

## Failure to find the relationship between dispersal and spatial autocorrelation in species abundance

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Spatial autocorrelation in species abundances indicates a lack of independence between sample locations and causes problems in distribution modelling. Knowing the cause of such spatial autocorrelation is vital for selecting the best suited modelling methods. Most autocorrelation in distributions is caused by autocorrelation in the underlying environmental conditions. The aim of the study was to determine whether dispersal could be responsible for additional spatial autocorrelation. I used data from 107 species of the North American Breeding Bird Survey covering the conterminous United States to investigate this question. As is the case for most species, no direct information on the dispersal activity of the study species was available. Therefore, I derived dispersal indices from three ecological theories: the deviation from an abundance-occupancy relationship, the spatial exponent of Taylor's power law, and density dependence. Spatial autocorrelation was captured in conditional autoregressive regression models (CAR) and measured with a standardized version of the regression coefficient  $\rho$ , the extent of the optimized neighbourhood, and the additional variance explained in CAR models over traditional regression models. No consistent association between these measures of autocorrelation and the indices for dispersal was found. Results indicated that the indirect ecological indices for dispersal carried too much noise and too little information for successful analysis. Future research on the effects of dispersal on autocorrelation need to be based on improved indirect indicators or direct, empirical dispersal information.

### Introduction

Dependence between observations across geographic space has long been identified as a source of error in statistical analyses (Student 1914). In geography, the universal spatial dependence or autocorrelation in measurements of a variable collected at different spatial locations has been termed the First Law of Geography (Tobler 1970). Ecologists have also recognized the

problem for decades (Legendre 1993), but only recently has the number of studies addressing spatial autocorrelation proliferated (Augustin *et al.* 1996, Leathwick 1996, Overton 1996, Thomson *et al.* 1996, Koenig 1999, Lennon 2000, Koenig 2001, Trenham *et al.* 2001, Keitt *et al.* 2002, Lichstein *et al.* 2002, Diniz-Filho *et al.* 2003, Peakall *et al.* 2003).

In the field of distribution modelling, spatial autocorrelation has been widely identified in

species' distributions and abundances (Legendre 1993) and statistical techniques have been developed to address the problem (Dale *et al.* 2002, Dale & Fortin 2002, Keitt *et al.* 2002, Lichstein *et al.* 2002, Dormann *et al.* 2007). However, as Austin (2002) points out, an understanding of the ecological processes that underlie spatial autocorrelation in species distributions is a prerequisite to the creation of adequate models. When all autocorrelation in a species' abundance is due to autocorrelation in the underlying environmental factors, and all factors are included in a distribution model, spatially explicit modelling is unnecessary (Austin 2002). Only when a major environmental factor is missing or when ecological processes lead to additional autocorrelation in a species' abundance are spatial models necessary. The questions thus become which ecological processes could lead to spatial autocorrelation in species abundances, and is there any empirical evidence for the effects of such processes?

The ecological process most likely to cause spatial autocorrelation in species abundances is dispersal in the widest sense (Austin 2002). I use dispersal in the sense of Lidicker (1975), including every movement that constitutes leaving the home area for breeding, but not short-term exploratory and "round-trip" migratory movements. The exchange of individuals between populations may synchronize population sizes (Paradis *et al.* 1998, Bjørnstad *et al.* 1999), an effect that is thought to decay with distance because dispersal strength also typically decays with distance. The behavioural motivations for dispersal vary widely (Stenseth & Lidicker 1992a). While it would be interesting and ultimately important to gain a detailed understanding of such motivations, I considered the motivation for dispersal a secondary question in this study and I focused solely on the consequences of dispersal.

Dispersal is difficult to study, particularly at large extents (Stenseth & Lidicker 1992b). Accordingly, very little information on long-distance dispersal is found in the literature. I therefore developed an indirect approach to predicting the dispersal activity of bird species and compared this dispersal index to autocorrelation found in their abundances. Because some of the most prominent ecological fields and theories — for example metapopulation dynamics,

island biogeography, and studies on population synchrony — have dispersal at their core, I used such theories to develop indirect predictors of dispersal. While such indirect predictors are not well-suited to determining unequivocal cause and effect, the use of several unrelated theories and approaches can still make a strong case (Levins 1966).

The goal of this study was to determine whether dispersal was related to spatial autocorrelation in species abundances above and beyond what can be explained through spatial autocorrelation in underlying environmental factors. To answer this question, it was necessary to find a way to predict dispersal activity consistently across a large number of species and to determine the amount of spatial autocorrelation in species abundances that could not be explained by autocorrelation in underlying environmental conditions.

## Materials and methods

### Empirical data

The species distribution data stemmed from the North American Breeding Bird Survey (BBS). I used averaged incidence values for each of 107 bird species (*see* complete list in Appendix) in the conterminous USA. Criteria for the selection were good coverage over the conterminous USA (> 150 occupied routes) and sensitivity to coarse-scale predictors covered in my dataset ( $R^2 > 0.5$  in initial regression tree models). Reasons for exclusion were extreme range shapes, such as long and narrow ranges along the border of the study area, or the extremely patchy distributions. Such distributions prevent meaningful spatial modelling. One bird species was dropped from the previous analysis (Bahn *et al.* 2006b) because of lack of data.

Incidence values are more robust than abundance measures (O'Connor *et al.* 1996) but are expected to correlate well with abundance (Wright 1991). Therefore, I used averaged incidence values over 10 years (1981 to 1990) in the distribution models and deviation from abundance-occupancy relationship (*see* below) rather than abundance as dependent variable. Oyler

(1993) and Boone (1991) used the same BBS data for calculating their indices (*see* below). However, they used time-series running from 1966 to 1990 rather than abundances averaged over 10 years. The data were summarized over 1189 BBS routes with the highest reliability rating, which were mapped to a hexagonal grid, with cells approximately 620 km<sup>2</sup> in size and 27 km apart from centre to centre (White *et al.* 1992).

The 207 independent variables comprised 160 variables summarizing land cover information, twelve climate variables (January and July temperatures, precipitation, and derived variables such as seasonality), four variables from digital elevation models, and thirty-one other variables characterizing the land cover in terms of spatial configuration and fragmentation indices. For more details on these variables see Bahn *et al.* (2006a).

The distribution of each bird species was modelled using the same procedure: first, variables were selected with regression tree models (Breiman 1984); second, these variables were included in third degree polynomial form in regular regression models; third, individual independent variables or their polynomials were selected in an AIC-based stepwise backward selection method leading to ordinary regression models based on a selection of environmental variables, henceforth called “traditional environmental models”; fourth, fully spatial CAR models were fit on these selected variables and their polynomials with a range of different neighbourhood sizes (in 50 km steps); fifth, the neighbourhood size leading to the model with the highest maximum likelihood was selected for the final model. All models were constrained to the ranges of the bird species as determined by the ranges published by NatureServe (Ridgely *et al.* 2003). These ranges are the typical filled-in polygons describing the maximum extent of species occurrences within which lie many locations at which the species was actually absent.

The high number of independent variables may seem to pose a danger of creating spurious results in this multi-step analysis process. However, bear in mind that 160 of these 207 variables were land cover variables that have zeros over most of the area. At any given loca-

tion, only few landcover variables will be relevant and able to enter the model. In addition, in contrast to multiple regressions, regression trees are very good at variable selection and do not tend to pick up spurious effects in random variables (Bahn & McGill 2007). Averaged over the 107 included species, the pruned regression tree models included  $4.9 \pm 0.3$  (SE) variables and  $12.3 \pm 0.74$  splits, while the multiple regressions retained  $4.6 \pm 0.29$  variables resulting in  $14.3 \pm 0.68$  parameters given that variables were included up to a 3rd degree polynomial. The average sample size was  $717 \pm 28.7$  routes per species (range: 161–1189), making the number of included parameters reasonable.

The methods of this study have two distinct components: First, the analysis of spatial autocorrelation patterns present in each species' distribution, and second, indices of dispersal activity.

## Measures of autocorrelation

The part of autocorrelation that was interesting in the context of this study was the part that went above and beyond the spatial autocorrelation stemming from the environment. Therefore, all measures of autocorrelation were based on fully spatial Conditional Autoregressive Regression (CAR) models (Cressie 1993) that included a comprehensive set of environmental variables. These models stemmed from previous research (Bahn *et al.* 2006b) and are described in detail there.

I derived three measures for autocorrelation from these models described in more detail below. The first measure was the extent of the neighbourhood included in the spatial model (from here on called “Extent”), which I selected for best fit of the model during the modelling process (*see* above). The second measure was the variation in distribution identified as purely spatial effect during the partitioning of variation following Borcard *et al.* (1992), from here on called “Space.” The third measure was a standardized version of  $\rho$  (from here on called “Rho.std”), which is the regression coefficient in front of the neighbourhood matrix in the CAR models (*see* Eq. 1).

$$Y = \mathbf{X}\beta + \rho\mathbf{C}(Y - \mathbf{X}\beta) + \varepsilon \quad (1)$$

where:  $Y$  is a vector of responses,  $\mathbf{X}$  is a matrix of predictor variables,  $\beta$  is a vector of parameters,  $\rho$  is a parameter,  $\mathbf{C}$  is a neighbourhood matrix, and  $\varepsilon$  is a vector of errors.

Extent is the maximum distance at which a significant autocorrelation effect can be measured. Extent does not give any indication of the strength of autocorrelation. Note that the way the maximum extent was determined here was not identical to the range of a variogram. In general, the optimal extents of neighbourhoods were smaller than the range in variograms on the same data, an effect also observed by van Teeffelen and Ovaskainen (2007).

The spatial partition of variation in species distributions (Space) was the  $R^2$  of the full CAR model (including environmental variables and the neighbourhood matrix) minus the  $R^2$  of the traditional environmental model. It describes the variation explained in the CAR model that is attributable neither to the environmental predictors nor to the spatial information implicit in the environmental predictors (which is also captured in the traditional environmental models). Thus, it does not necessarily measure spatial autocorrelation *per se*, but is an indirect index for purely spatial variation in the distribution patterns that could not be explained through environmental variables or their spatial structure or expressed in a different way: autocorrelation in the species' distribution that goes above and beyond the autocorrelation in the distribution attributable to autocorrelation in the underlying environmental gradients.

The coefficient  $\rho$  (see Eq. 1) indicates the strength of inclusion of the neighbourhood matrix (which was distance weighted with a spherical model reaching a weight of zero at the specified neighbourhood extent) in the CAR model, and thus indirectly captures both the strength and the extent of spatial autocorrelation. However, as in other regression coefficients,  $\rho$  was also dependent on the magnitude of and variation in the dependent and independent variables, and the neighbourhood matrix. Therefore, I standardized  $\rho$  analogously to the standardization of regular regression coefficients (Zar 1996: 420):  $b_i' = b_i \times s_{X_i}/s_Y$  where  $b_i'$  is the standard-

ized regression coefficient of the  $i$ th independent variable,  $b_i$  is the non-standardized regression coefficient,  $s_{X_i}$  is the standard deviation of the independent variable  $X_i$ , and  $s_Y$  is the standard deviation of the dependent variable  $Y$ . In the case of the coefficient  $\rho$  in CAR regressions,  $\mathbf{X}$  is not simply a variable but an expression describing neighbourhood effects:  $\mathbf{C}(Y - \mathbf{X}\beta)$ , where  $\mathbf{C}$  is the neighbourhood matrix,  $Y$  is the dependent variable,  $\mathbf{X}$  is a matrix of all independent variables and  $\beta$  is a vector of regression coefficients for the independent variables. In practice, I used the observed values of the dependent variable  $Y$  minus the predictions from the purely environmental part of the model  $\mathbf{X}\beta$  minus the residuals  $\varepsilon$  to calculate the spatial signal  $\rho\mathbf{C}(Y - \mathbf{X}\beta)$  (Kaluzny *et al.* 1996). Taking the standard deviation of the spatial signal is equal to the  $b_i \times s_{X_i}$  part of the standardized coefficient equation because  $\rho$  is a constant multiplier. Therefore, I only needed to divide this value by the standard deviation of  $Y$  to arrive at the standardized coefficient Rho.std.

## Indices of relative dispersal activity

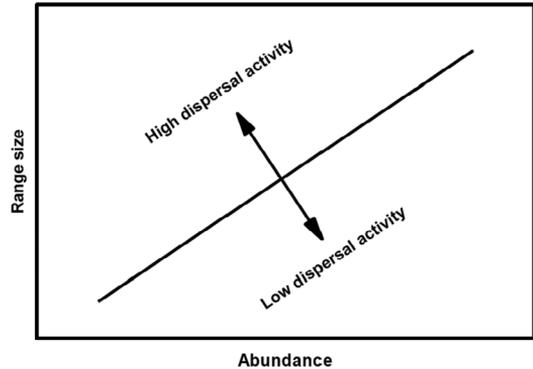
### Density dependence

The first index of dispersal activity was based on density dependence. I hypothesized that an increase in density dependence would correlate with an increase in dispersal because dispersal was identified as one of the mechanisms through which density dependence is attained (Taylor & Taylor 1977). Boone (1991) derived density dependence scores for breeding birds of the conterminous United States using Pollard *et al.*'s (1987) Monte Carlo randomization estimate (from here called "Poll"). He used annual censuses at all locations available for a given species. He detected density dependence by correlating changes in population size with population size and comparing this against a theoretical expectation under density independence derived from Monte Carlo randomization. In this measure, higher values meant less density dependence. Therefore, I expected this measure to correlate negatively with my measures of autocorrelation.

## Spatio-temporal population dynamics

The second index for dispersal activity used population dynamics characterized by Taylor's Power Law. McArdle *et al.* (1990) used Taylor's power law to characterize species according to their spatial and temporal variation in population densities. In particular the spatial exponent is relevant to dispersal. This exponent is estimated by the equation:  $s^2 = am^b$  (Taylor 1961), where  $s^2$  is the variance in abundance at all locations in a given year,  $a$  is a scaling coefficient thought to be related to sampling or computing,  $m$  is the mean in abundance across all locations in a given year, and  $b$  is the spatial exponent. The exponent  $b$  is determined as the slope of a log-log regression of variance vs. mean with individual data points stemming from different years.

When the mean and variance are independent, the expected spatial exponent is two (McArdle *et al.* 1990). That means that the variance quadruples when the mean doubles across sites. If the exponent is larger than two, the variance more than quadruples, which means that the high-density sites must be extremely packed and the low density sites must stay disproportionately sparsely populated in a good year. In contrast, if the exponent is lower than two, the variance across space increases less than expected with mean abundance meaning that high-density sites are not very high and low density sites are higher than expected. Taylor and Taylor (1977) and Taylor *et al.* (1983) attributed the variation in the power coefficient to aggregation and dispersal. Accordingly, an exponent smaller than two suggests a reduction in variance among sites potentially through more dispersal from high-density sites to low-density sites than an exponent larger than two. Alternatively, a similar reduction in variance among sites could be achieved with other mechanisms of density dependence such as reduced birth or increased death rates, weakening the connection between the exponent and dispersal. Nevertheless, my hypothesis was that species with a spatial exponent  $> 2$  will have lower indicators of autocorrelation than species with a spatial exponent  $\leq 2$ . I used the spatial exponent (from here called "Bspatial") calculated by Oyler (1993) for birds of the United States and correlated them with the three measures of auto-



**Fig. 1.** Relationship between average abundance and occupancy (here labelled distribution). While the main relationship is attributed to niche width, deviations from it are caused by rates of dispersal. Adapted from Hanski *et al.* (1993).

correlation using Spearman's rank correlation and expecting a negative correlation.

## Hanski's deviation from abundance-occupancy relationship

The third indirect index for dispersal activity was derived according to a hypothesis put forward by Hanski *et al.* (1993). They presented possible explanations for the positive abundance-occupancy relationship, which is a widely documented macroecological pattern within homogeneous taxonomic assemblages (Gaston *et al.* 2000, Holt *et al.* 2002). One of the explanations was based on metapopulation dynamics and, in addition to explaining the relationship, it led to the expectation of a deviation from the relationship. According to their equations, they expected that species with low dispersal activity (i.e., a relatively low percentage of individuals dispersing over a relatively low average distance) would be above the predicted abundance-occupancy relationship, while those with high dispersal (i.e., a relatively high percentage of individuals dispersing over a relatively high average distance) would fall below. This hypothesis is supported by Boehning-Gaese *et al.* (2006).

I turned the relationship around so that abundance was on the  $x$ -axis and range size was on the  $y$ -axis (Fig. 1) because high average abundance causing a large range is more plau-

sible than a large range causing high average abundance. In my version, species that failed to achieve large ranges despite high average abundances were assumed to be poor dispersers while species that had unusually large ranges compared to their average abundances were assumed to be very active dispersers (Fig. 1). In this theory and layout of the relationship, positive residuals signified active dispersers, while negative residuals stood for poor dispersers. Therefore, the working hypothesis was that the residuals of a simple linear regression between abundance and range size (from here called “Ao.resid”) would correlate positively with measures of spatial autocorrelation.

I used incidence values over 10 years rather than abundance in the calculation of Ao.resid. I calculated the average incidence values for each species only across sites with non-zero incidence values (Gaston *et al.* 2000). Range size was derived from the NaturServe maps (Ridgely *et al.* 2003), also used in the range determination for the distribution models.

## Confounding variables

Two variables deserved attention because of their potentially confounding effects on the relationship between dispersal and autocorrelation. The first one was the number of sampling locations. Species with larger ranges also had more sampling locations and thus larger sample sizes. Several of the independent and dependent variables described above were substantially correlated with sample size. These correlations were taken into consideration by using partial correlations, controlling for sample size. The second potentially confounding variable was the potential

population growth rate  $R$ . Bahn *et al.* (2006a) showed that  $R$  influences the effect of dispersal on spatial patterns species distributions. Here clutch size (hereafter called “Max.clutch”) taken from Ehrlich *et al.* (1988) was used as a proxy for  $R$ .

All statistics were programmed in S-PLUS 6.2 (Insightful 2003). Rather than presenting hypothesis tests on the Spearman rank correlations I calculated bootstrap bias-corrected, adjusted 95% confidence limits (Efron & Tibshirani 1998) to give the reader an impression of the uncertainty in the regression coefficients. The number of bootstrap resamples was 10 000.

## Results

The three measures of autocorrelation only showed partial agreement (Table 1). While the standardized regression coefficient for neighbourhood inclusion (Rho.std) and the pure spatial partition (Space) correlated fairly well ( $r = 0.513$ , 95% CI = 0.366–0.641), the two measures did not correlate meaningfully with the maximum neighbourhood extent. This result underscores the lack of any systematic relationship between the overall strength of autocorrelation and its extent.

The confounding variables had few effects on the three measures of autocorrelation (Table 2). The only moderately strong correlation was between extent and the sample size of locations ( $n$ ). Larger  $n$  occurred in larger ranges, which can accommodate larger neighbourhoods. In addition, larger  $n$  allowed better models, which were more capable of profiting from small effects

**Table 1.** Spearman rank correlation coefficients among three different measures of autocorrelation. Confidence intervals are bootstrap bias-correct, adjusted 95% probability limits.  $N = 107$ .

Variable 1	Variable 2	$r$	Lower CI	Upper CI
Space	Extent	0.111	−0.081	0.297
Space	Rho.std	0.513	0.366	0.641
Extent	Rho.std	0.124	−0.086	0.320

**Table 2.** Spearman rank correlation coefficients among three confounding variables and three measures of dispersal. Confidence intervals are bootstrap bias-correct, adjusted 95% probability limits.  $N = 107$ .

Variable 1	Variable 2	$r$	Lower CI	Upper CI
$n$	Space	−0.030	−0.218	0.168
$n$	Extent	0.376	0.175	0.538
$n$	Rho.std	0.025	−0.190	0.233
Max.clutch	Space	0.098	−0.097	0.292
Max.clutch	Extent	0.042	−0.161	0.231
Max.clutch	Rho.std	0.210	0.008	0.381

caused by distant neighbours. Another weak but interesting positive correlation existed between the maximum clutch size (Max.clutch) and Rho.std. When Max.clutch is seen as an index for potential population growth rate, such a correlation is predicted by Bahn *et al.* (2008).

The three indices for dispersal were only weakly correlated with each other, with some of the correlations having the opposite sign than expected (Table 3). I hypothesized that Ao.resid would correlate positively with dispersal, while Poll and Bspatial were hypothesized to correlate negatively with dispersal. According to these expectations, Poll and Bspatial should have correlated positively, but correlated negatively instead. Poll and Ao.resid should have correlated negatively, but did not show any consistent correlation pattern within the confidence limits. Bspatial and Ao.resid were expected to correlate negatively. While the point estimate for the regression coefficient was consistent with this expectation, the direction of the correlation was inconclusive within the confidence interval. The abundance-occupancy relationship held up fairly well in the Breeding Bird Survey data ( $R^2 = 0.11$ ,  $F_{1,105} = 12.33$ ,  $p = 0.0007$ ).

**Table 3.** Spearman rank correlation coefficients among three different indices for dispersal derived from three different ecological theories. Confidence intervals are bootstrap bias-correct, adjusted 95% probability limits.  $N = 107$ .

Variable 1	Variable 2	<i>r</i>	Lower CI	Upper CI
Poll	Bspatial	-0.221	-0.378	-0.039
Poll	Ao.resid	0.140	-0.060	0.313
Bspatial	Ao.resid	-0.114	-0.292	0.085

**Table 4.** Spearman rank correlation coefficients among three confounding variables and three measures of dispersal. Confidence intervals are bootstrap bias-correct, adjusted 95% probability limits.  $N = 107$ .

Variable 1	Variable 2	<i>r</i>	Lower CI	Upper CI
<i>n</i>	Poll	0.321	0.120	0.490
<i>n</i>	Bspatial	-0.234	-0.414	-0.033
<i>n</i>	Ao.resid	0.787	0.688	0.858
Max.clutch	Poll	0.009	-0.178	0.197
Max.clutch	Bspatial	0.033	-0.158	0.228
Max.clutch	Ao.resid	0.013	-0.185	0.207

The three indices of dispersal showed some correlations with confounding variables (Table 4). All three indices correlated with sample size (*n*), but only Ao.resid correlated strongly. Poll and Bspatial had different signs in front of their correlation coefficients with *n*, which may partly explain why they unexpectedly correlated negatively with each other. Maximum clutch size (Max.clutch) did not show strong correlations with the three indices.

No meaningful correlations between measures of autocorrelation and indices of dispersal were found (Table 5). I found only one moderately strong correlation, which was between Extent and Ao.resid. The most likely cause for this positive correlation was, however, the positive correlation of both variables with *n*. Partial correlations controlling for *n* lowered regression coefficient in this relationship but left the other correlation coefficients virtually unchanged (Table 6).

## Discussion

This study was unable to find a connection between autocorrelation and indirect indices of dispersal. The absence of correlations prevented conclusions about a possible relationship between dispersal and spatial autocorrelation in species distributions above and beyond what can be explained through spatial autocorrelation in underlying environmental factors. The failure to find the predicted correlations could have had

**Table 5.** Spearman rank correlation coefficients among three measures of spatial autocorrelation and three indices of dispersal. Confidence intervals are bootstrap bias-correct, adjusted 95% probability limits.  $N = 107$ .

Variable 1	Variable 2	<i>r</i>	Lower CI	Upper CI
Space	Poll	0.048	-0.146	0.227
Space	Bspatial	0.082	-0.103	0.260
Space	Ao.resid	0.051	-0.145	0.243
Extent	Poll	0.107	-0.092	0.296
Extent	Bspatial	-0.144	-0.328	0.045
Extent	Ao.resid	0.488	0.319	0.632
Rho.std	Poll	0.123	-0.083	0.303
Rho.std	Bspatial	-0.094	-0.271	0.094
Rho.std	Ao.resid	0.075	-0.128	0.262

multiple causes, which can be broadly assigned to two categories: the hypothesized relationship did not exist, or, the relationship existed but the selected methods were unsuitable for detecting it. Given that the selected methods were very indirect and that a connection between dispersal and spatial patterning was shown in theory in Bahn *et al.* (2006a) and hypothesized by several authors (e.g., Paradis *et al.* 1998, Bjørnstad *et al.* 1999, Trenham *et al.* 2001), I interpret the results predominately as a failure of the methods and not as strong evidence for the absence of an effect.

Despite the failure to find meaningful correlations, there are some lessons to be learned from this study. Therefore, I will discuss the methods in detail, and elucidate the parts that were most likely responsible for the failure and the parts that seemed to be valuable methodological contributions and offer interesting insights.

A mismatch in scale between the observed effect and the investigated process can prevent meaningful results in ecology (Levin 1992). The data used for deriving the autocorrelation measures were of large spatial extent and coarse grain (the North American Breeding Bird Survey): 27 km from centre to centre of the hexagons. Paradis *et al.* (1998) found the natal and breeding dispersal of many European birds to average in the few to tens of kilometres, with much further distance dispersal in the tails of the distance distributions, making the resolution of my analysis fine enough to be able to detect the effects of dis-

persal under the assumption that North American birds exhibit similar dispersal distances.

The first two indices of dispersal, density dependence (Poll) and the spatial exponent of Taylor's power law (Bspatial) were calculated from the same dataset as the measures of autocorrelation. Therefore, the scale should have matched, although sometimes the scale at which a phenomenon can be observed is coarser than the scale at which the underlying processes take place (Huston 2002). The last index for dispersal, the deviation from an abundance-occupancy relationship, was not an unequivocal scale match. Abundance-occupancy relationships have been shown at coarse scales that would match the present study (Bock & Ricklefs 1983, Gaston *et al.* 1999, Gaston *et al.* 2000). However, Hanski *et al.*'s (1993) hypothesis concerning the relationship between the residuals from the abundance-occupancy regression and dispersal was based on metapopulation dynamics equations, which are typically concerned with smaller extents than covered here. At these smaller extents, considerable dispersal connects populations. However, overall, a mismatch in scale was likely not a major flaw of this study.

A more obvious weakness of the approach was the indirect nature of the indices of dispersal. How well did the selected measures express dispersal? In the case of dispersal being responsible for the deviation from the abundance-occupancy relationship hypothesized by Hanski *et al.* (1993), some support was found by Matter *et al.* (2002) and Boehning-Gaese *et al.* (2006), while Gaston and Blackburn (2003) failed to support this theory. Also in disagreement with Hanski *et al.*'s (1993) theory, Paradis *et al.* (1998) found in a study of dispersal that wide-spread and abundant species exhibited lower dispersal activity than species with small ranges and low abundances. In addition, the ranges of many of the bird species investigated were only partly in the study area of the conterminous United States. Therefore, some of the range sizes entered in the abundance-occupancy relationship were considerably smaller than the species' entire range. Hanski *et al.* (1993) considered this point but concluded that partial ranges should also work in this relationship. It remains unclear, though, whether the predicted dispersal is dependent on

**Table 6.** Partial Spearman rank correlation coefficients among three measures of spatial autocorrelation and three indices of dispersal. The correlations are controlled in respect to sample size  $n$ . Confidence intervals are bootstrap bias-correct, adjusted 95% probability limits.  $N = 107$ .

Variable 1	Variable 2	$r$	Lower CI	Upper CI
Space	Poll	0.061	-0.146	0.246
Space	Bspatial	0.077	-0.116	0.255
Space	Ao.resid	0.121	-0.072	0.314
Extent	Poll	-0.016	-0.195	0.191
Extent	Bspatial	-0.062	-0.248	0.133
Extent	Ao.resid	0.336	0.162	0.504
Rho.std	Poll	0.121	-0.075	0.320
Rho.std	Bspatial	-0.091	-0.267	0.121
Rho.std	Ao.resid	0.089	-0.078	0.254

the proportion of range included in the relationship. In addition, the relationship between dispersal and spatial autocorrelation may be dependent on the specific part of the range included in the study area.

The connection between density-dependence and dispersal has, to my knowledge, no direct empirical support. Population regulation dependent on density is a well supported and universally documented phenomenon (Murdoch 1994). However, it is unclear whether the mechanisms of regulation are mostly local, through birth and death rates, or whether dispersal among populations, as in metapopulation dynamics, is mainly responsible for density-dependence (Murdoch 1994). Although most models implement density-independent dispersal (Amarasekare 2004), organisms typically exhibit density-dependent dispersal (Sutherland *et al.* 2002). If dispersal is density-dependent, it is fair to assume that dispersal is also at least part of the population density regulation mechanism (Taylor & Taylor 1977). Therefore, using density-dependence as a proxy for dispersal activity is likely not wrong but may be a weak approach dependent on how important local mechanisms of density-dependence are compared to dispersal. For example, Rodenhouse *et al.*'s (1997) theory of density-dependence through site dependence relies on dispersal as the primary mechanism. However, the dispersal exhibited in the context of density-dependence may be of relatively short range and thus may be a scale mismatch to the observed spatial autocorrelation. In addition, an improvement to Pollard *et al.*'s (1987) method became available (Link & Hoover 1991) after Boone (1991) used it to calculate density dependence indices for North American breeding birds.

My hypothesis on the negative correlation between the spatial exponent  $b_s$  in Taylor's power law and dispersal agrees with Taylor and Taylor's (1977) view, although they called what I defined as dispersal "migration". My approach agreed with their concept of dispersal as a process generally counteracting aggregation and thus leading to more uniformly distributed population sizes. However, Taylor and Taylor (1977) also introduced another form of dispersal that leads to more aggregation, which they called congregatory migration and which is caused by

intraspecific attraction. In addition, they note that many behaviours, such as the search for food, mates and shelter, antagonistic interactions, and predator avoidance, can lead to movements that obscure the effects of dispersal. Other species-specific characteristics that potentially influence  $b_s$  independently of dispersal are the spatial and temporal patterns of relevant environmental conditions, and population growth rate. Therefore, while the basic hypothesis was probably correct, there are many reasons why the connection could have been weak.

Another issue that could have caused the lack of meaningful correlations was the variability in sample size  $n$  among species. Each species had a different range size and accordingly a different number of included sample points. While I did consider correlations with  $n$  (Tables 2 and 4) and controlled for  $n$  where appropriate (Table 6), not all problems arising from differences in sample size were obvious or easily controlled. Most importantly, sample size influenced the quality of the models and thus variable selection, efficiency of models in differentiating between noise and signal, and parameter estimates. In brief, the uncertainty encompassed in the models of the different species varied because  $n$  varied, and this additional variation may well have weakened existing correlations between indices of dispersal and measures of autocorrelation.

Another source of unexplained variation in measures of autocorrelation could have been environmental factors that were missed in the distribution models. While I used an extensive set of independent variables, they were all remotely sensed or interpolated and may have missed very fine-scaled and local ecological constraints on species. Conceivably, this effect could have been different for different species, thus introducing additional uncertainty in my estimation of spatial autocorrelation that went above and beyond the autocorrelation found in environmental factors.

Finally, the three measures of autocorrelation showed some agreement, in contrast to the three measures of dispersal. In particular, the two measures aiming at a general "strength" of autocorrelation, the standardized regression coefficient for neighbourhood inclusion (Rho.std) and the pure spatial partition (Space), correlated well. However, the extent of autocorrelation did not

agree well with these two measures. This suggests that strong effects of autocorrelation do not necessarily coincide with a large extent of autocorrelation. Assuming that the autocorrelation in the underlying environmental determinants is similar across species, one can only speculate that the relative independence of autocorrelation strength and extent stems from variations among species in the shape of dispersal kernels with the extremes being some species having low overall dispersal but very long tails and others having strong local dispersal, but short tails. Alternatively, biotic interactions such as interspecific competition or brood parasitism could be responsible for spatial autocorrelation and a decoupling between autocorrelation strength and extent.

In conclusion, the selected indices for dispersal were likely neither inappropriate, nor at a wrong scale. The most likely explanation for the absence of results was the indirect nature of the ecological indices. While each relationship of the three indices to dispersal may have some merit, other processes than dispersal may have been more influential, with each of these being quite different in the three indices. Thus, the noise or unwanted variation in the indices may have overwhelmed the information in these approaches, a conclusion supported by the absence of correlation among the three indices. Future research needs to be based on direct, empirical dispersal information such as used for British birds in Paradis *et al.* (1998).

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**Appendix.** List of common and scientific names of the 108 bird species used in this study. Names from the 7th edition of the Checklist of North American Birds (American Ornithologists' Union, 1998, Washington, DC, USA).

Common name	Scientific name	Common name	Scientific name
Little blue heron	<i>Egretta caerulea</i>	White-throated sparrow	<i>Zonotrichia albicollis</i>
Cattle egret	<i>Bubulcus ibis</i>	Chipping sparrow	<i>Spizella passerina</i>
Green heron	<i>Butorides virescens</i>	Clay-colored sparrow	<i>Spizella pallida</i>
Common snipe	<i>Gallinago delicata</i>	Field sparrow	<i>Spizella pusilla</i>
Northern bobwhite	<i>Colinus virginianus</i>	Song sparrow	<i>Melospiza melodia</i>
California quail	<i>Callipepla californica</i>	Swamp sparrow	<i>Melospiza georgiana</i>
Black vulture	<i>Coragyps atratus</i>	Eastern towhee	<i>Pipilo erythrophthalmus</i>
Burrowing owl	<i>Athene cucularia</i>	Northern cardinal	<i>Cardinalis cardinalis</i>
Yellow-billed cuckoo	<i>Coccyzus americanus</i>	Rose-breasted grosbeak	<i>Pheucticus ludovicianus</i>
Black-billed cuckoo	<i>Coccyzus erythrophthalmus</i>	Black-headed grosbeak	<i>Pheucticus melanocephalus</i>
Downy woodpecker	<i>Picoides pubescens</i>	Blue grosbeak	<i>Passerina caerulea</i>
Yellow-bellied sapsucker	<i>Sphyrapicus varius</i>	Indigo bunting	<i>Passerina cyanea</i>
Pileated woodpecker	<i>Dryocopus pileatus</i>	Painted bunting	<i>Passerina ciris</i>
Red-headed woodpecker	<i>Melanerpes erythrocephalus</i>	Dickcissel	<i>Spiza americana</i>
Red-bellied woodpecker	<i>Melanerpes carolinus</i>	Lark bunting	<i>Calamospiza melanocorys</i>
Chuck-will's-widow	<i>Caprimulgus carolinensis</i>	Western tanager	<i>Piranga ludoviciana</i>
Common nighthawk	<i>Chordeiles minor</i>	Scarlet tanager	<i>Piranga olivacea</i>
Chimney swift	<i>Chaetura pelagica</i>	Summer tanager	<i>Piranga rubra</i>
Western kingbird	<i>Tyrannus verticalis</i>	Purple martin	<i>Progne subis</i>
Western wood-pewee	<i>Contopus sordidulus</i>	Tree swallow	<i>Tachycineta bicolor</i>
Acadian flycatcher	<i>Empidonax virescens</i>	Violet-green swallow	<i>Tachycineta thalassina</i>
Least flycatcher	<i>Empidonax minimus</i>	Northern rough-winged swallow	<i>Stelgidopteryx serripennis</i>
Blue jay	<i>Cyanocitta cristata</i>	Cedar waxwing	<i>Bombcilla cedrorum</i>
Fish crow	<i>Corvus ossifragus</i>	Loggerhead shrike	<i>Lanius ludovicianus</i>
Bobolink	<i>Dolichonyx oryzivorus</i>	Red-eyed vireo	<i>Vireo olivaceus</i>
Yellow-headed blackbird	<i>Xanthocephalus xanthocephalus</i>	Warbling vireo	<i>Vireo gilvus</i>
Eastern meadowlark	<i>Sturnella magna</i>	White-eyed vireo	<i>Vireo griseus</i>
Western meadowlark	<i>Sturnella neglecta</i>	Black-and-white warbler	<i>Mniotilta varia</i>
Orchard oriole	<i>Icterus spurius</i>	Prothonotary warbler	<i>Protonotaria citrea</i>
Bullock's oriole	<i>Icterus bullockii</i>	Nashville warbler	<i>Vermivora ruficapilla</i>
Brewer's blackbird	<i>Euphagus cyanocephalus</i>	Orange-crowned warbler	<i>Vermivora celata</i>
Common grackle	<i>Quiscalus quiscula</i>	Yellow warbler	<i>Dendroica petechia</i>
Evening grosbeak	<i>Coccothraustes vespertinus</i>	Magnolia warbler	<i>Dendroica magnolia</i>
Purple finch	<i>Carpodacus purpureus</i>	Chestnut-sided warbler	<i>Dendroica pensylvanica</i>
House finch	<i>Carpodacus mexicanus</i>	Blackburnian warbler	<i>Dendroica fusca</i>
American goldfinch	<i>Carduelis tristis</i>	Black-throated green warbler	<i>Dendroica virens</i>
Lesser goldfinch	<i>Carduelis psaltria</i>	Pine warbler	<i>Dendroica pinus</i>
Pine siskin	<i>Carduelis pinus</i>	Prairie warbler	<i>Dendroica discolor</i>
Vesper sparrow	<i>Pooecetes gramineus</i>	Ovenbird	<i>Seiurus aurocapilla</i>
Savannah sparrow	<i>Passerculus sandwichensis</i>	Mourning warbler	<i>Oporornis philadelphia</i>
Grasshopper sparrow	<i>Ammodramus savannarum</i>		
Lark sparrow	<i>Chondestes grammacus</i>		

continued

**Appendix.** Continued.

Common name	Scientific name	Common name	Scientific name
MacGillivray's warbler	<i>Oporornis tolmiei</i>	Sedge wren	<i>Cistothorus platensis</i>
Common yellowthroat	<i>Geothlypis trichas</i>	White-breasted nuthatch	<i>Sitta carolinensis</i>
Yellow-breasted chat	<i>Icteria virens</i>	Red-breasted nuthatch	<i>Sitta canadensis</i>
Hooded warbler	<i>Wilsonia citrina</i>	Brown-headed nuthatch	<i>Sitta pusilla</i>
Canada warbler	<i>Wilsonia canadensis</i>	Tufted titmouse	<i>Baeolophus bicolor</i>
American redstart	<i>Setophaga ruticilla</i>	Black-capped chickadee	<i>Poecile atricapillus</i>
Northern mockingbird	<i>Mimus polyglottos</i>	Carolina chickadee	<i>Poecile carolinensis</i>
Gray catbird	<i>Dumetella carolinensis</i>	Blue-gray gnatcatcher	<i>Poliopitla caerulea</i>
Brown thrasher	<i>Toxostoma rufum</i>	Wood thrush	<i>Hylocichla mustelina</i>
Carolina wren	<i>Thryothorus ludovicianus</i>	Veery	<i>Catharus fuscescens</i>
Bewick's wren	<i>Thryomanes bewickii</i>	Hermit thrush	<i>Catharus guttatus</i>
House wren	<i>Troglodytes aedon</i>	American robin	<i>Turdus migratorius</i>
Winter wren	<i>Troglodytes troglodytes</i>	Eastern bluebird	<i>Sialia sialis</i>