitat suitability (as estimated with a MaxEnt SDM) through time are accompanied by parallel changes in colonization probability and 2) inverse changes in extirpation probability over a relatively short time scale (one to a few years). Finally, we compared the predictive ability of MaxEnt to that of a simple spatial model based on occupancy of neighbouring sites by conspecifics, to assess how much temporal variability in species occupancy can be explained by MaxEnt beyond what can be explained by the spatial structure of species distributions alone.

Material and Methods

Species data

The species data we used came from the North American Breeding bird survey (Pardieck et al., 2017). The data consist of observations of the presence (and estimated abundance) of bird species on approximately 4900 routes in the U.S. and southern Canada. Observation are made each year by skilled volunteers during birds' breeding season (May to June). Most routes are sampled several years in a row. The BBS survey started in 1966, but we only use data from 1979 to 2009, because our environmental data only covered that range. BBS sampling covers much of North America, but some regions are better sampled than others. Sampling intensity tends to follow road density and human population density. We only used observations that met BBS criteria of quality (i.e. Runtype = 1).

The BBS contains observations on > 700 species, but we used only 21 species for the following reasons. First, we only included Passerine species because they are the species most reliably detected using the BBS protocol (Cunningham et al., 1999). Second, we excluded non-native species from the study since they are unlikely to meet MaxEnt's assumption that the species is in equilibrium with its environment. Third, because we wished to observe distribution shifts in all directions, we eliminated species whose potential breeding range extended beyond the area sampled by the BBS (i.e., into Mexico or northern Canada). Following Currie & Venne (2017), we defined the potential breeding range of each bird as the union of the breeding range map depicted by BirdLife International (http://www.birdlife.org/datazone/info/spcdownload) and the BBS routes at which the species was observed at least once between 1979 and 2009, plus a 100 km buffer around each of those routes (most, but not all, BBS presences fall within the BirdLife ranges). Finally, we excluded any species that was observed on fewer than 20 routes during any given year because species with very small ranges are unlikely to be constrained by climate (Stockwell & Peterson, 2002; Proosdij et al., 2016), and because SDMs based on <20 points have low precision. This left 21 species. Range shifts have been reported over the study period for those 21 species, making them good candidates for this study (Currie & Venne, 2017). A list of the 21 species included in this study, as well as map of each species' potential range, are provided in appendices B and E respectively.

MaxEnt estimates the relative suitability of sites for a given species by comparing environmental conditions at occupied sites to the available environmental conditions in the study region (the "background"). The background should include "the area that has been accessible to the species of interest over relevant time period" (Barve et al., 2011). The area included in the background can have an important influence on the MaxEnt model fit (Royle et al., 2012; Merow et al., 2013). We used each species' potential breeding range to define its "background" in our MaxEnt models (below). We used a buffer of 100 km around occupied sites (see above) to defined species' potential breeding range because smaller buffers often produced fragmented ranges, while larger buffers could overestimate the area accessible to the species over the study period.

Environmental data

Monthly environmental data come from the National Center for Environmental Prediction (Saha et al., 2010) and have a spatial resolution of 0.5° (~ 50 km). We calculated the average of each environmental variable during the breeding season (May to June) for each year from 1979 to 2009. The seven environmental variables we used in the MaxEnt models are average temperature, average precipitation rate, average transpiration, soil type, vegetation type, average percent vegetation cover, and elevation (Appendix D).

MaxEnt models

We produced species-specific distribution models using MaxEnt (version 3.4.0) (Phillips et al., 2017) carried out with the dismo package (Hijmans et al., 2015) in R version 3.4.0 (R Core Team, 2018) with the default settings (i.e. all feature classes except threshold). MaxEnt output (which we refer to as *habitat suitability*) is proportional to the density of individuals per unit area (raw output), and it is monotonically related to the probably of presence (logistic output) (Elith et al., 2011; Yackulic et al., 2013).

MaxEnt is often viewed as a “black-box” and is too often used with little consideration of its limitations (Yackulic et al., 2013). It was originally described as a machine-learning method (Phillips et al., 2006). However, Renner & Warton (2013) have demonstrated that MaxEnt is mathematically equivalent to an inhomogeneous Poisson process (IPP), a type of generalized linear model, and it is thus based on the same assumptions. Sampling of presence is assumed to be random or representative of the available environmental condition in the background. BBS sample sites are not distributed randomly in space. Therefore, rather than using random samples of the background in our MaxEnt models, we used all the sampled BBS routes (presence and absence) within the *potential breeding range* of a species to characterize the background, following Thibaud et al. (2014). This way, the presence and background points are subject to the same sampling bias and are comparable (Elith et al., 2011).

We evaluated MaxEnt models using AUC (Area Under the Curve). This statistic measures the ability of the model to discriminate between sites where a species is present and sites where it is absent. More precisely, AUC corresponds to the probability that a randomly chosen presence has a greater habitat suitability than a randomly selected absence (in the present case, a randomly selected BBS site within the potential range at which the species was not detected). A random ranking would produce a value of 0.5, while a perfect model would produce a value of 1. When AUC is calculated with presence and background points (instead of absence), the relative abundances of presences and background points can affect the AUC (Yackulic et al., 2013). We therefore used the same number of presences and non-detections (presumed absences) when calculating AUCs.

To be consistent with the literature, we used cross-validation to calculate model AUC**.** Optimally, AUC should be calculated using test data that are independent (both spatially and temporally) from the data used to train the model, but this is rarely possible in practice (Araújo et al., 2005). Since MaxEnt assumes stationarity and equilibrium, the year when a presence was observed should not be important to the model fit. Because most BBS routes are sampled in multiple years, when a species was present on given route one or more times during the study period, we randomly selected one presence-year, and we recorded the environmental conditions. This generated a sample of presences (i.e. training presence data) that does not include the same route twice. We similarly generated a sample of absence-years. To produce the MaxEnt background sample (i.e. training background data), we combined the samples of absences and presences because the background represents the range of conditions available in the potential range. The model AUC was calculated using the set of presences that were not used during model fitting and the set of absences that were not part of the background. Before calculating AUC, we resampled the data to have equal numbers of absences and presences. We repeated this process 10 times, and site suitability was then estimated as the average of the 10 model's predictions, weighting each model based on its AUC.

Colonization and extinction models

After fitting the MaxEnt models, we used logistic regressions to model (separately) the probability of colonization and the probability of extinction of each bird as functions of the habitat suitability estimated by MaxEnt. The extinction model predicts the probability of presence of a species in a particular year, given that it was present before, while the colonization model predicts the probability of presence of a species given that it was absent before.

The dependent variable in the *colonization models* indicates if a BBS route was colonized or not colonized. Colonization occurs when a species that was absent (not observed) on a BBS route for k consecutive years becomes present the following year. Non-colonization occurs when a species that was absent on a BBS route for k consecutive years remains absent the following year.

The dependent variable in the *extinction models* indicates if a species went extinct from a BBS route, or if it persisted. We defined extinction as occurring when a species that was present on a BBS route becomes absent (not observed) the following year and remains absent for k consecutive years. Persistence occurs when a species that was present on a BBS route is still present in at least one year during the next k consecutive years.

BBS sampling is subject to detection errors, when a species is present on a route but is undetected. A false absence is more likely than a false presence (Lobo et al., 2008). To reduce the risk of false absence, we consider a species absent only if it has not been observed on a given route for k consecutive years. When a route is not sampled one or more years during a period of k years, the occupation status of the species on that route is unknown for that period and the observation is not used. Consequently, colonization and extinction status can only be determined on routes sampled for a minimum of $k + 1$ consecutive years. We repeated all analyzes with $k = 1, 2, 3$ and 4 years to ensure that our conclusions are minimally affected by false absences. Using *k* > 4 years led to excessively small sample sizes (see Appendix B). Below, we present the results for *k* = 2 years unless stated otherwise.

The independent variable in colonization and extinction models is habitat suitability, estimated by MaxEnt models for each species. We separated habitat suitability into two components: 1) *previous suitability*, which is the suitability in the year(s) before the colonization or extinction event, and 2) Δ*suitability*, the change in habitat suitability, which is the difference between suitability in the years(s) prior to the colonization or extinction event and the suitability in the year(s) of the event. When *k*>1, suitability is averaged over the period of *k* years. For colonization, that period includes the *k* years before the event, while for extinction it includes the year of the event and the following (*k*-1) years. Positive values of *Δsuitability* indicate an increase in habitat suitability and negative values of *Δsuitability* indicate a decrease.

Most estimated Δ*suitability* are small, and the error on Δsuitability must be, on average, twice the error on suitability (because Δsuitability combines the errors of two measures of suitability). This is a problem since logistic models assume that independent variables are measured without error. To reduce this issue, we restricted the data for colonization and extinction models to cases where *Δsuitability* was unambiguous, defined as follow. For each species, we calculated mean *Δsuitability* using the prediction of the 10 MaxEnt models produced during the cross-validation procedure*,* and we only kept cases where all 10 models predicted Δ*suitability* in the same direction. This eliminated ≈ 45% of cases for analyses of colonization vs. non-colonization, and 50% for extinction vs. persistence.

The number of non-colonizations is much greater than the number of colonizations (the same is true for persistence vs extinction). Logistic regression models underestimate the probability of rare events (colonization or extinction in this case) because the probability tends to be biased toward the majority class of event (non-colonization or persistence) (King & Zeng, 2001;

Maalouf & Trafalis, 2011; Komori et al., 2015). We dealt with this problem before fitting the logistic models by resampling the data such that the numbers of colonizations and non-colonizations (or extinctions and persistences) were equal.

We modeled the probabilities of colonization and extinction in relation to Δ*suitability* and *previous suitability*. The expected effects of *previous suitability* and Δ*suitability* are the same because they both measure the effect of the same variable: habitat suitability. Increase in habitat suitability should increase the probability of colonization and decrease the probability of extinction. The hypothesis that MaxEnt models capture a causal relationship between species occurrence and environmental variables predicts positive correlations between occurrence and the two components of habitat suitability (i.e. *previous suitability* + Δ*suitability)*. Further, if the relationship is causal, the correlation should be maintained through time. This prediction of a positive correlation between Δ*occurrence and* Δ*suitability* provides a particularly strong test of the hypothesis.

Bahn & McGill (2007) showed that "many explanatory variables with suitable spatial structure can work well in species distribution models" and that "the predictive power of environmental variables is not necessarily mechanistic" (see also Bahn & McGill, 2007; Beale, 2008; Chapman, 2010; Fourcade et al., 2017). Because habitat suitability predicted by MaxEnt is always spatially autocorrelated, we added a spatial autocovariate (*SA*) to the colonization and extinction models. This allows us to ask: how much of the variability in colonization and extinction can be explained by habitat suitability, beyond what can be explained simply by proximity of conspecifics? To answer this question, we partitioned the deviance in the colonization and extinction models related to *previous suitability,* Δ*suitability,* and *SA*.

The spatial autocovariate (*SA*) is intended to capture the spatial autocorrelation in occupancy among neighboring BBS routes. It is an estimate of neighborhood occupancy. We calculated *SA* as the proportion of occupied BBS routes within the neighborhood of a focal route, weighting the importance of each neighbor according to its distance from the focal route. We calculated *SA* before colonization or extinction events occurred, because if we had calculated *SA* during the same year as the events it would have no predictive value through time. The calculation of *SA* requires arbitrary decisions regarding the definition of neighborhood and the distance-weighting function (for details see Appendix C). *SA* can be calculated using either presence/absence or estimated abundances. We repeated our analyses using both measures of occupancy (presence-absence and abundance), various definitions of neighborhood and distance-weighting functions to verify that those choices did not affect our conclusions (Appendix A). For the results presented here, neighborhood is defined as every route within a 200-km radius, occupancy is based on presence-absence, and the distance-weighting function uses an exponent of 2 (i.e. a neighbour's weight is inversely proportional to the square of the distance from the focal route).

Finally, we tested whether the apparent quality of MaxEnt models is indicative of their capacity to predict temporal changes in species' distributions. To do this, we determined the correlation between the AUC of MaxEnt models and two measures of the predictive accuracy of the colonization and the extinction models (AUC and Brier score, estimated with cross-validation) and one measure of goodness of fit (McFadden R^2).

Results

MaxEnt models

By the standard criterion used to judge MaxEnt models (viz., AUC>0.7 represents acceptable quality: but see Raes & Ter Steege, 2007; Lobo et al., 2008), the models for the 21 species in this study described their geographic distributions well. AUC ranged from 0.72 to 0.90 (median =

0.84; mean = 0.83). It therefore seems reasonable to use these MaxEnt models to calculate habitat suitability at each BBS site, for each of our 21 species, in each year. Of the seven environmental variables used in the MaxEnt models, % vegetation cover, temperature and elevation most frequently ranked among the most important predictors, based on permutation importance (Searcy & Shaffer, 2016).

Extinction models

Local extinctions occur fairly frequently (median = 408 local extinctions per species over the study period; mean = 470). The number of persistences is always greater than the number of extinctions, but the ratio of extinctions to persistences varies greatly among species, from 0.027 to 0.472 (median ratio = 0.106, mean ratio = 0.084).

The variation in extinction probability among sites is related to habitat suitability. In regressions of extinction probability as a function of Δ*suitability* + *previous suitability*, the coefficients are always in the predicted direction when they are significant (Table 1). The effect of *previous suitability* is always significant, while the effect of Δsuitability is significant for most species (15 out of 21). However, extinctions are strongly spatially structured. Adding *previous SA* (the spatial autocovariate in the year preceding extinction or persistence) to the model reduces the importance of *previous suitability*, and it causes the effect of Δ*suitability* to become non-significant for most species (Table 1). In models including all three predictors, the effect of *previous SA* is significant for 15 out 21 species (Table 1).

The largest amount of deviance is explained by the collinearity of *previous suitability* and *previous SA* (Fig. 1). Although there is important variation among species, on average the amount of deviance uniquely explained by *previous suitability* is similar to that of *previous SA* (paired t-test, two tail p-value = 0.951). Very little deviance is explained by Δ*suitability* (alone or shared with other predictors) (Fig. 1)

Habitat suitability estimated from better MaxEnt models does tend to better predict extinction and persistence (Fig. 2). We evaluated the predictive accuracy of the suitability-only extinction models using cross-validation and two different statistics: AUC and Brier score. We also evaluated goodness of fit using McFadden R^2. The AUC of extinction models varied among species from 0.52 to 0.94 (mean = 0.73, median = 0.73). The Brier score ranged from 0.11 to 0.25 (mean = 0.20, median = 0.21), and McFadden R^2 ranged from 0.007 to 0.49 (mean = 0.15, median = 0.13). All three statistics correlate with MaxEnt's AUC (Fig. 2).

Based on the three metrics (AUC, Brier score and McFadden R^2) models tend to be better when k -- the time window used to define absence -- is larger (Appendix A). This indicates that longer-term extinctions are generally better predicted than short term extinctions.

Colonization models

Colonizations also occur fairly frequently (median = 415 colonizations per species over the study period; mean = 461). The number of non-colonizations is always much greater than the number of colonizations, but the ratio of colonizations to non-colonizations varies greatly among species, from 0.020 to 0.244 (median ratio = 0.076; mean ratio = 0.061).

Variation in colonization probability among sites is related to habitat suitability. In the suitability-only model (i.e. Δ*suitability* + *previous suitability*), the effects of Δ*suitability* and *previous suitability* on colonization probability are always in the predicted direction when they are significant (Table 2). While previous suitability has a significant effect for all species, Δ*suitability* has a significant effect only for 5 of 21 species. The largest amount of deviance is again explained by the collinearity of *previous suitability* and spatial autocorrelation (*previous SA)*, and secondly, by *previous SA* independently of habitat suitability (Fig. 3). The spatial autocovariate independently explains more deviance than *previous suitability* (Fig. 3, but see

Appendix A). Again, very little deviance is explained by Δ*suitability* (alone or shared with other predictors) (Fig. 3)

The quality of MaxEnt models is unrelated to their ability to predict colonization (Fig. 4). We evaluated the predictive accuracy of the suitability-only colonization model the same way we did for the extinction model. The colonization models' AUC values varied among species from 0.59 to 0.85 (mean = 0.73, median = 0.74), the Brier score ranged from 0.16 to 0.27 (mean = 0.21, median = 0.21), and McFadden R^2 ranged from 0.02 to 0.27 (mean = 0.14, median = 0.14). None of those three measures of colonization model quality correlates with the MaxEnt AUC when $k > 1$ years. However, when $k = 1$ year, we observe a weak correlation in the expected direction.

For the colonization models, the three metrics (AUC, Brier score and McFadden R^2) tend to be better when $k = 1$ year compared to other values of k (Appendix A). In other words, habitat suitability has some predictive value for colonization of sites that have been unoccupied for one year, but not much predictive value when sites have been unoccupied longer.

Discussion

Does Maxent capture a causal relationship?

Extinction and colonization probabilities both relate to *previous suitability* in the expected way (i.e. higher *previous suitability* increases the probability of colonization and decreases the probability of extinction). However, *previous suitability*, extinction and colonization are all spatially structured and the correlations among them may be due in part to spatial autocorrelation, rather than the quality of the environment per se. As such, the effect of *previous suitability* provides only a weak test of the hypothesis that SMDs capture causal relationships.

If there is a causal link, then changing the independent variable will lead to a change in the dependent variable. Thus, the test of the relationship between Δ*suitability* and the probability of extinction and colonization provides a stronger test of the causal link. While the effect of *previous suitability* is generally quite large, the effect of Δ*suitability* is very small, often undetectable. In fact, once the spatial structure of species ranges is accounted for, extinctions and colonization are only rarely detectably related to Δ*suitability*. Like Boucher-Lalonde et al. (2014b), we found that very little of the interannual variability in species occupancy can be explained by interannual variation in abiotic conditions. For most of our species, either there is no causal link, or the effect of Δ*suitability* was too small to be detected.

In this light, are projected changes in species' geographic ranges based on SDM and projected climate change likely to be accurate? Many studies have argued that species' geographic ranges track changing climate, and temperature in particular. Generally, studies that report species' range shifts toward the poles and/or toward higher elevation attribute those ranges shifts to climate warming without explicitly testing that hypothesis (Parmesan et al., 1999; Parmesan & Yohe, 2003; Hitch & Leberg, 2007; Chen et al., 2011; Virkkala & Lehikoinen, 2014; Kerr et al., 2015; Mason et al., 2015; but see Taheri et al., 2016; Currie & Venne, 2017; Zhu et al., 2012). Our MaxEnt models included temperature as a component of habitat suitability. Our results suggest that observed range shifts are not necessarily related to climate and that the effect of environmental variables explains only a small portion of between-year variability in species' occupancy. Changes in occupancy over a short period appear to be largely random. This suggests that SDM predictions of climate change effects over the scale of a few years or decades (e.g. Matthews et al., 2011; Reese & Skagen, 2017) are unlikely to be very accurate.

One might argue that the test of the link between colonization / extinction and habitat suitability is weak because: a) changes in suitability over time were generally quite small, and b) there may be a lag between change in environment suitability and species' responses (Devictor et al., 2008, 2012; La Sorte & Jetz, 2012), limiting our ability to detect an effect. However, the fact that many extinctions and colonizations occurred despite environmental conditions changing very little indicates that changes in occupancy are mostly unrelated to change in environmental condition. It is possible that lagged models might make better predictions of extinction, but this seems unlikely for colonization since increasing *k* (i.e. the number of years preceding the event, over which suitability is averaged) did not improve the predictive value of the colonization models. For extinction models, we could not test the possibility of a lagged response by increasing *k* because the period of *k* years includes the year of the event and the following (*k*-1) — i.e., increasing *k* does not change the number of years preceding the extinction over which suitability is averaged.

Some might argue that the effect of change in suitability would be greater over a longer period. Changes in suitability between years were generally very small and were not more frequently negative than positive (Fig. 5A), and route-wise non-parametric correlations between suitability and years show that suitability very rarely changed monotonically over the study period (Fig. 5B). Thus, there would be little point in analyzing effect of change in suitability over longer periods. Nevertheless, for each bird, we compared the trend in suitability to the trend in occupancy over the whole period on each routes. The result did not affect our conclusion, that changes in occupancy are mostly unrelated, or weakly related, to change in environmental condition (Appendix F).

It is also possible that important determinants of habitat suitability may be missing from our MaxEnt models. However, this argument implies that the main determinants of species' geographic ranges are neither the climatic variables typically included in MaxEnt models (we used average temperature, average precipitation rate, average transpiration, soil type, vegetation type, average percent vegetation cover, and elevation), nor variables strongly collinear with them (e.g., temperature extremes).

Finally, we recognize that our 21 species may not be representative as they are all mid-latitude, fairly large-ranged species. Our conclusion should be interpreted in light of that.

Does Maxent AUC relate to model transferability?

Model transferability is a critical aspect of distribution modelling when SDMs developed in one time or area are applied to different times or areas (Phillips, 2008; Wenger & Olden, 2012). Numerous studies have used SDMs to predict changes in species' distributions under different climate change scenarios, often without any assessment of transferability (*e.g.* Thomas et al., 2004; Ledig et al., 2010; Matthews et al., 2011; Reese & Skagen, 2017). The method proposed to evaluate transferability generally relies on non-random cross-validation (where the test data come from a different geographic region than the data used to develop the model). Spatial transferability is then assumed to be a surrogate for temporal transferability. We evaluated transferability of MaxEnt models in a novel way by looking at the models' ability to predict change in occupancy through time (i.e. colonization and extinction). We found that common measure of SDM performance, AUC, is related to MaxEnt models' ability to predict extinction, but it is unrelated to the models' ability to predict colonization. Further, a MaxEnt model's ability to predict extinction is unrelated to its ability to predict colonization (correlation between AUCs : $r = -0.273$, $p = 0.231$). Thus, the best MaxEnt models do not tend to better predict where species will go, but they do seem to better predict where species will disappear. The predictive value of species distribution models may be overestimated when evaluated through space only. Consequently, future prediction of species' responses to climate change should make a distinction between colonization and extinction, recognizing that the two processes are not equally well predicted by SDMs.

How does Maxent perform compared to a simple spatial model?

Like Eaton et al. (2014), we found that estimates of neighborhood occupancy (i.e., *SA*) positively relate to colonization probability and negatively to extinction probability. Furthermore, we found that the effect of *SA* was generally similar to, or greater than, the effect of habitat suitability. The important effect of *SA* in both colonization and extinction models indicates that species distributions exhibit spatial structure beyond that owing to the environmental variables in the MaxEnt model (Phillips et al., 2017). The effect of *SA* could reflect exogenous factors, i.e., be caused by spatially structured variables that were not included in the MaxEnt model. In other words, the presence of conspecifics at neighbouring sites could be an indicator of regional habitat suitability. The effect of *SA* could also reflect endogenous population processes such as dispersal and rescue effects (Eaton et al., 2014; Eriksson et al., 2014). If the effect of *SA* were due to missing spatially structured habitat variables, we would expect the effect of *SA* to be of similar size in both the colonization model and the extinction model, or perhaps smaller in the former, since a BBS route that was unoccupied could remain unoccupied if there is no nearby source of colonists, despite a suitable environment. In contrast, a decrease in suitability should have more immediate impact on an occupied route. We found the opposite: that the effect of *SA* tends to be greater for colonization than extinction (when *SA* is based on presence). This, and the lack of correlation between the predictive ability of colonization models and MaxEnt models suggests that colonization is more strongly driven by endogenous factors that are not captured by the SDMs. Since the link between dispersal and colonization is obvious, while the link between extinction and dispersal only exists via the rescue effect, we propose that the difference could reflect a greater effect of dispersal on colonization than extinction. Given that birds are among the most mobile organisms, we expect that dispersal limitation will be an even more important factor in the response of other taxa to climate change.

When projecting species response to climate change, the spatial structure of the species' distribution should be considered. The use of a spatial autocovariate (*SA*) had been proposed as a way to account for dispersal limitations (Yackulic et al., 2015). Although it is unclear whether *SA* measures dispersal limitations or some other process, one thing is clear: including the *SA* generally increase the predictive ability of species distribution models.

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Table 1. Direction and statistical significance of the coefficients of the predictor variables in two different extinction models. The first model includes the effects of Δ*suitability* and *previous suitability.* The second model includes the effects of Δ*suitability*, *previous suitability* and *previous spatial autocovariate (SA)*. Values in each cell indicate the numbers of species (out of 21) for which the effect of the variable is in the expected (negative) or unexpected (positive) direction. Values in parentheses () indicate the number of species for which the effect is statistically significant after applying a Bonferroni correction (i.e. multiplying p-value by 21). n.a. indicates that the variable is not included in the model.

	Δsuitability		*Previous suitability*		*Previous SA*	
Model	Positive	Negative	Positive	Negative	Positive	Negative
Δsuitability + Previous suitability	1 (0)	20 (15)	0 (0)	21 (21)	n.a.	n.a.
Δsuitability + Previous suitability + Previous SA	3 (0)	18 (2)	0 (0)	21 (13)	0 (0)	21 (15)

Table 2. Direction and statistical significance of predictor variables in the two different colonization models. The first model includes the effects of Δ*suitability* and *previous suitability*. The second model includes the effects of Δ*suitability*, *previous suitability* and *SA*. Values in the cell indicate the numbers of species (out of 21) for which the effect of the variable is in the expected (positive) or unexpected (negative) direction. Values in parentheses () indicate the number of species for which the effect was statistically significant after applying Bonferroni correction (i.e. multiplying p-value by 21). n.a. indicates that the variable is not in the model.

	Δsuitability		*Previous suitability*		*Previous SA*	
Model	Positive	Negative	Positive	Negative	Positive	Negative
Δsuitability + Previous suitability	21 (5)	0 (0)	21 (21)	0 (0)	n.a	n.a
Δsuitability + Previous suitability + Previous SA	20 (4)	1 (0)	21 (13)	0 (0)	20 (13)	1 (0)

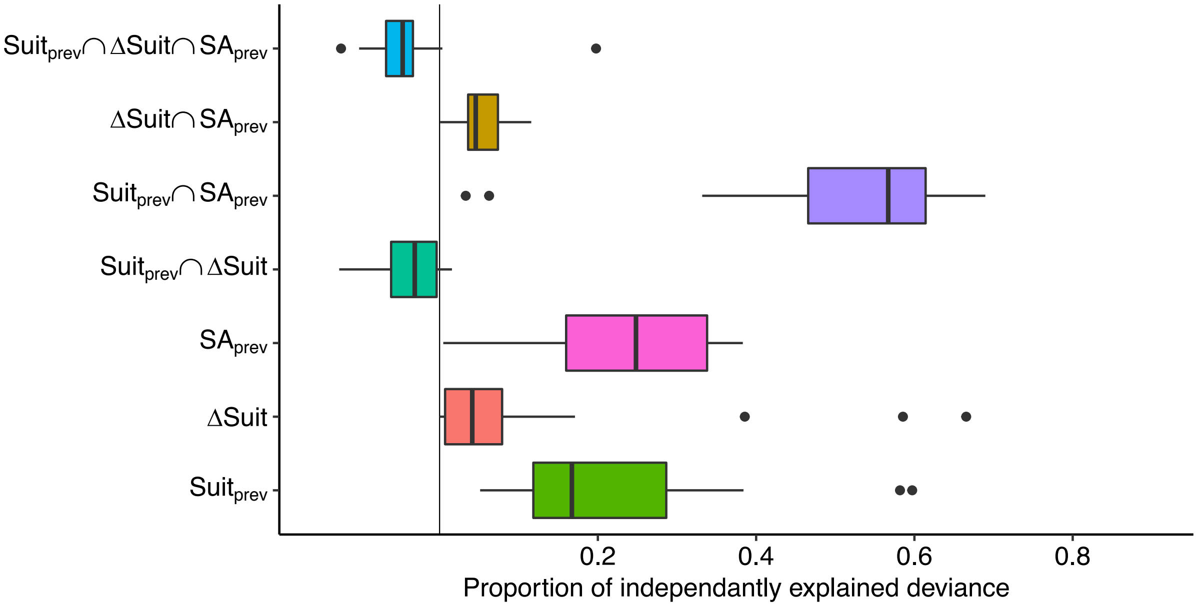

Figure 1. Partitioning of the explained deviance in models of extinction for 21 species of passerine birds. Extinction was modeled as a function of previous habitat suitability ($\mathrm{Suit}_{\mathrm{prev}}$), change in habitat suitability (ΔSuit) and previous spatial autocovariate ($\mathrm{SA}_{\mathrm{prev}}$). For each species, the total explained deviance is divided into the proportion uniquely explained by each predictor and the proportion that is jointly explained by different combinations of predictors. The symbol $\cap$ indicates the proportion of explained deviance that is shared between predictors. For example, $\mathrm{Suit}_{\mathrm{prev}} \cap \mathrm{SA}_{\mathrm{t-1prev}}$ shows the deviance that may be explained by either $\mathrm{Suit}_{\mathrm{prev}}$ or $\mathrm{SA}_{\mathrm{prev}}$, but not by ΔSuit. The boxplots represent the variation of explained deviance among the 21 species.

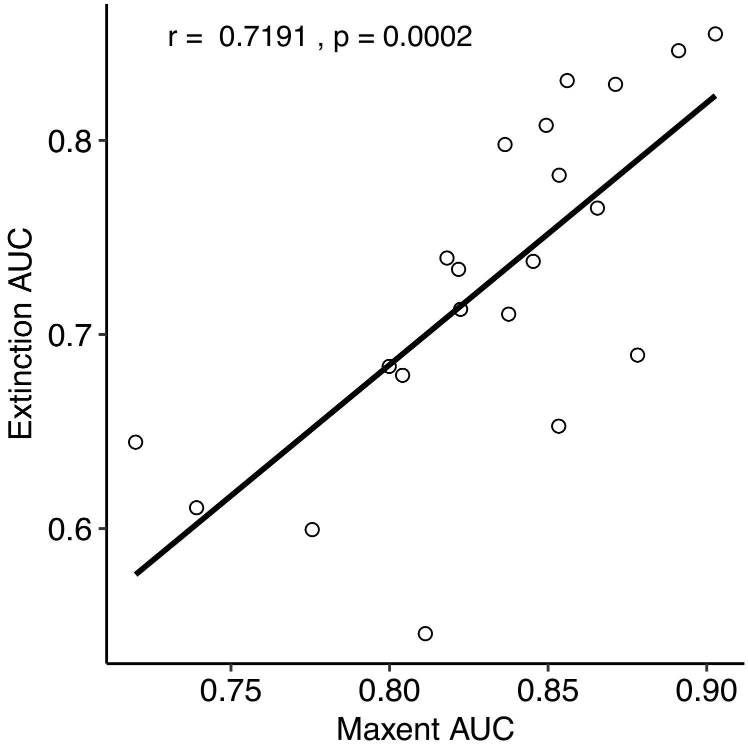

Figure 2. Does habitat suitability, estimated from MaxEnt models, make better predictions of extinctions when the MaxEnt models are better (i.e., have higher AUC)? Here, we show one measure of the strength of the extinction ~ habitat suitability relationship (extinction AUC) as a function of the AUC of the MaxEnt model for 21 species of Passeriformes. The relationships with the two other measures (Brier score and McFadden R^2) were nearly identical to this one.

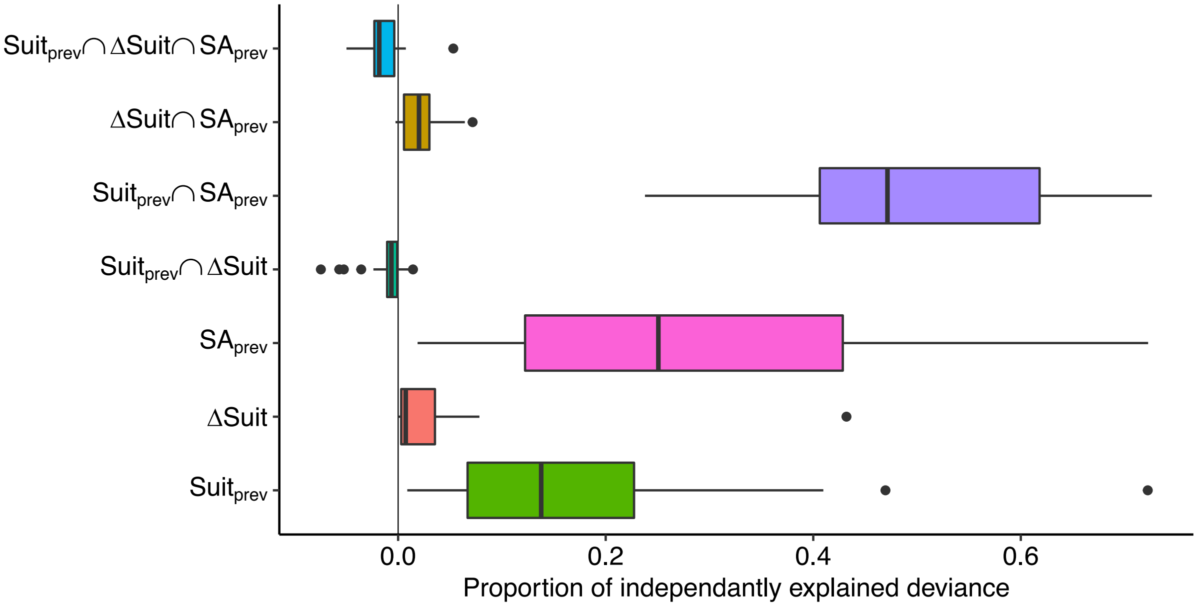

Figure 3. Partitioning of the explained deviance in models of colonization for 21 species of Passeriformes. Extinction was modeled as a function of previous habitat suitability ($\mathrm{Suit}_{\mathrm{prev}}$), change in habitat suitability (ΔSuit) and previous spatial autocovariate ($\mathrm{SA}_{\mathrm{prev}}$). For each species, the total explained deviance is divided into the proportion uniquely explained by each predictor and the proportion that is jointly explained by different combinations of predictors. The symbol ∩ is not an interaction; rather, it indicates the proportion of explained deviance that is shared between predictors. For example, $\mathrm{Suit}_{\mathrm{prev}} \cap \mathrm{SA}_{\mathrm{prev}}$ shows the deviance that may be explained by either $\mathrm{Suit}_{\mathrm{prev}}$ or $\mathrm{SA}_{\mathrm{prev}}$, but not by ΔSuit. The boxplots represent the variation of explained deviance among the 21 species.

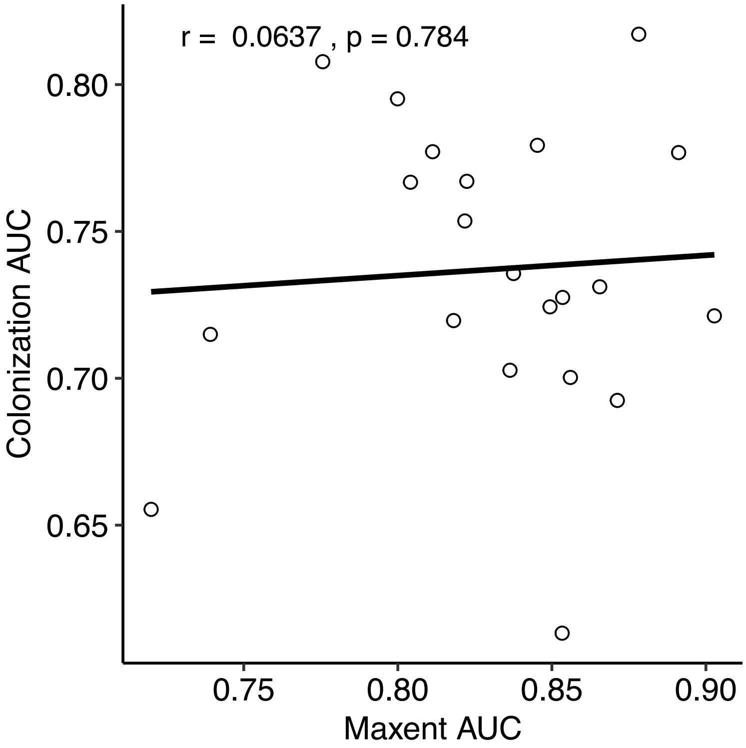

Figure 4. Does habitat suitability, estimated from MaxEnt models, make better predictions of colonization when the MaxEnt models are better (i.e., have higher AUC)? Here, we show one measure of the strength of colonization ~ habitat suitability relationship (colonization AUC) as a function of the AUC of the MaxEnt model for 21 species of Passeriformes. The relationships with the two other measures (Brier score and McFadden R^2) were nearly identical to this one.

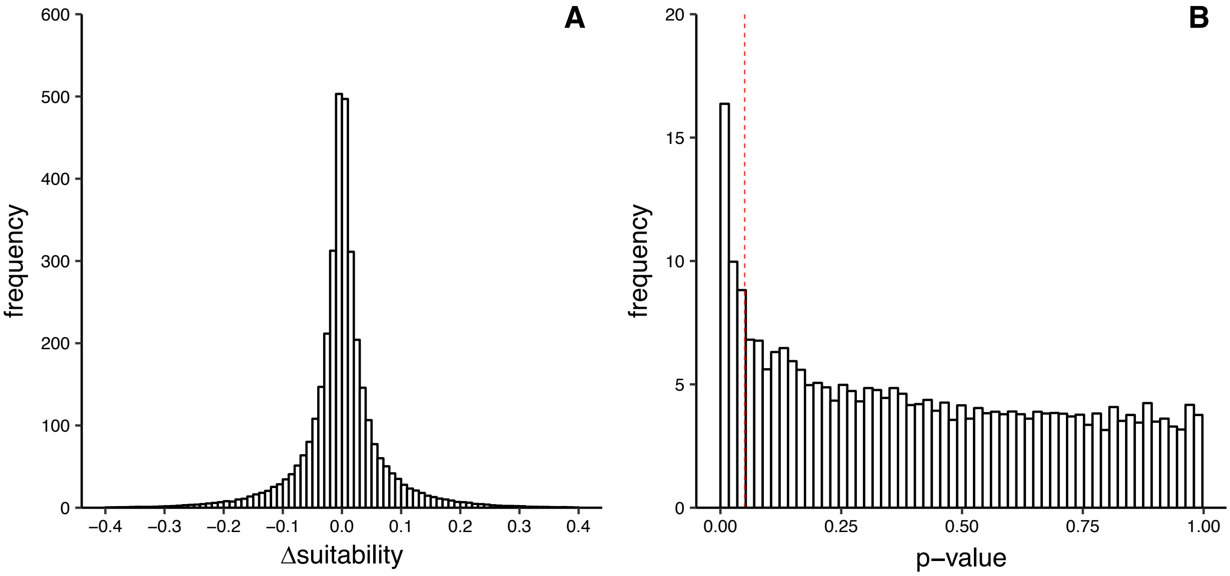

Figure 5. Histogram showing (A) the distribution of Δsuitability values, and (B) the distribution of p-values of route-wise non-parametric correlations between suitability and year (i.e., Spearman correlations used to test for monotonic trends). Frequency is in hundreds. The red dashed line in panel B indicates the typical significance level of 0.05. At this level, we can reject the null hypothesis of no monotonic trend for only 12.5% of routes.

Appendix A – Sensitivity Analysis

Because our analysis relies on some arbitrary methodological decisions, we carried a sensitivity analysis, where we repeated the analysis while varying those methodological decisions. Here is a list of those methodological decision along with the rational for them.

1. **Using balanced or unbalanced data**.
   Our raw data are very unbalanced, the number of non-colonizations is much greater than the number of colonizations (the same is true for extinctions vs persistences). Logistic regression models underestimate the probability of rare events (colonizations) because probability tends to be bias toward the majority class of events (i.e., non-colonizations) (King & Zeng, 2001; Maalouf & Trafalis, 2011; Komori et al., 2015) We dealt with this problem by resampling the data such that the number of colonizations and non-colonizations was the same before fitting the logistic models. We also carried the analysis with the raw data to evaluate how that decision might have impacted our result.
2. **Only using data for which all the Maxent models agreed on the direction of change in suitability (i.e. same.sign = T) or not filtering the data (i.e. same.sign = F).**
   Logistic models assume that the independent variables are measured without error, but this is clearly not the case for Δ*suitability*. When all models do not agree on the direction of Δsuitability (some model estimate negative change, while some other estimate positive change) the error surrounding Δsuit is likely to be greater than average Δsuit. We therefore repeated our analyses, filtering the data to use only cases in which we can be quite confident that Δ*suitability* is at least in the right direction. In the rest of this document, **same.sign = T** indicates that we filtered the data in such way. While **same.sign = F** indicated that we did not filter the data
3. **Using a time window of *k* years to define absence**.
   The purpose of using a time window to define absence is to reduce the chance of false absence (i.e. non-detection of a species that is, in fact, present), which are much more likely than false presence. We don't have a strong basis for deciding which size of the time window to use, so we repeated the analysis with four different sizes (1 to 4 years). We didn't go beyond four years because sample size decreases quite rapidly as we increase the time window (see section *sample size*).
4. **Using different definitions of the spatial autocovariate**.
   This only concern models that include the effect of *previous spatial autocovariate* (*SA*). Calculation of the *SA* relies upon three arbitrary decisions: the measure of species occupancy (presence-absence or estimated abundance), the definition of neighborhood and the exponent in the distance-weighting function (see section *calculation of the spatial autocovariate* for details). We tried five different ways of calculating the spatial autocovariates by using different combinations of those decisions (see table 1). We used two different distances to define neighborhood (200 km and 1000 km), two different exponents for the distance-weighting function (2 and 0 [i.e. not weighted]), and two measures of species occupancy (presence-absence and estimated abundance). Three of the five *SA* are based on presence, and the two other are based on estimated abundance.

   We based our choice of distance (200 km and 1000 km) on an examination of the distribution of nearest neighbor distance. We wanted to only keep routes for which *SA* calculation was based on at least 5 neighboring routes.

   In 1978, at the beginning of the period covered by our study (when the fewest routes were sampled), 95% of fifth nearest neighbor distances were less than 175 km. In order to keep a reasonable number of routes in the analysis, we decided to use a distance of 200 km as the minimum distance to define the neighborhood. If we wanted all the routes to have at least 5 neighbors, we would need to use a radius of about 1130 km. We decided to use 1000 km as the maximum distance used to define the neighborhood.

Table A.0. The five measures of *spatial autocovariate* used in the sensitivity analysis. Each measure is based on a different combination of three choices: 1) measure of species occupancy, 2) neighborhood distance and 3) exponent of the distance weighing function.

	Measure of species occupancy	Neighborhood distance (km)	Exponent Distance-weighing function
1	Estimated abundance	200	2
2	Estimated abundance	1000	2
3	Presence-absence	200	2
4	Presence-absence	1000	2
5	Presence-absence	200	0

Direction of effects

The table below summarize the results obtained with different combinations of those four methodological decisions. They are separated into two sections. The first section contains results for **colonization** models. The second contains results for **extinction** models. Within each section, we grouped the table into four sub-sections based on the first two methodological decisions (e.g. unbalanced data and same.sign = T).

In the table, **Δsuit** stands for *change in suitability*, **prev.suit** stands for *previous suitability* and **prev.SA** stands for *previous spatial autocovariates*.

Each table shows the direction and statistical significance of the effect of predictor variables in two different colonization (or extinction) models. The first model is the suitability-only model (first row of the table), which includes the effects of Δ**suit** and **prev.suit**. The second model (second row of the table) includes the effects of Δ**suit**, **prev.suit** and **prev.SA**.

Values in the cell indicate the numbers of bird species (out of 21) for which the effect of the variable is in the expected or unexpected direction. Values in parentheses () indicate number of species for which the effect was statistically significant (using alpha = 0.05) after applying a Bonferroni correction for multiple comparisons (multiplying p-values by 21).

In the **colonization** models the effects of Δ**suit** and **prev.suit** are expected to be positive. In the **extinction** models the effects are expected to be negative.

For the second model (second row), a range of values (e.g. 13-21) is presented instead of a single value. The range indicates the minimum and maximum numbers of species obtained when repeating the analysis with the different definitions of *SA*. We decided to present the results using ranges because producing a table for each definition of *SA* would have required five times more tables (5 * 16 = 80 tables).

Cells are **gray** when the variable is not in the model. Cells are **red** when there are more than 3 species for which the estimated effect of Δ**suit** was in the unexpected direction (ignoring statistical significance).

Colonization models

unbalanced data and same.sign = T

Table A.1. Colonization models, unbalanced data, same.sign = T, and *k* = 1.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	21 (19)	0 (0)	21 (21)	0 (0)	/	/
Δsuit + prev.suit + prev.SA	21 (10-19)	0 (0)	21 (19-21)	0 (0)	18-21 (13-21)	0-3 (0)

Table A.2. Colonization models, unbalanced data, same.sign = T, and *k* = 2.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	21 (6)	0 (0)	21 (20)	0 (0)	/	/
Δsuit + prev.suit + prev.SA	19-20 (2-3)	1-2 (0)	21 (18-20)	0 (0)	19-21 (9-18)	0-2 (0)

Table A.3. Colonization models, unbalanced data, same.sign = T, and *k* = 3.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	20 (2)	1 (0)	20 (14)	1 (0)	/	/
Δsuit + prev.suit + prev.SA	16-18 (2)	3-5 (0)	20-21 (10-19)	0-1 (0)	18-20 (8-18)	1-3 (0)

Table A.4. Colonization models, unbalanced data, same.sign = T, and *k* = 4.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	14 (2)	7 (0)	20 (14)	1 (0)	/	/
Δsuit + prev.suit + prev.SA	13-14 (2)	7-8 (0)	19-20 (9-19)	1-2 (0)	17-21 (6-14)	0-4 (0)

balanced data and same.sign = T

Table A.5. Colonization models, balanced data, same.sign = T, and *k* = 1.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	21 (17)	0 (0)	21 (21)	0 (0)	/	/
Δsuit + prev.suit + prev.SA	20-21 (8-16)	0-1 (0)	21 (19-21)	0 (0)	18-21 (11-18)	0-3 (0)

Table A.6. Colonization models, balanced data, same.sign = T, and *k* = 2.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	21 (5)	0 (0)	21 (21)	0 (0)	/	/
Δsuit + prev.suit + prev.SA	16-20 (1-3)	1-5 (0)	20-21 (14-20)	0-1 (0)	19-21 (8-15)	0-2 (0)

Table A.7. Colonization models, balanced data, same.sign = T, and *k* = 3.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	15 (2)	6 (0)	20 (20)	1 (0)	/	/
Δsuit + prev.suit + prev.SA	11-17 (2)	4-10 (0)	20-21 (8-16)	0-1 (0)	17-21 (5-14)	0-4 (0)

Table A.8. Colonization models, balanced data, same.sign = T, and *k* = 4.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	15 (2)	6 (0)	20 (16)	1 (0)	/	/
Δsuit + prev.suit + prev.SA	13-15 (0-2)	6-8 (0)	19-20 (4-16)	0-2 (0)	16-21 (2-11)	0-5 (0)

unbalanced data and same.sign = F

Table A.9. Colonization models, unbalanced data, same.sign = F, and *k* = 1.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	21 (19)	0 (0)	21 (21)	0 (0)	/	/
Δsuit + prev.suit + prev.SA	21 (13-19)	0 (0)	21 (21)	0 (0)	21 (18 -21)	0 (0)

Table A.10. Colonization models, unbalanced data, same.sign = F, and *k* = 2.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	21 (7)	0 (0)	21 (21)	0 (0)	/	/
Δsuit + prev.suit + prev.SA	20-21 (2)	1-2 (0)	21 (18-21)	0 (0)	21 (17-20)	0 (0)

Table A.11. Colonization models, unbalanced data, same.sign = F, and *k* = 3.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	18 (2)	3 (0)	21 (20)	0 (0)	/	/
Δsuit + prev.suit + prev.SA	14-18 (2)	4-7 (0)	21 (14-19)	0 (0)	20-21 (15-20)	0-1 (0)

Table A.12. Colonization models, unbalanced data, same.sign = F, and *k* = 4.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	15 (2)	6 (0)	21 (20)	0 (0)	/	/
Δsuit + prev.suit + prev.SA	13-15 (1-2)	6-8 (0)	20-21 (12-18)	0-1 (0)	20-21 (11-18)	0-1 (0)

balanced data and same.sign = F

Table A.13. Colonization models, balanced data, same.sign = F, and *k* = 1.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	21 (16)	0 (0)	21 (21)	0 (0)	/	/
Δsuit + prev.suit + prev.SA	19-21 (7-14)	0-2 (0)	21 (20-21)	0 (0)	21 (19-21)	0 (0)

Table A.14. Colonization models, balanced data, same.sign = F, and *k* = 2.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	20 (3)	1 (0)	21 (21)	0 (0)	/	/
Δsuit + prev.suit + prev.SA	15-19 (2)	2-6 (0)	21 (16-20)	0 (0)	21 (15-19)	0 (0)

Table A.15. Colonization models, balanced data, same.sign = F, and *k* = 3.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	17 (2)	4 (0)	21 (20)	0 (0)	/	/
Δsuit + prev.suit + prev.SA	11-15 (2)	6-10 (0)	20-21 (11-18)	0-1 (0)	20-21 (15-18)	0-1 (0)

Table A.16. Colonization models, balanced data, same.sign = F, and *k* = 4.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	13 (1)	8 (0)	21 (19)	0 (0)	/	/
Δsuit + prev.suit + prev.SA	10-14 (1-2)	7-11 (0)	19-20 (8-15)	1-2 (0)	20-21 (10-16)	0-1 (0)

Extinction models

unbalanced data and same.sign = T

Table A.17. Extinction models, unbalanced data, same.sign = T, and *k* = 1.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	1	20	0	21	/	/
	(0)	(13)	(0)	(18)		
Δsuit + prev.suit + prev.SA	1	20	0-2	19-21	0-2	19-21
	(0)	(6-7)	(0)	(17-18)	(0)	(16-18)

Table A.18. Extinction models, unbalanced data, same.sign = T and *k* = 2.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	1	20	0	21	/	/
	(0)	(14)	(0)	(17)		
Δsuit + prev.suit + prev.SA	1	20	0-1	20-21	0-3	18-21
	(0)	(6-10)	(0)	(15-16)	(0)	(15-16)

Table A.19. Extinction models, unbalanced data, same.sign = T and *k* = 3.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	0	21	0	21	/	/
	(0)	(12)	(0)	(18)		
Δsuit + prev.suit + prev.SA	1-2	19-20	0-1	20-21	0-1	20-21
	(0)	(5-7)	(0)	(15-16)	(0)	(14-16)

Table A.20. Extinction models, unbalanced data, same.sign = T and *k* = 4.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	0	21	0	21	/	/
	(0)	(9)	(0)	(18)		
Δsuit + prev.suit + prev.SA	0-1	20-21	0-1	20-21	0-1	20-21
	(0)	(4-6)	(0)	(13-17)	(0)	(13-17)

balanced data and same.sign = T

Table A.21. Extinction models, balanced data, same.sign = T, and *k* = 1.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	1 (0)	20 (12)	0 (0)	21 (18)	/	/
Δsuit + prev.suit + prev.SA	1-3 (0)	18-20 (2-5)	0-1 (0)	20-21 (13-18)	0-2 (0)	19-21 (13-18)

Table A.22. Extinction models, balanced data, same.sign = T, and *k* = 2.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	1 (0)	20 (15)	0 (0)	21 (21)	/	/
Δsuit + prev.suit + prev.SA	1-3 (0)	18-20 (1-4)	0-1 (0)	20-21 (13-15)	0-3 (0)	18-21 (12-15)

Table A.23. Extinction models, balanced data, same.sign = T, and *k* = 3.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	0 (0)	21 (8)	0 (0)	21 (17)	/	/
Δsuit + prev.suit + prev.SA	0-3 (0)	18-21 (2-6)	0-1 (0)	20-21 (9-14)	0-2 (0)	19-21 (9-14)

Table A.24. Extinction models, balanced data, same.sign = T, and *k* = 4.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	2 (0)	19 (7)	0 (0)	21 (18)	/	/
Δsuit + prev.suit + prev.SA	0-3 (0)	18-21 (1-3)	0-1 (0)	20-21 (9-13)	0-1 (0)	20-21 (9-13)

unbalanced data and same.sign = F

Table A.25. Extinction models, unbalanced data, same.sign = F, and *k* = 1.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	1 (0)	20 (13)	0 (0)	21 (21)	/	/
Δsuit + prev.suit + prev.SA	1 (0)	20 (6-9)	0-1 (0)	20-21 (19-20)	0-1 (0)	20-21 (17-20)

Table A.26. Extinction models, unbalanced data, same.sign = F, and *k* = 2.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	1 (0)	20 (14)	0 (0)	21 (21)	/	/
Δsuit + prev.suit + prev.SA	1 (0)	20 (6-9)	0-1 (0)	20-21 (19-20)	0-1 (0)	20-21 (17-20)

Table A.27. Extinction models, unbalanced data, same.sign = F, and *k* = 3.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	1 (0)	20 (16)	0 (0)	21 (21)	/	/
Δsuit + prev.suit + prev.SA	1-2 (0)	19-20 (4-9)	0-1 (0)	20-21 (20)	0-1 (0)	20-21 (17-20)

Table A.28. Extinction models, unbalanced data, same.sign = F, and *k* = 4.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	1 (0)	20 (11)	0 (0)	21 (20)	/	/
Δsuit + prev.suit + prev.SA	1 (0)	20 (3-5)	1 (0)	20 (19-20)	0-1 (0)	20-21 (17-20)

balanced data and same.sign = F

Table A.29. Extinction models, balanced data, same.sign = F, and *k* = 1.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	2 (0)	19 (14)	0 (0)	21 (20)	/	/
Δsuit + prev.suit + prev.SA	1-3 (0)	18-20 (3-6)	0 (0)	21 (18-20)	0-1 (0)	20-21 (16-20)

Table A.30. Extinction models, balanced data, same.sign = F, and *k* = 2.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	0 (0)	21 (13)	0 (0)	21 (21)	/	/
Δsuit + prev.suit + prev.SA	1-2 (0)	19-20 (4-5)	0-1 (0)	20-21 (16-18)	0-1 (0)	20-21 (16-19)

Table A.31. Extinction models, balanced data, same.sign = F, and *k* = 3.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	0 (0)	21 (9)	0 (0)	21 (21)	/	/
Δsuit + prev.suit + prev.SA	1-4 (0)	17-20 (2-5)	0-1 (0)	20-21 (16-19)	0-2 (0)	19-21 (15-19)

Table A.32 Extinction models, balanced data, same.sign = F, and *k* = 4.

	Δsuit		***Prev.suit***		***Prev.SA***	
	Positive	Negative	Positive	Negative	Positive	Negative
Δsuit + prev.suit.	2 (0)	19 (6)	0 (0)	21 (20)	/	/
Δsuit + prev.suit + prev.SA	1-3 (0)	18-21 (2-4)	0-1 (0)	20-21 (13-17)	0-1 (0)	20-21 (13-17)

In summary, methodological choices do not have a large influence on the results. The only methodological decision that has a notable effect is the choice of *k*: we tend to detect fewer significant effects as *k* increases and more effect in the wrong direction. However, effects in the wrong direction are never significant.

Deviance partitioning

We compared the amount of deviance independently explained by the spatial autocovariate (*SA*) to the amount independently explained by *previous suitability* using paired t-tests.

We repeated the analysis using different ways of calculating *SA* and different combinations of methodological decisions. In total, we repeated the analysis with 80 different combinations of methodological decisions.

Extinction models

We found that the way *SA* is calculated has minimal influence on the results. Other methodological decisions also had minimal influence on the results. In almost all cases, there was no significant difference between the amount of deviance explained by *SA* and *previous suitability*. In the rare instance where we found a significant difference (5/80), *SA* explained more than *previous suitability*. We only found significant differences when same.sign = F and *k* =1 or 2.

Colonization models

We found that the way *SA* is calculated does have an influence on the results. In comparison, other methodological decisions had very little influence. In general, models in which *SA* is based on presence accounted for more deviance than models in which *SA* is based on abundance. Consequently, *previous suitability* explains more deviance than *SA* when *SA* is based on abundance.

The choice of *k* is the only other decision that has a notable influence. When *k* = 1, there is generally no significant difference between the deviance explained by *SA* and *previous suitability.* While for other values of *k* there generally is a difference.

Before making the analyses, we expected that abundance would contain more information regarding the effect of neighbours on colonization than does presence. Yet, when the spatial covariate is calculated with presence-absence, it independently explains more deviance than *previous suitability*, but the situation is reversed (*previous suitability* explains more than *previous SA*) when *SA* is calculated with estimated abundance.

Our observation that *SA* is more important in colonization models than in extinction models may indicate that dispersal limitation is more important for colonization than for extinction. Yet, if the statistical effect of *SA* reflects the proximity of sources of colonists, shouldn't *SA* explain even more deviance when it is based on abundance? Yes, but only if abundance truly contains more information regarding sources of colonists than presence-absence. In theory, abundance data should have greater information content. However, in practice it may not be the case because abundance data also comes with greater uncertainty and might be biased (Sauer et al., 2013).

Also, the effect of *SA* may not be linear when *SA* is based on abundance (and thus poorly estimated by logistic regression). Therefore, we don't give too much importance to the results based on *SA* calculated with abundance.

Comparing suitability-only models based on different *k*

To test if *k* influenced the performance of colonization models and extinction models, we fitted simple linear models with *k* — the time window used to define absence — and species as the independent variables, and one of the three measures of extinction models' performance (McFadden R^2, Brier or AUC) as the independent variables

Extinction models

All three measures of model performance produced congruent results: the effect of *k* is highly significant and extinction models tend to be better when *k* is larger, indicating that longer-term extinctions are generally better predicted than short term extinctions. These results are not affected by methodological decisions.

Colonization models

We found that the *k* generally had a significant effect on model performance. However, methodological choices did affect the conclusion. The estimated effect of *k* was always in the same direction when using balanced data: models tend to be worse as *k* increases. However, when using unbalanced data, the result depends on which measure of model performance is used. When using Brier score, the effect of *k* in the opposite direction to the other measure (AUC and McFadden R^2) : models tend to be better as *k* increases.

Cited Literature

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Appendix B – Sample Size and Taxonomic Information

Sample size

Table B.1. Median, mean, minimum and maximum number of **extinctions** and **persistences** per species over the study period for different values of *k* (1-4 years). Numbers in parentheses () show those same statistics after limiting data to cases where same.sign = T (i.e. when all MaxEnt models agree on the direction of *Δsuitability*).

	Persistence				**Extinction**			
K	median	mean	min	max	median	mean	min	max
1	5935 (2546)	6525 (3259)	528 (52)	16603 (10716)	719 (362)	1068 (558)	86 (30)	2491 (1867)
2	5663 (2413)	6095 (3010)	588 (49)	15398 (10078)	408 (152)	470 (247)	48 (14)	1159 (750)
3	5140 (2246)	5445 (2739)	566 (61)	13708 (9230)	274 (99)	272 (145)	29 (10)	690 (394)
4	4557 (2054)	4839 (2422)	470 (60)	12179 (8169)	193 (69)	176 (93)	21 (9)	451 (227)

Table B.2. Median, mean, minimum and maximum number of **colonizations** and **non-colonizations** per species over the study period (1979-2009) for different values of *k* (1-4 years). Numbers in parentheses () show those same statistics after limiting data to cases where same.sign = T (i.e. all MaxEnt models agree on the direction of *Δsuitability*).

	Non-colonization				**Colonization**			
K	median	mean	min	max	median	mean	min	max
1	6723 (3503)	7990 (4439)	2596 (552)	20091 (12098)	732 (385)	1060 (551)	81 (22)	2512 (1829)
2	5478 (2861)	6321 (3511)	2070 (493)	16034 (9769)	415 (165)	461 (244)	37 (9)	1151 (692)
3	4548 (2588)	5159 (2893)	1681 (376)	13118 (8176)	271 (112)	264 (141)	22 (3)	684 (342)
4	3690 (2146)	4289 (2376)	1381 (305)	10906 (6794)	158 (73)	170 (89)	17 (5)	446 (195)

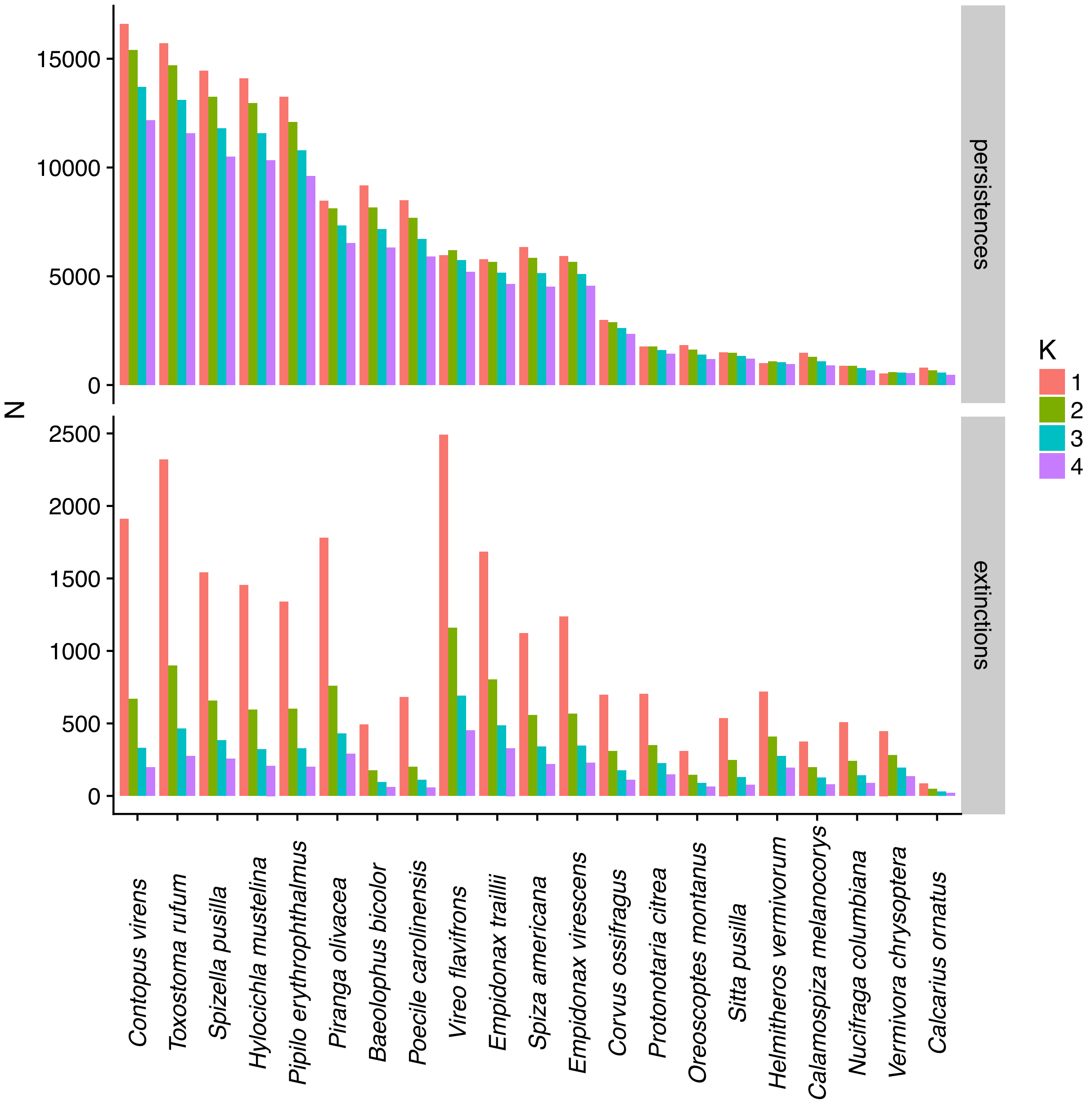

Figure B.1. Barplots showing the number of persistences (top panel) and extinctions (bottom panel) that were observed over the study period (1979-2009) for each of the 21 species included in the study. The length of the time window used to define absence (*k*) is indicated by the color of the bar. Note that the scale of the y-axis differs between the panels.

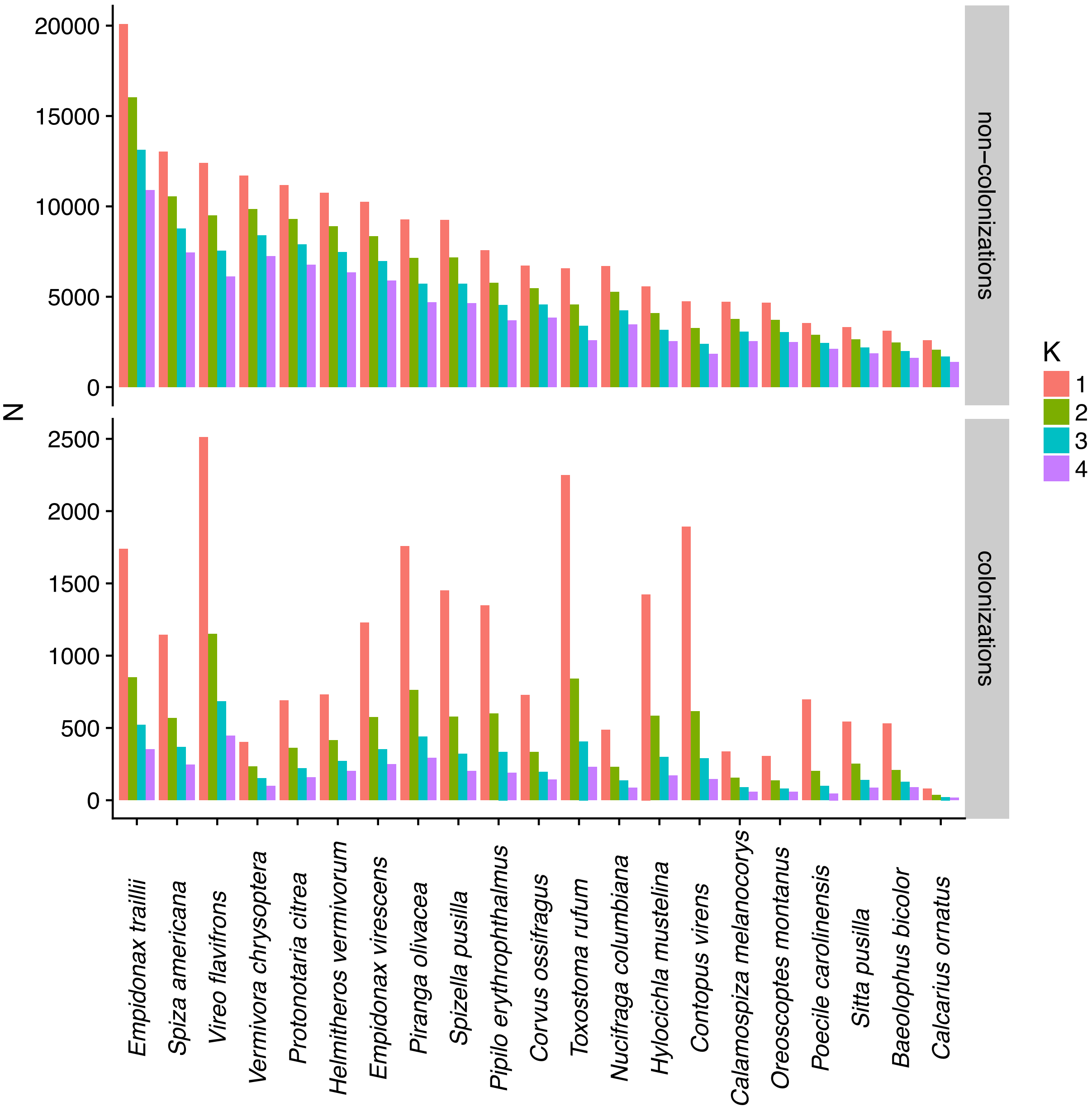

Figure B.2. Barplots showing the number of non-colonizations (top panel) and colonizations (bottom panel) that were observed over the study period (1979-2009) for each of the 21 species included in the study. The length of the time window used to define absence (*k*) is indicated by the color of the bar. Note that the scale of the y-axis differs between the panels.

Taxonomic Information

Table B.3. Taxonomic classification and common names of the 21 species of bird included in the study.

Order	Family	*Genus*	*species*	French common name	English common name
Passeriformes	Emberizidae	*Spizella*	*nusilla*	Bruant des champs	Field sparrow
Passeriformes	Emberizidae	*Pipilo*	*erythrophthalmus*	Tohi à flancs roux	Easter towhee
Passeriformes	Calcariidae	*Calcarius*	*ornatus*	Bruant à ventre noir	Chestnut-collared longspur
Passeriformes	Emberizidae	*Calamospiza*	*melanocorys*	Bruant noir et blanc	Lark bunting
Passeriformes	Corvidae	*Nucifraga*	*columbiana*	Cassenoix d'Amérique	Clark's nutcracker
Passeriformes	Corvidae	*Corvus*	*ossifragus*	Corneille de rivage	Fish crow
Passeriformes	Vireonidae	*Vireo*	*flavifrons*	Viréo à gorge jaune	Yellow-throated vireo
Passeriformes	Cardinalidae	*Spiza*	*americana*	Dickcissel d'Amérique	Dickcissel
Passeriformes	Tyrannidae	*Empidonax*	*virescens*	Moucherolle vert	Acadian flycatcher
Passeriformes	Tyrannidae	*Empidonax*	*traillii*	Moucherolle des saules	Willow flycatcher
Passeriformes	Tyrannidae	*Contopus*	*virens*	Pioui de l'Est	Eastern wood pewee
Passeriformes	Turdidae	*Hylocichla*	*mustelina*	Grive des bois	Wood thrush
Passeriformes	Cardinalidae	*Piranga*	*olivacea*	Tangara écarlate	Scarlet tanager
Passeriformes	Sittidae	*Sitta*	*pusilla*	Sittelle à tête brune	Brown-headed nuthatch
Passeriformes	Parulidae	*Vermivora*	*chrysoptera*	Paruline à ailes dorées	Golden-winged warbler
Passeriformes	Parulidae	*Protonotaria*	*citrea*	Paruline orangée	Prothonotary warbler
Passeriformes	Parulidae	*Helmitheros*	*vermivorum*	Paruline vermivore	Worm-eating warbler
Passeriformes	Paridae	*Poecile*	*carolinensis*	Mésange de Caroline	Carolina chickadee
Passeriformes	Paridae	*Baeolophus*	*bicolor*	Mésange bicolore	Tufted titmouse
Passeriformes	Mimidae	*Toxostoma*	*rufum*	Moqueur roux	Brown thrasher
Passeriformes	Mimidae	*Oreoscoptes*	*montanus*	Moqueur des armoises	Sage thrasher

Appendix C – Calculation of the Spatial Autocovariate

The occupation of the neighborhood can be calculated in several ways and its calculation is based on arbitrary decisions.

First, we need to choose a definition of the neighborhood. We decided to base our definition of the neighborhood on distance: all the BBS routes located within a radius of *X* km around the focal routes are neighbors. This definition guarantees the symmetry of neighborhood relationships. That is, if A is neighbor to B, then B is necessarily neighbor to A. Once the definition of neighborhood is established, the neighborhood occupancy of route j can be calculated as follows:

$$SA_j = \frac{1}{n_j}\sum_{i=1}^{n_j} a_i$$

a_i is an attribute of route i , where $i = 1, \ldots, n_j$, and n_j is the number of routes in the neighborhood of routes j. a_i can be the occupation status (absence = 0 and presence = 1) or the estimated abundance. This choice of metric is the second arbitrary decision. If a_i is the occupancy status, then SA is the proportion of occupied routes in the neighborhood. If a_i is the estimated abundance, then SA is the average abundance in the neighborhood.

These measures of SA_j can be weighted by distance so that the nearest routes have more weight than the more distant routes. To do this, we add a weighting factor (w_i) that modifies the relative importance of the neighboring routes in the calculation of SA_j.

$$SA_j = \frac{1}{n_j}\sum_{i=1}^{n_j} a_i w_{ij}$$

The weighting factor for the neighbor i of the focal route j is calculated as follows:

$$w_{ij} = \frac{{d_{ij}}^{x}}{\sum_{i=1}^{n_j} d_{ij}}$$

d_{ij} is the distance between the neighbor i and the focal route j.

The choice of x is the third arbitrary decision. The exponent x determine how w_{ij}varies with distance. For example, if $x = -1$, the weight of neighboring routes is inversely proportional to their distance from route j.

Division by $\sum_{i=1}^{n_j} d_i$ ensures that $\sum_{i=1}^{n} w_i = 1$. Without this adjustment, SA_j would be unduly dependent on n_j. This would be a problem since not all routes have the same number of neighbors, and this variation is unrelated to neighborhood occupancy. It is rather due to spatial variability in sampling intensity.

Neighbor occupancy is calculated in the same way as the spatial autocovariate of autologistic models (Bardos et al., 2015). In these models, a spatial autocovariate is used to model the dependence between neighboring observations, i.e. spatial autocorrelation. The autocovariate is calculated from the dependent variable and then added to the model as an independent variable. In some way, it measures how the dependent variable varies as a function of itself, hence the prefix "auto".

Some authors have argued that this method produces biased results (Dormann et al., 2007; Dormann, 2009): that when a spatial autocovariate is included in a model, the effects of the other independent variables are systematically underestimated. However, Bardos et al. (2015) have recently shown that these criticisms were unfounded. The biases observed were due to incorrect weighting of neighboring observations when calculating the spatial autocovariate, and not to the method itself. When adequate weighting is used (as is the case here), the results obtained are unbiased.

All the measures of SA_j assume that the probability of a detection error is the same on all routes and is independent of the year. Due to the spatial distribution of BBS routes, some routes have very few or no neighbors within an X km radius. For these routes, SA_j is calculated with very little accuracy or simply cannot be calculated (division by zero). For this reason, we used only routes with at least 5 neighbors.

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Bardos D.C., Guillera-Arroita G., & Wintle B.A. (2015) Valid auto-models for spatially autocorrelated occupancy and abundance data. *Methods in Ecology and Evolution*, **6**, 1137‑1149.

Dormann C., M. McPherson J., B. Araújo M., Bivand R., Bolliger J., Carl G., G. Davies R., Hirzel A., Jetz W., Daniel Kissling W., Kühn I., Ohlemüller R., R. Peres-Neto P., Reineking B., Schröder B., M. Schurr F., & Wilson R. (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. *Ecography*, **30**, 609‑628.

Dormann C.F. (2009) Response to comment on « methods to account for spatial autocorrelation in the analysis of species distributional data: A review ». *Ecography*, **32**, 379‑381.

Appendix D – Environmental Data

Table D.1. Name, type (categorical or continuous), unit and values range of values for the seven environmental variables used in the MaxEnt model. When a variable is categorical, the number of categories is indicated in parentheses. The definition of those categories is given in table D.2 and D.3.

Name	Type	Units	Range (min – max)
Temperature	Continuous	K	274.6– 308.2
Precipitation rate	Continuous	kg m^{-2} s^{-1}	0.00 – 1.83
Transpiration	Continuous	W m^{-2}	0.0 –125.9
Soil type	Categorical(9)	—	1–9
Vegetation type	Categorical(13)	—	1–13
Vegetation cover	Continuous	%	1.00 – 97.68
Elevation	Continuous	m	-37 – 3687

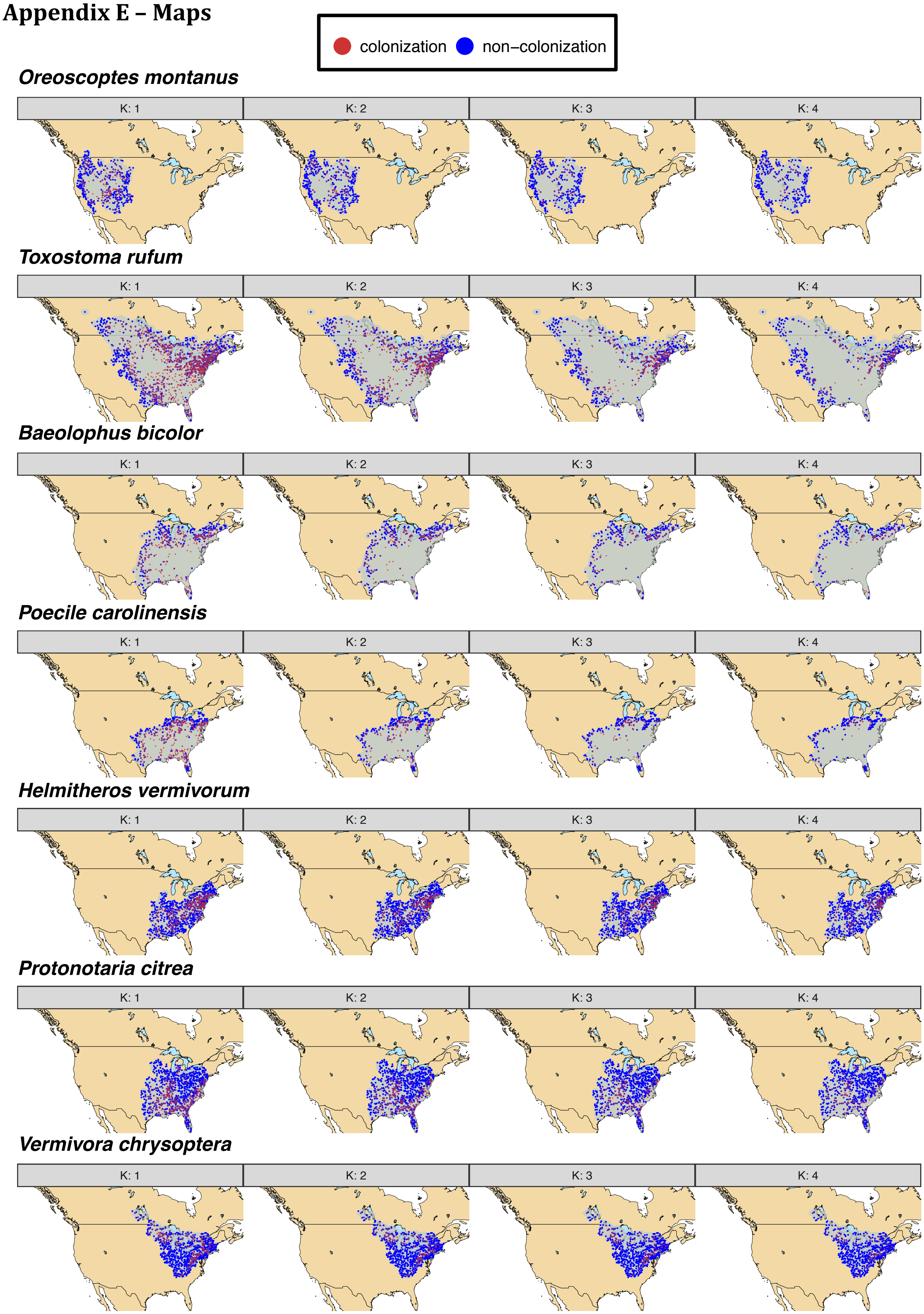
Table D.2. Definition of the different vegetation type values

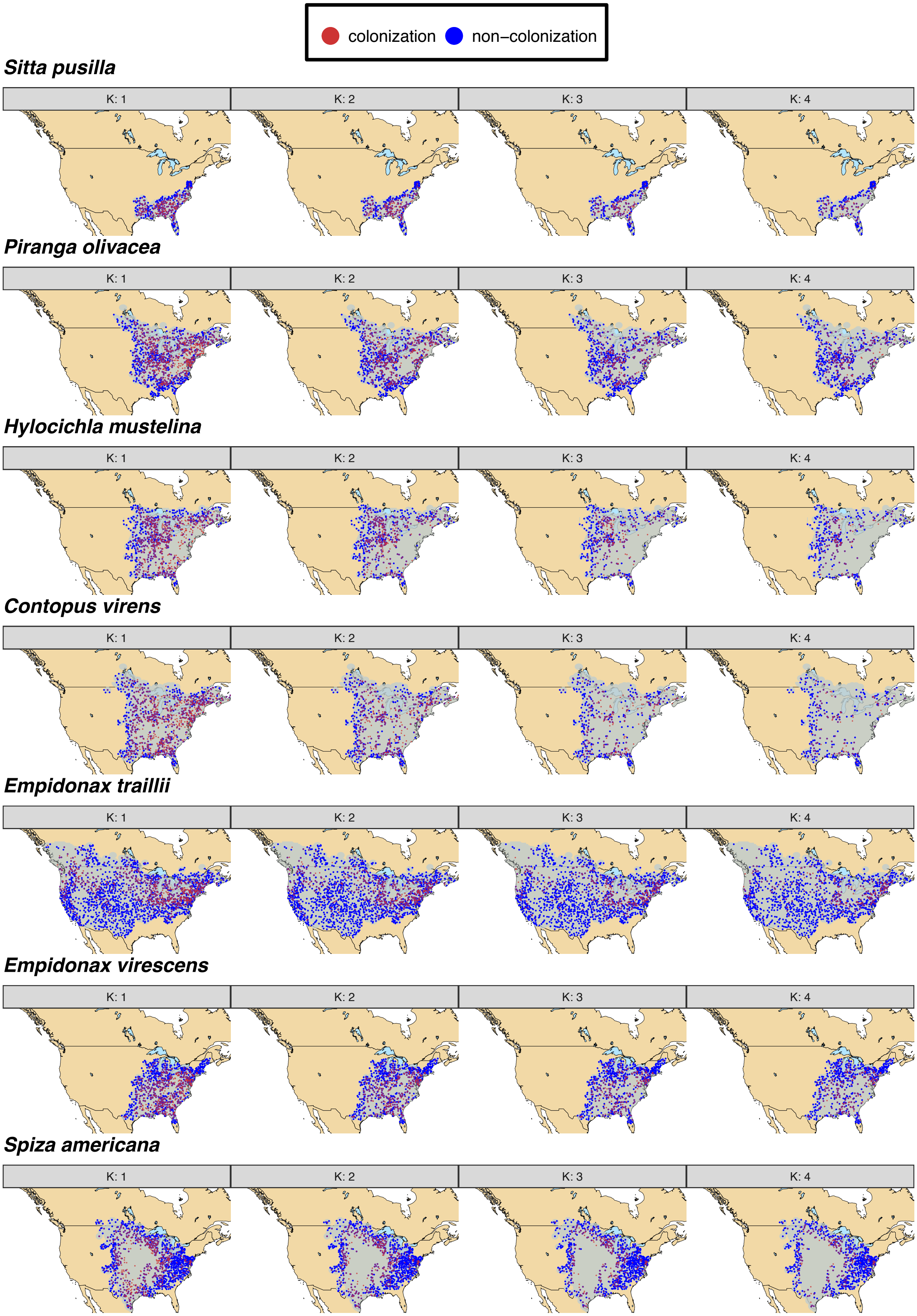
VALUE	DESCRIPTION
1	Broadleaf-evergreen trees (tropical forest)
2	Broadleaf-deciduous trees
3	Broadleaf and needleleaf trees (mixed forest)
4	Needleaf-evergreen trees
5	Needleaf-deciduous trees (larch)
6	Broadleaf trees with groundcover (savanna)
7	Groundcover only (perennial)
8	Broadleaf shrubs with perennial groundcover
9	Broadleaf shrubs with bare soil
10	Dwarf trees and shrubs with groundcover (tundra)
11	Bare soil
12	Cultivations (same as for type 7)
13	Glacial (same as for type 11)

Table D.3. Definition of the different soil type values

VALUE	DESCRIPTION
1	Coarse texture, loamy sand, 0.82 quartz content
2	Medium texture, silty clay loam, 0.10 quartz content
3	Fine texture, light clay, 0.25 quartz content
4	Coarse-medium texture, sandy loam, 0.60 quartz content
5	Coarse-fine texture, sandy clay, 0.52 quartz content
6	Medium-fine texture, clay loam, 0.35 quartz content
7	Coarse-medium-fine texture, sandy clay loam, 0.60 quartz content
8	Organic texture, 0.40 quartz content
9	Glacial land ice, loamy sand, 0.82 quartz content

Appendix E – Maps




● colonization ● non–colonization
Sitta pusilla
K: 1
K: 2
K: 3
K: 4
Piranga olivacea
K: 1
K: 2
K: 3
K: 4
Hylocichla mustelina
K: 1
K: 2
K: 3
K: 4
Contopus virens
K: 1
K: 2
K: 3
K: 4
Empidonax traillii
K: 1
K: 2
K: 3
K: 4
Empidonax virescens
K: 1
K: 2
K: 3
K: 4
Spiza americana
K: 1
K: 2
K: 3
K: 4

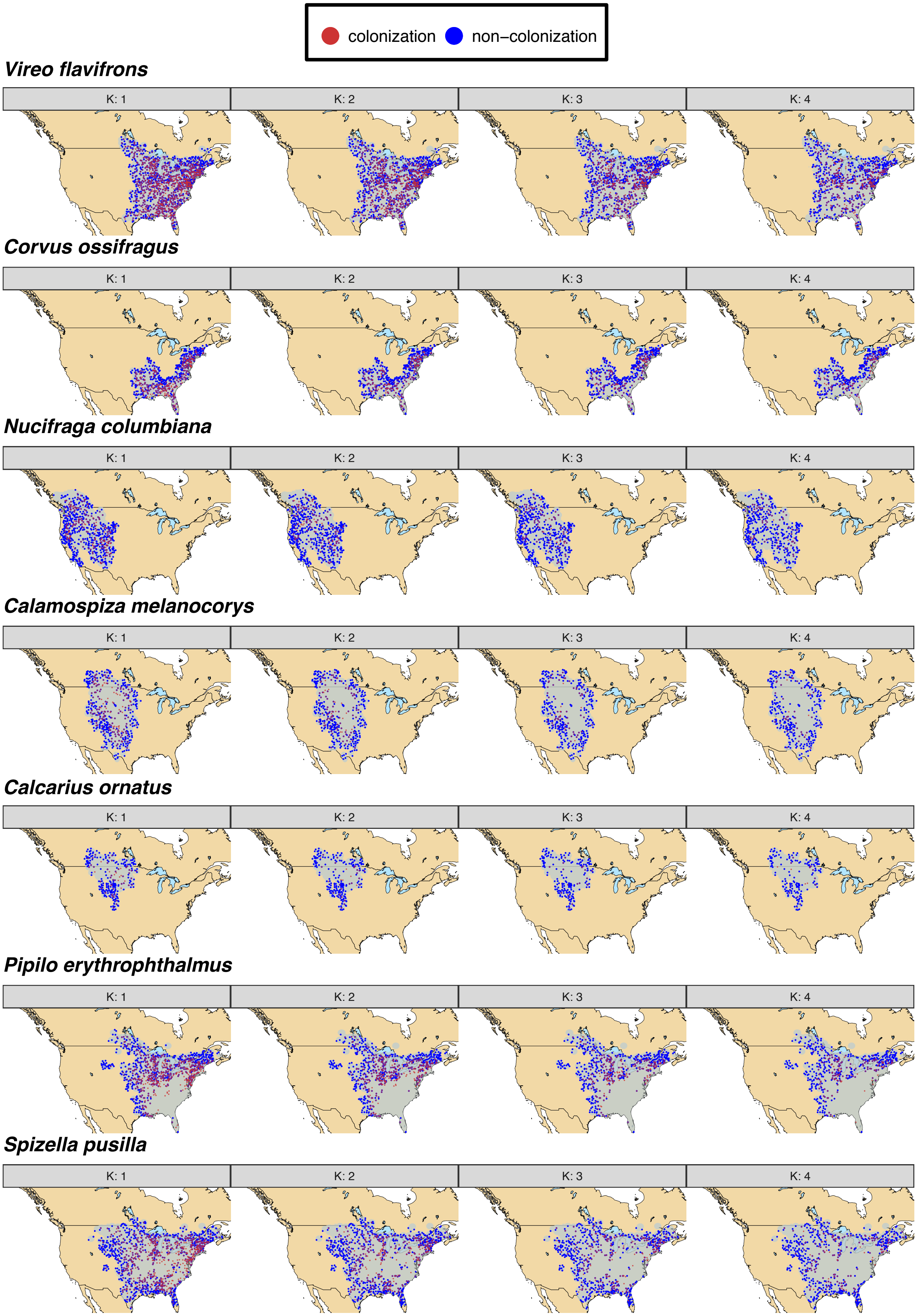
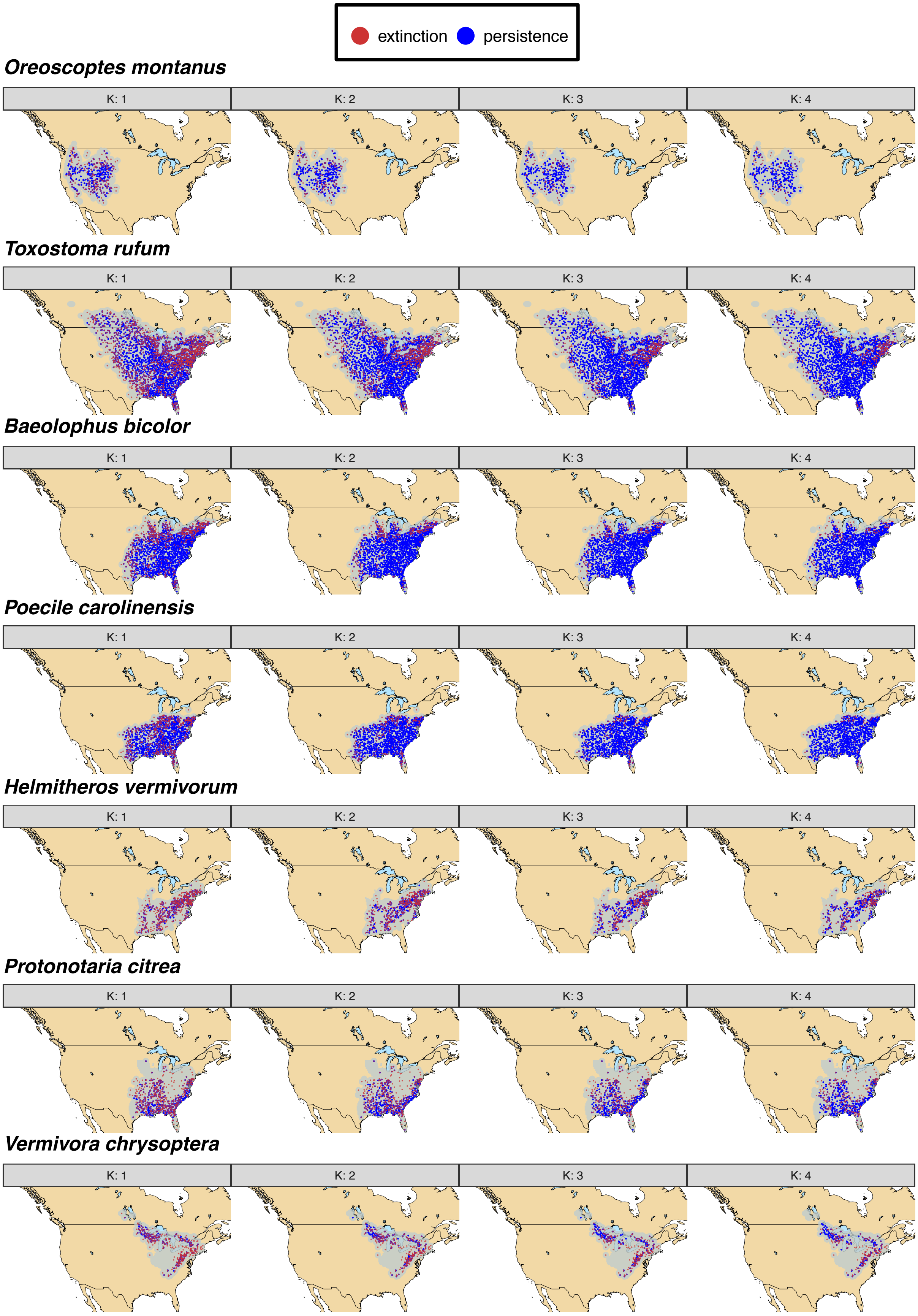
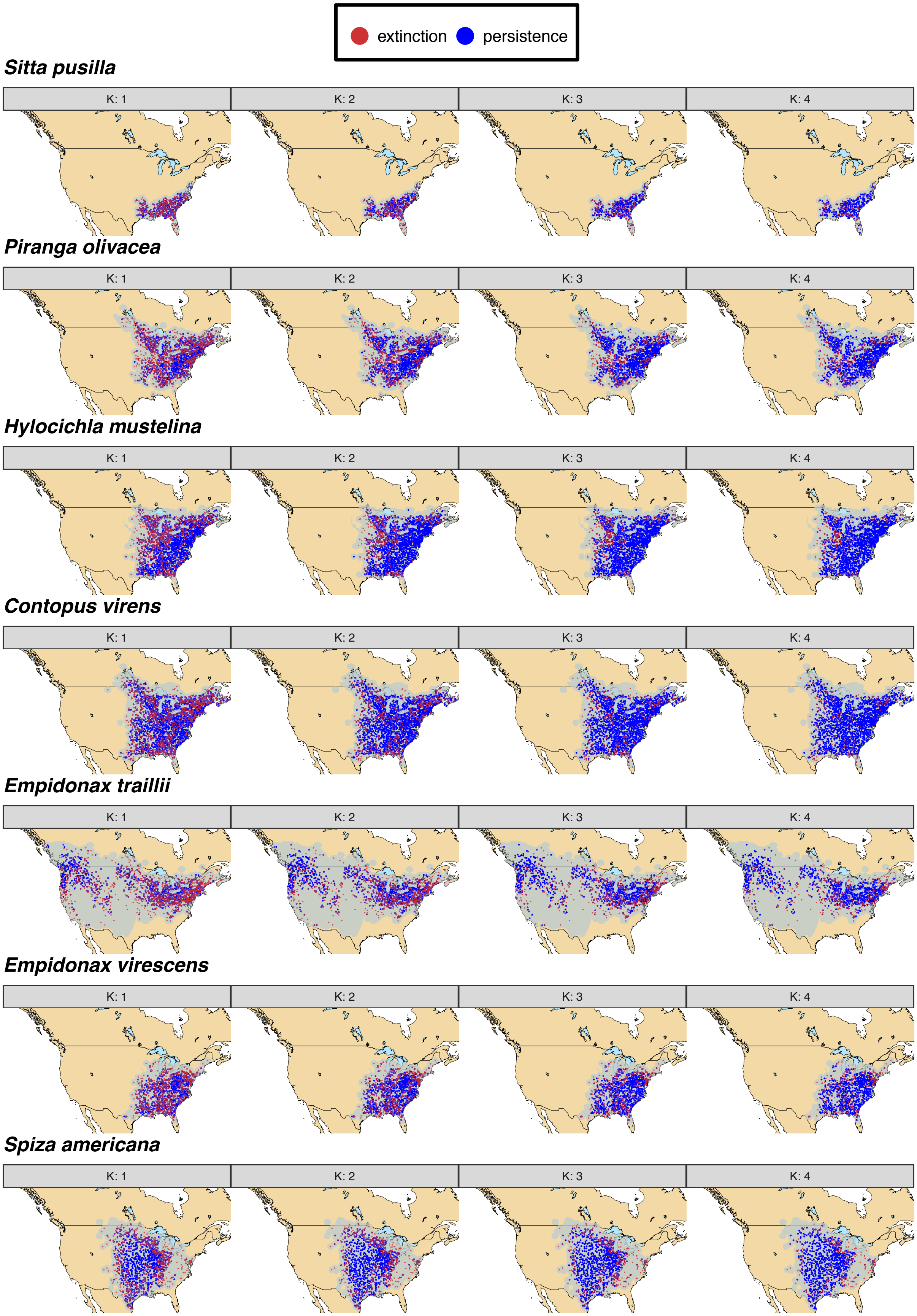

colonization
non–colonization
Vireo flavifrons
K: 1
K: 2
K: 3
K: 4
Corvus ossifragus
K: 1
K: 2
K: 3
K: 4
Nucifraga columbiana
K: 1
K: 2
K: 3
K: 4
Calamospiza melanocorys
K: 1
K: 2
K: 3
K: 4
Calcarius ornatus
K: 1
K: 2
K: 3
K: 4
Pipilo erythrophthalmus
K: 1
K: 2
K: 3
K: 4
Spizella pusilla
K: 1
K: 2
K: 3
K: 4

Figure E.1. Maps showing the potential breeding range (gray area), colonization (red) and non-colonization (blue) of the 21 bird species included in our study. Colonization is defined on a BBS routes as a period of absence (i.e. non-detection) of *k* successive years followed by a presence. For each species, four maps are shown: one for each value of *k* used in our study (1 - 4 years). Over the study period (1979-2009), both colonizations and non-colonizations can have occurred on the same BBS route. To be able to see when it is the case, we plotted colonizations on top of non-colonizations and used points of smaller size for colonization. We defined the potential breeding range of each bird as the union of the breeding range map depicted by BirdLife International (http://www.birdlife.org/datazone/info/spcdownload) and the BBS routes at which the species was observed at least once between 1979 and 2009, plus a 100 km buffer around each of those routes (most, but not all, BBS presences fall within the BirdLife ranges).


● extinction
● persistence
Oreoscoptes montanus
K: 1
K: 2
K: 3
K: 4
Toxostoma rufum
K: 1
K: 2
K: 3
K: 4
Baeolophus bicolor
K: 1
K: 2
K: 3
K: 4
Poecile carolinensis
K: 1
K: 2
K: 3
K: 4
Helmitheros vermivorum
K: 1
K: 2
K: 3
K: 4
Protonotaria citrea
K: 1
K: 2
K: 3
K: 4
Vermivora chrysoptera
K: 1
K: 2
K: 3
K: 4


● extinction ● persistence
Sitta pusilla
K: 1
K: 2
K: 3
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Piranga olivacea
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Hylocichla mustelina
K: 1
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K: 3
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Contopus virens
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Empidonax traillii
K: 1
K: 2
K: 3
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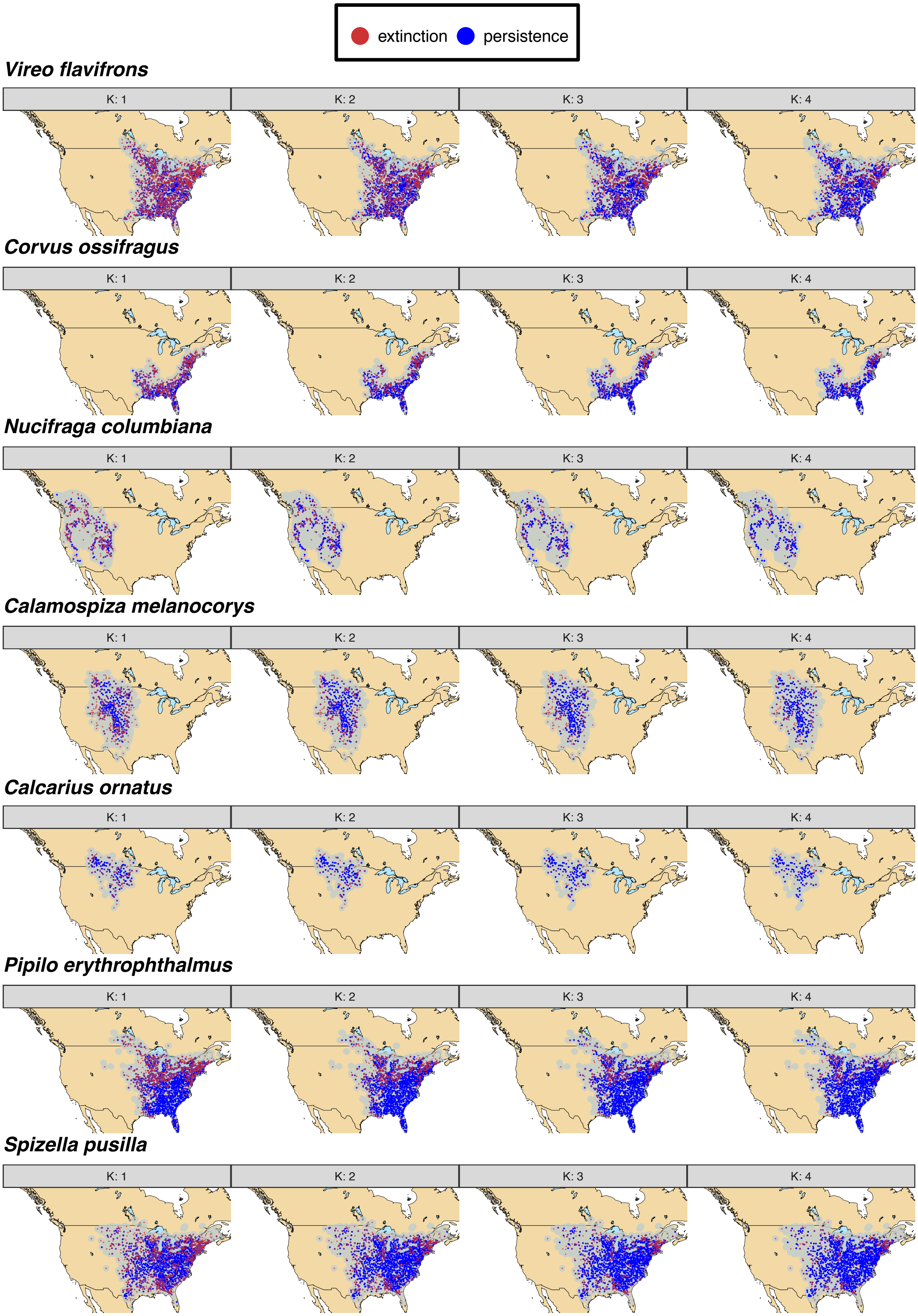

Vireo flavifrons

Corvus ossifragus

Nucifraga columbiana

Calamospiza melanocorys

Calcarius ornatus

Pipilo erythrophthalmus

Spizella pusilla

Figure E.2. Maps showing the potential breeding range (gray area), extinctions (red) and persistences (blue) of the 21 bird species included in our study. Extinction is defined on a BBS routes as a presence followed by a period of absence (i.e. non-detection) of *k* successive years. For each species, four maps are shown: one for each value of *k* used in our study (1 - 4 years). Over the study period (1979-2009), both persistence and extinction can have occurred on the same BBS route. To be able to see when it is the case, we plotted extinctions on top of persistences and used points of smaller size for extinction. We defined the potential breeding range of each bird as the union of the breeding range map depicted by BirdLife International (http://www.birdlife.org/datazone/info/spcdownload) and the BBS routes at which the species was observed at least once between 1979 and 2009, plus a 100 km buffer around each of those routes (most, but not all, BBS presences fall within the BirdLife ranges).

Appendix F – Supplementary Analysis

Some might argue that the effect of change in suitability would be greater over a longer period. This cannot be tested simply by increasing *k* (the period of absence) because this reduces sample sizes too much for most birds. Another way of testing if change is suitability is related to change in occupancy is to compare the rate of change in suitability to the rate of change in occupancy over the same period. This allows us to consider the entire period over which a route was sampled. However, this analysis suffers from many problems.

First, it assumes that suitability changed linearly over the study period, such that changes in suitability on a given route can be described by a single number (i.e. the slope of suitability over time estimated with linear regression). We know that this is likely not the case for most routes since route-wise non-parametric correlation between suitability and years show that suitability very rarely changed monotonically over the study period (Fig. 5B).

Similarly, it assumes that trend in occupancy though time can be described using logistic regression. In fact, time is not a significant predictor of probability of presence on most routes.

Nevertheless, ignoring those issues, we looked at the relationship between the trend in suitability through time and the trend in occupancy through time on each route.

We created a binary variable based on the direction of change in occupancy over time (estimated with logistic regression). The variable identifies whether the occupancy increased or decreased (1 or 0) on a route over the study period.

Then, for each bird, we fitted a logistic regression model using this new variable as the dependent variable, and the rate of change in suitability as the independent variable. The expectation is that an increase in suitability would cause an increase in occupancy. Thus, the probability of an increase in occupancy should be higher when suitability increased. When analyzed in this way, the effect of change in suitability on change in occupancy is rarely significant (Fig. F.1), but generally in the right direction.

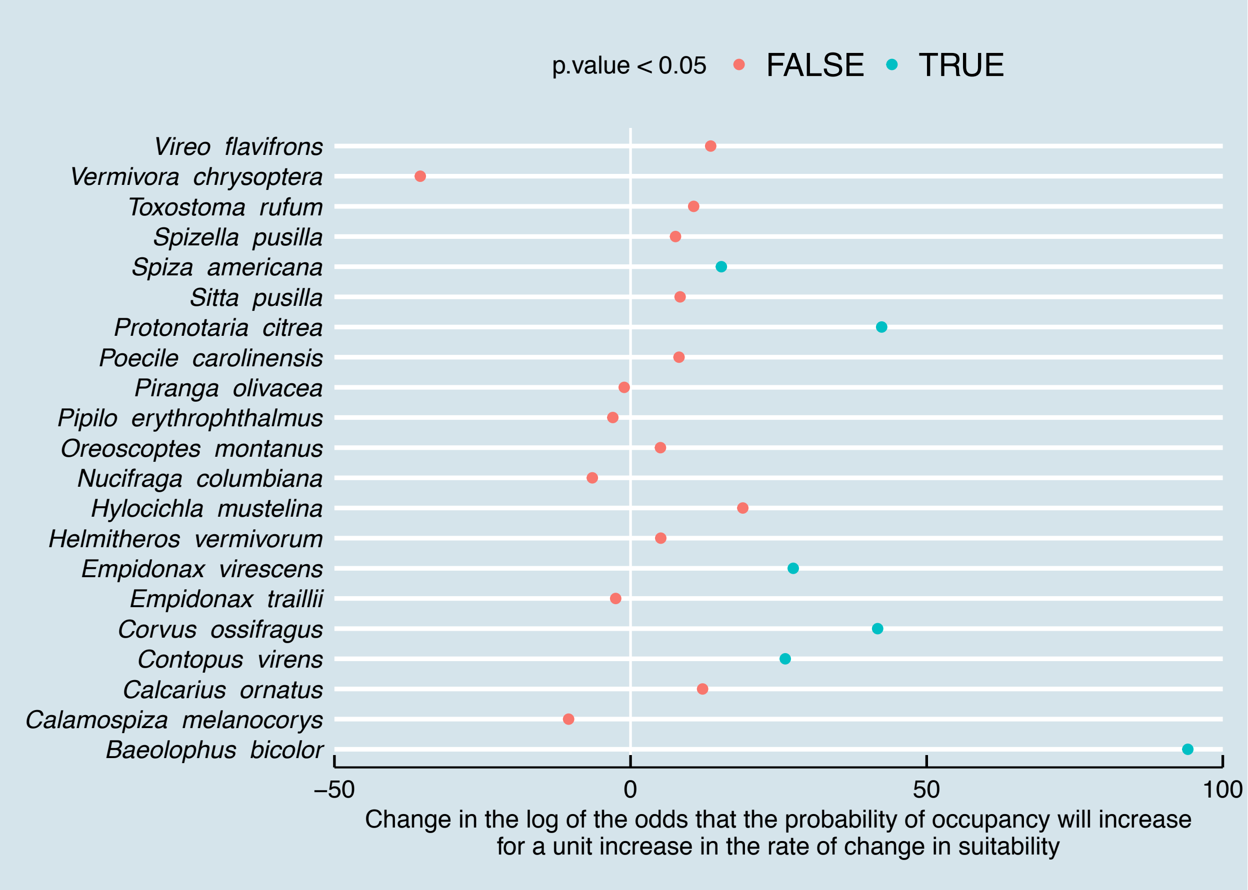

Figure F.1. Change in the log of the odds that the probability of occupancy will increase for a unit increase in the rate of change in suitability, for the 21 bird species included in our study. For a given species, on each route within the species'potential range, the trend in suitability is estimated using linear regression. Similarly, the trends in occupancy through time are estimated using logistic regression and then converted into a binary variable (increase or decrease). Logistic regression is then used to estimate how changes in occupancy relate to changes in suitability. A blue dot indicates a significant effect of change in suitability.