Habitat Relations

Overlapping Landscapes: A Persistent, But Misdirected Concern When Collecting and Analyzing Ecological Data

BENJAMIN ZUCKERBERG,[1] *Cornell Lab of Ornithology, Cornell University, Ithaca, NY 14850, USA*

ANDRÉ DESROCHERS, *Université Laval, Centre D'étude de la Forêt, Université Laval, Québec, QC, Canada G1V 0A6*

WESLEY M. HOCHACHKA, *Cornell Lab of Ornithology, Cornell University, Ithaca, NY 14850, USA*

DANIEL FINK, *Cornell Lab of Ornithology, Cornell University, Ithaca, NY 14850, USA*

WALTER D. KOENIG, *Cornell Lab of Ornithology, Cornell University, Ithaca, NY 14850, USA*

JANIS L. DICKINSON, *Cornell Lab of Ornithology, Cornell University, Ithaca, NY 14850, USA*

ABSTRACT A primary focus of wildlife ecology is studying how the arrangement, quality, and distribution of habitat influence wildlife populations at multiple spatial scales. A practical limitation of conducting wildlife–habitat investigations in the field, however, is that sampling points tend to be close to one another, resulting in spatial clustering. Consequently, when ecologists seek to quantify the effects of environmental predictors surrounding their sampling points, they encounter the issue of using landscapes that are partially or completely overlapping. A presumed problem of overlapping landscapes is that data generated from these landscapes, when used as predictors in statistical modeling, might violate the assumption of independence. However, the independence of error is the critical assumption, not the independence of predictor variables. Nonetheless, many researchers strive to avoid such overlaps through sampling design or alternative analytical procedures and specialized software programs have been created to assist with this. We present theoretical arguments and empirical evidence showing that changing the amount of overlap does not alter the degree of spatial autocorrelation. Using data derived from 2 broad-scaled avian monitoring programs, we quantified the relationship between forest cover and bird abundance and occurrence at multiple landscapes ranging from 100 m to 24 km across. We found no clear evidence that increasing overlap of landscapes increased spatial autocorrelation in model residuals. Our results demonstrate that the concern of overlapping landscapes as a potential cause of violation of spatial independency among sampling units is misdirected and represents an oversimplification of the statistical and ecological issues surrounding spatial autocorrelation. Overlapping landscapes and spatial autocorrelation are separate issues in the modeling of wildlife populations and their habitats; non-overlapping landscapes do not ensure spatial independency and overlapping landscapes do not necessarily lead to greater spatial autocorrelation in model errors. © 2011 The Wildlife Society.

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Wildlife ecologists are often interested in testing the influence of the surrounding landscape context on species' presence or abundance at sampling sites (Turner et al. 2001, Brennan et al. 2002), where landscape context is a representation of a surrounding area that is based on the life-history of the study species (Vos et al. 2001, McGarigal and Cushman 2002, Fahrig 2005). When scales relevant to a species' life-history are not known or less certain, however, investigators will often quantify habitat heterogeneity at multiple spatial scales (Cunningham and Johnson 2006, Koper and Schmiegelow 2006, Buler et al. 2007, Thogmartin

and Knutson 2007, Boscolo and Metzger 2009, Desrochers et al. 2010). The data used in such studies often consist of sampling sites that are spatially clustered and, as such, modeling wildlife-habitat associations poses potential analytical problems. First, a highly clustered sample of observations may not be representative of the distribution over which we want to make inference. Second, the analysis of these data must deal with the issue of spatial autocorrelation.

Much of statistical inference is based on the assumption of independence of errors. When dealing with correlative models, this assumption relates to the independence of residual errors that represent the portion of variation not adequately explained by the predictors in the model (Draper and Smith 1998, Banerjee et al. 2004). In many ecological studies, ecologists are concerned with the independence of individual sites (Hurlbert 1984), and when dealing with spatially distributed sampling sites, a lack of

independence is most likely the result of spatial autocorrelation where sites that are closer together have a tendency to be more alike (Legendre 1993, Diniz-Filho and Telles 2002).

Spatial autocorrelation in the distribution or abundance of wildlife populations results from a mixture of both inherent (endogenous) and induced (exogenous) processes (Fortin and Dale 2005, Beale et al. 2010). Inherent processes of spatial autocorrelation can lead to individuals of a population being spatially clustered in a patchy non-random fashion, and are often due to some characteristic or trait of that species or population such as conspecific attraction or juvenile philopatry (Campomizzi et al. 2008, Nocera et al. 2009, Nocera and Forbes 2010). Alternatively, the spatial distribution of an organism or population may be due to induced processes imposed by gradients in the environment, such as the distribution of forest cover or elevation. In this case, the species or population is spatially and functionally dependent on an environmental predictor and the resultant autocorrelation is referred to as induced spatial dependence (Lennon 2000, Fortin and Dale 2005). This induced spatial dependency can result from spatially structured environmental processes that could be occurring at multiple spatial scales, from local abundance to regional patterns of distribution. Both sources of spatial autocorrelation in species' distributions, inherent and induced, may be problematic for parametric and randomization tests that require independent errors (Lennon 2000, Diniz-Filho et al. 2003, Bini et al. 2009, Beale et al. 2010).

In applied settings, researchers have employed 3 basic approaches to avoid the perceived problems associated with induced spatial autocorrelation. First, in the planning stages of a study, sampling sites are spaced far enough apart such that non-overlapping landscapes of interest can be delineated around them (Fahrig 2005, Eigenbrod et al. 2011). Alternatively, sites have been removed later, prior to analysis, if the landscape size of interest results in overlap (Koper and Schmiegelow 2006, Yamaura et al. 2006). A special case of this approach is outlined by Holland et al. (2004), whose program FOCUS uses repeated random sub-sampling of data to create multiple data sets with non-overlapping landscapes; the accumulated results from analyses of all of these subsets are used to make inferences. Planning to avoid overlap has proven problematic for the required distance between sites to ensure spatial independency is not always clear. Moreover, collecting evenly spaced data for many studies is not often practical, especially those over broad spatial scales that rely on opportunistic sampling. As a result of these challenges, ecologists have employed a third approach by using a plethora of analytical procedures to control for residual spatial autocorrelation including methods that explicitly account for the spatial neighborhood of sampling sites (Dormann et al. 2007, Bini et al. 2009, Beale et al. 2010) or information-theoretic approaches that are thought to have less stringent assumptions of independency (Pan 2001, Cunningham and Johnson 2006, Thogmartin and Knutson 2007).

The need to avoid spatial overlap of landscapes during data collection or prior to analysis can be questioned for multiple reasons. First, in an empirical example of cactus bugs (*Chelinidea vittiger*) Schooley (2006) noted that the use of non-overlapping landscapes does not guarantee the elimination of residual spatial autocorrelation, and concluded that the problem of spatially correlated areas depends on the size of the sampling units. Second, as noted above, numerous analytical methods are available to explicitly account for autocorrelation that may exist (Dormann et al. 2007, Bini et al. 2009, Beale et al. 2010). Third, the criticism that landscape overlap will induce a violation of independency can be questioned for theoretical reasons. In classic linear models, the crucial assumption to be met is independence of residuals of the dependent (or response) variable, not independence among regressor values (Draper and Smith 1998, Wagner and Fortin 2005). Fourth, in many cases spatial autocorrelation is often unavoidable and should not be considered a statistical artifact in need of correction or removal, but rather an indication of a spatially explicit biological or environmental process (Legendre 1993).

Despite these findings and theoretical considerations, researchers continue to advocate avoiding overlapping landscapes both in planning their data collection or by removing sites from analysis after the data have been collected. Recently, Eigenbrod et al. (2011) performed an empirical test highlighting what they considered 3 of the more common pitfalls associated with sub-optimal study designs: overlapping landscapes, truncated range of predictor values, and multicollinearity in predictors. With respect to the first of these, they stated that overlapping landscapes are a form of pseudoreplication because values of the predictor variables from nearby landscapes are used as multiple observations in the dataset resulting in non-independence of the residuals, and that the degree of pseudoreplication depends on the degree of the overlap. Using data from 2 broad-scaled surveys, they tested the relationship between anuran abundance and percent forest cover and compared coefficient shifts under scenarios meant to replicate these design pitfalls. Despite finding that overlapping landscapes did not lead to shifts in the sign of their parameter estimates, their first recommendation for future studies is the subset of non-overlapping sites. In spite of mensurative studies on landscape fragmentation that have gone to great lengths to have spatially discrete, replicated landscapes (e.g., McGarigal and McComb 1995), whether the use of overlapping landscapes leads to an automatic violation of spatial dependency remains to be demonstrated. If it does not, then the issue of landscape overlap may have had exaggerated effects on the field of wildlife ecology by constraining sample sizes and analyses, and reducing the power of inference for a large number of studies.

Our objective was to offer empirical evidence of whether overlapping landscapes violate the assumption of induced spatial independence, and further test whether greater overlap in landscapes will lead to greater spatial autocorrelation. Although this general question has been addressed by a small number of studies already (Holland et al. 2004, Schooley 2006), many of these studies either maintain non-overlapping landscapes or change the sampling size of measurement

for the predictor and response variable when altering spatial scale. Our novel contributions are to examine these issues using field-collected abundance and occurrence data to test explicitly whether a relationship exists between the magnitude of spatial autocorrelation and the degree of landscape overlap. We use data from 2 avian monitoring programs and hundreds of sample sites to test for a violation of spatial independency in modeling wildlife-habitat relationships when environmental predictor data are generated from overlapping landscapes.

STUDY AREA

Data Sources (Bird Data)
We investigated bird species distribution and abundance patterns using data from 2 independent monitoring schemes, Project FeederWatch (Wells et al. 1998) and the Ontario Forest Bird Monitoring Program (FBMP; Cadman et al. 1998). Both projects were created to monitor bird populations based on information provided by volunteers. They share useful properties for analyses at multiple spatial scales: large spatial extent, long duration, large sample sizes, and the availability of detailed information on land cover. Although using artificial data are useful for modeling a range of known spatial structures and multiple comparisons (Beale et al. 2010), we chose to use data from 2 empirical biological surveys whose data would better reflect the complexities that are inherent in real-world monitoring programs and to compare our results to other findings based on empirical data (Holland et al. 2004, Schooley 2006, Eigenbrod et al. 2011).

Project FeederWatch (PFW) is a citizen science program operated by the Cornell Lab of Ornithology and Bird Studies Canada (Wells et al. 1998, Dickinson et al. 2010). In brief, program participants record the maximum number of each species seen from a single location near a supplemental feeding station during periodic, 2-day counts. More than 10,000 PFW sites exist across the United States and Canada, with as many as 22 counts submitted from each site between mid-November of one calendar year and early April of the next calendar year. We have limited our analyses to 649 sites located in New York State monitored between November 2000 and April 2001 (Fig. 1). We chose this study area because the sampling points were spatially clustered and offered a reasonable sampling layout for testing the effects of overlapping landscapes. We focused on counts conducted during this time period to correspond with the time frame over which the land cover data were collected.

The Ontario FBMP was created to monitor breeding bird population changes in Ontario forests (Cadman et al. 1998). It consists of annual point count surveys of all forest songbirds and covers most of the southern part of the province and part of the northwestern region (Fig. 2). Our study used 1,147 point count stations grouped in 240 FBMP sites located in mature forest. Sites generally consisted of 5 point count stations located more than 100 m from forest edges. Each station was marked and visited twice each year between
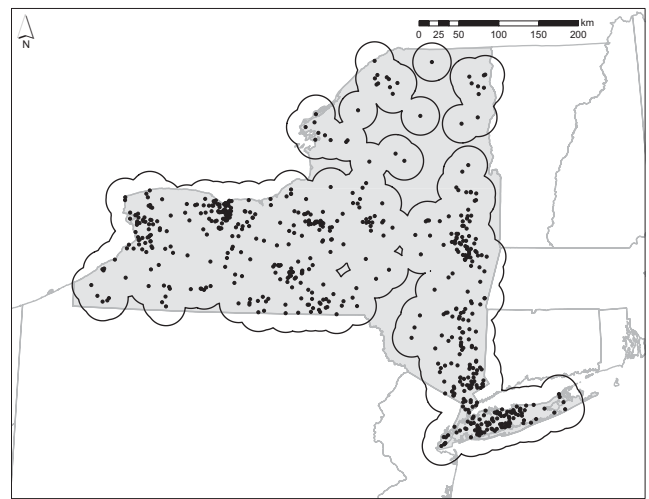
Figure 1. Project FeederWatch sites used in this study. We restricted our data to sites in New York State from which data were collected during the winter of 2000–2001. Overlapping sample landscapes with 24-km radius are shown (gray lines).

1987 through 2005. The first visit was done between 24 May and 17 June and the second between 13 June and 10 July. During these visits, volunteers reported all bird species seen or heard at an unlimited distance in 10 minutes. Visits to the same site were separated by a mean of 17.6 days. Surveys were conducted between sunrise and 5 hours after sunrise, in the absence of heavy rain or wind. The average number of volunteers for sites with more than 5 years of monitoring was 1.2. All sites were not visited every year. The sites retained for analysis were visited 5.8 years in average (median = 5 yr), over a mean period of 7.2 years (median = 7 yr).
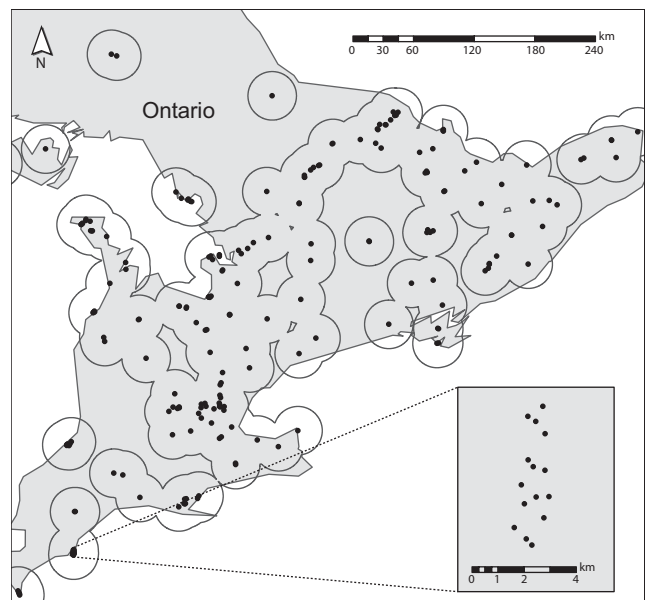
Figure 2. Point count sites for Ontario's Forest Bird Monitoring Program. Most of the visible points consist of several individual point count stations, as exemplified by the insert; overlapping sample landscapes with 24-km radii are shown (gray lines).

Data Sources (Land Cover Data)

For analyses using data from PFW, we used the 2001 National Land Cover Data (NLCD) to characterize the composition of different land cover types in the surrounding landscape. The 2001 NLCD consists of 16 land cover classes modeled over the conterminous United States at a 30-m cell resolution and a 0.40-ha minimum mapping unit (Homer et al. 2007). For the purposes of this study, we quantified the percent of the landscape that was classified as forested upland (deciduous, coniferous, and mixed forested areas where tree canopy accounts for 25–100% of the cover). We calculated all landscape metrics using FRAGSTATS (McGarigal et al. 2002). We conducted land cover analyses using ArcMap 9.2 (Environmental Systems Research Institute, Inc., Redlands, CA).

For analyses using data from FBMP, we acquired forest cover from a land cover classification map based on a composite Landsat Thematic Mapper image of Ontario, with a resampled cell size of 25 m × 25 m (Spectranalysis, Inc. 1999). This spatial database was produced under 3 separate programs of the Ontario Ministry of Natural Resources between 1991 and 1998 and represented the most recent land cover data available. Forest cutovers and burns were updated from 1996. The image was originally classified in 28 land cover classes. We reclassified it into 4 vegetation classes (coniferous, deciduous, mixed, and non-forest) plus an unknown land cover category, using ArcMap 9.2. The accuracy of the original, high-resolution land cover data was estimated at 90% for the forest classes (Spectranalysis, Inc. 1999), and we assumed classification accuracy was substantially greater than 90% after merging original classes into 4 broader groups. The positional accuracy of the map was within 2 pixels (50 m; Spectranalysis, Inc. 1999); thus, we assumed that forest area estimates were accurate. Although changes must have occurred from 1987 to 2005 in the landscapes studied, we assumed that such changes were sufficiently small to be ignored; the southern part of the area had a largely agricultural matrix and the timber harvest throughout the area was done using selective logging.

METHODS

For both PFW and FBMP, we calculated the percent area of forest measured around the center of each count station in concentric circles of different radii (100 m, 200 m, 400 m, 800 m, 1.6 km, 3.2 km, 6.4 km, 12.8 km, and 24.0 km). The grid resolution of the land cover map was constant among radii. If more than 20% of the landscape area was classified as unknown, then data from that station were not used for analyses at that specific radius. Given the different spatial distribution of sampling points for PFW and FBMP, these landscapes of increasing radii presented a range of total landscape overlap. For each landscape radius, we calculated the total percent overlap of the landscapes in the study area (calculated as the area of intersecting overlap/total area covered by landscapes).

For PFW and FBMP data, we selected bird species that were well-sampled by both surveys, occupied forest as a wintering habitat, and were directly comparable across the 2 data sets. The final list of species included hairy woodpecker (*Picoides villosus*), downy woodpecker (*Picoide pubescens*), blue jay (*Cyanocitta cristata*), black-capped chickadee (*Poecile atricapillus*), white-breasted nuthatch (*Sitta carolinensis*), and red-breasted nuthatch (*Sitta canadensis*). For PFW, we modeled the relative abundance as the average of maximum counts (N) for a species seen at a single site throughout the 2000–2001 winter sampling season as an index of relative abundance. The counts were $\ln(N + 0.1)$ transformed effectively producing residuals with normal distributions (Poisson modeling was not appropriate for non-integer averaged count data). We used a generalized linear model (GLM) with a Gaussian error distribution followed by residual analyses to detect for signs of non-normality in the residuals or evidence of heteroscedasticity (Faraway 2006, McCulloch et al. 2008). We generated 9 separate GLMs (1 for each landscape radius), and used the proportion of forest as the predictor variable (linear and quadratic effect forms) in each model.

For FBMP, the response variable of the models was the proportion of years of survey in which the species was recorded, which we modeled using a generalized linear mixed model (GLMM). We fit these models using penalized quasi-likelihood. To account for the repeated sampling of the FBMP data, we used mixed-models with site as a variance-components random effect (PROC GLIMMIX, SAS Institute, Inc., Cary, NC) and area of mixed, conifer, and deciduous forest as fixed effects. A species was considered to occur at a point count station in a given year if it was recorded during at least 1 of the 2 annual visits made by the observer. We omitted songbird and woodpecker species with frequencies <10% from analyses, thus leaving 37 species for analysis (Appendix 1, available online at www.onlinelibrary. wiley.com).

For models using data generated from both PFW and FBMP, we assessed patterns of spatial autocorrelation by calculating spatial correlograms (Moran's *I*) of model residuals across increasing distance classes (Cliff and Ord 1973, Bjørnstad et al. 1999, Bjørnstad and Falck 2001). At each distance class, we ran 1,000 permutations to conduct a 2-sided significance test of whether the value for Moran's *I* differed from zero ($\alpha = 0.05$). We ran analyses using R (R Foundation for Statistical Computing, Vienna, Austria) and package "ncf" was used for spatial analyses. In addition, given the large number of species analyzed with FBMP data (Appendix 1, available online at www.onlinelibrary.wiley. com), we calculated a single value of Moran's *I* for each species-radius combination to look for systematic relationships between autocorrelation and the amount of overlapping landscapes across all species. We tested the overall relationship between landscape overlap and Moran's *I* for residuals using a generalized mixed effect model with overlap (%) as a fixed effect and species as a random effect, using Kenward–Roger degrees of freedom (Schaalje et al. 2001).

RESULTS

Large numbers of sampling sites were in close proximity in both PFW and FBMP datasets, leading to significant spatial
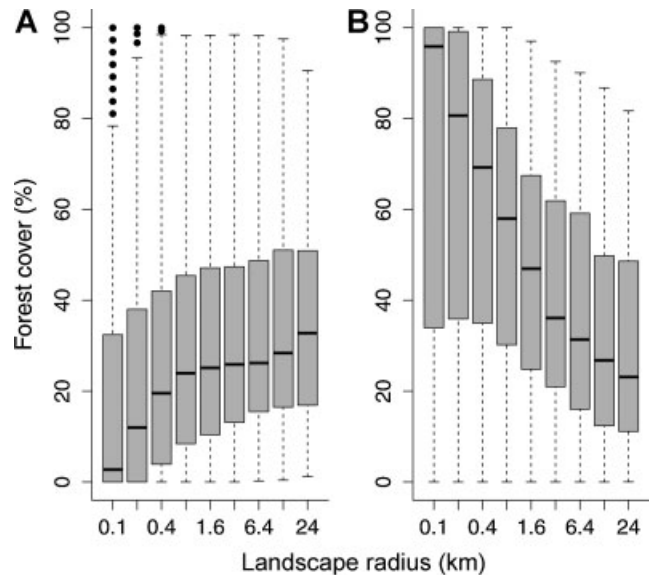
overlaps of larger landscapes surrounding sampling sites (Table 1; Figs. 1 and 2). The percentages of overlap for landscapes of different sizes ranged from 0.7% to 82.5% for PFW and 1.1% to 70.0% for FBMP points (Table 1). The range and variation of the percentage of forest cover changed as a result of the size of the landscape radius, but the direction of this change differed between the PFW and FBMP study areas (Fig. 3). For the PFW sites, the mean forest cover increased from 20.19% (SE 1.11) at the smallest landscape radius to 34.35% (0.79) at the largest landscape radius. For FBMP sites, the mean forest cover decreased from 69.05% (SE 0.45) to 30.73% (0.28). In both cases, however, the range in the variation of forest cover generally decreased as the size of the landscape radius increased (Fig. 3).

Significant spatial autocorrelation in model residuals was present for PFW data, but its amount and extent were highly variable among the 6 species examined (Fig. 4). As expected, sites in closer proximity were generally more alike (positive autocorrelation) than more distant sites (Fig. 4). For most species, significant autocorrelation in the model residuals persisted at inter-site distances of 100 km or more. In all cases, however, spatial autocorrelation did not differ notice-ably between models using small (non-overlapping) land-scapes or large (overlapping landscapes). Counter to the predictions of an increase in spatial autocorrelation with a greater degree of landscape overlap, some species including blue jay, black-capped chickadee, and white-breasted nut-hatch, demonstrated less spatial autocorrelation with the larger, overlapping landscapes (Fig. 4). As an example, the abundance of black-capped chickadees exhibited a high degree of spatial autocorrelation at distance classes ranging from 5 km to 100 km with models using small, non-over-lapping landscapes, but spatial autocorrelation decreased to 0 at 40 km when larger, overlapping landscapes were used (Fig. 4).

We found similar patterns of spatial autocorrelation in the residuals of models using the FBMP data set (Fig. 5). Although significant positive spatial autocorrelation was clear for the 6 study species common to both data sets, none showed a difference in the patterns of spatial autocor-relation in relation to sizes of landscapes. Similarly, although data from all 37 FBMP species exhibited residual spatial autocorrelation, we found no relationship between landscape
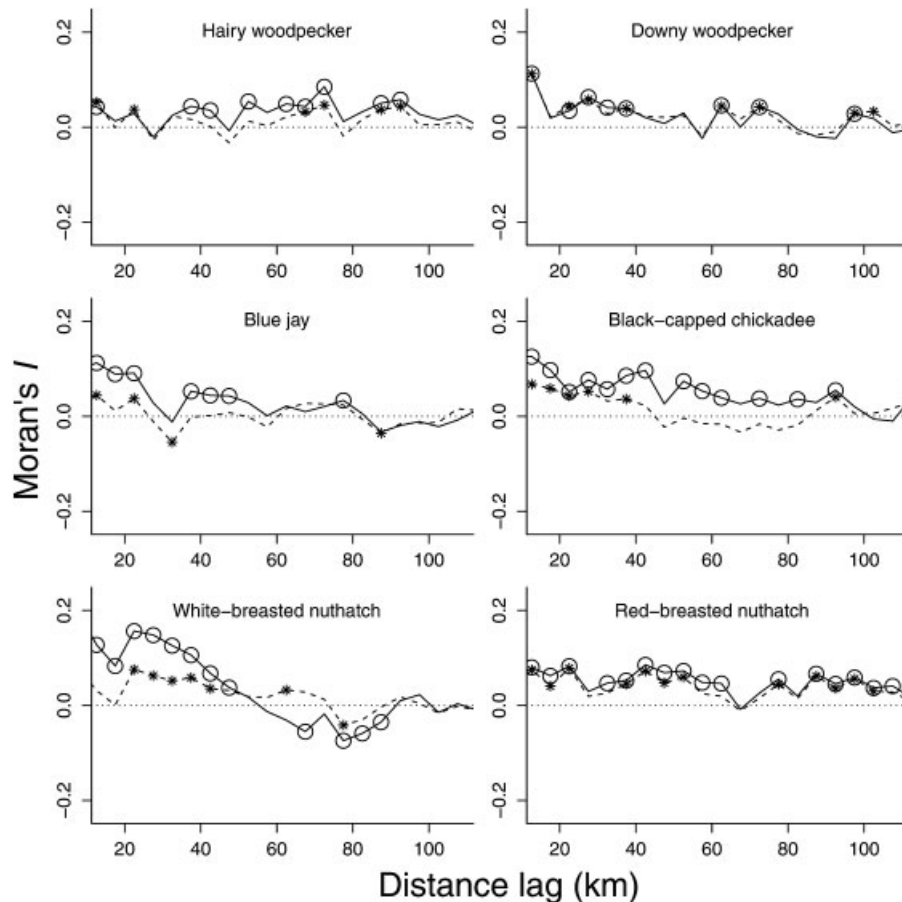

Figure 3. Box-and-whisker plots of the percentage of forest cover (%) calculated using the 9 separate radii (0.1–24 km) for the Project FeederWatch (A) and Ontario's Forest Bird Monitoring Program (B) sites. The plots demonstrate how the percentage of forest cover increases with increasing landscape scale in Project FeederWatch sites, but with the oppo-site trend observed with Ontario's Forest Bird Monitoring Program sites.

overlap and residual spatial autocorrelation ($F_{1,259.1} = 0.01$, $P = 0.9$; Fig. 6).

DISCUSSION

We found significant residual spatial autocorrelation in pat-terns of species occurrence or abundance in data from both FeederWatch and Ontario FBMP even after accounting for forest cover composition. An initial inspection of these patterns may provide grounds for concerns that overlapping landscapes lead to a violation of spatial independence (Holland et al. 2004). However, we found no evidence of a relationship between the extent of landscape overlap and the degree of spatial autocorrelation among model errors even though overlap was sometimes extensive. The lack of any relationship between spatial autocorrelation and the degree of overlap among sampling sites suggests that elimi-nating or sub-sampling sites to avoid pseudoreplication in this case would be unnecessary, leading only to smaller sample sizes and weaker inference in modeling wildlife-habitat relationships.

We found that for some species in this study, residual spatial autocorrelation actually was less significant when larger, overlapping landscapes with more spatial overlap were used compared to analyses using predictors with less (or no) landscape overlap. This could be a function of larger landscapes capturing a greater amount of relevant environ-mental variability, which, in turn, explains more of the spatial dependency among sites (Lennon 2000, Desrochers et al. 2010). The pattern of less spatial autocorrelation using the larger landscapes was most apparent in the PFW data set (Fig. 4). In these sites, the composition of forest cover generally increased with increasing landscape radius; an opposite pattern was found with FBMP sites (Fig. 3).

Table 1. Spatial overlap among landscapes centered on bird feeding stations (Project FeederWatch) or point count stations (Ontario Forest Bird Monitoring Program).

Landscape radius (m)	Spatial overlap (%)	
	Project FeederWatch	Ontario Forest Bird Monitoring Program
100	0.7	1.1
200	0.9	2.3
400	1.7	5.8
800	4.3	14.7
1,600	11.1	25.0
3,200	24.4	35.2
6,400	43.3	45.9
12,800	63.7	56.7
24,000	82.5	70.0

Figure 4. Spatial correlograms of model residuals from a selection of 6 species from Project FeederWatch. Moran's *I* values as a function of distance classes are shown from models with the smallest 100-m landscape (solid lines) and the largest 24-km landscape (dashed lines). Significant autocorrelation (*P* < 0.05) at each distance class is represented for the smallest landscapes (open circles) and largest landscapes (star).

Eigenbrod et al. (2011) found that the numerical range of the predictor variable, forest cover in their study, had the largest effect on parameter estimates and the strength of the inferred relationships. As such, if resources are available for intensive sampling, larger numbers of samples within a geographical extent will not lead to design flaws or statistical violations. On the contrary, it should lead to a more representative sample of habitat availability and greater precision of estimates for the effects of environmental predictors.

Although we found no evidence of greater overlap of landscapes leading to greater spatial autocorrelation, attempting to minimize overlapping landscapes has several advantages. The use of landscapes with limited overlap will generally be indicative of a larger study area with greater variation of habitat characteristics, a desirable statistical property when assessing wildlife–habitat associations. However, restricting data collection to sites with non-overlapping landscapes could also lead to a loss of sample size and a subsequent reduction in the range of a predictor variable. As such, a study design dictated by landscape overlap could conflate spatial scale and spatial overlap of samples. In addition, another potential problem of overlapping landscapes is the issue of using nested landscapes in a single model to evaluate species responses to habitat at multiple scales (Dungan et al. 2002).

In this case, when data are generated from landscapes of multiple, nested radii the predictor variables tend to be highly correlated with one another (i.e., multicollinearity; Graham 2003, Williams and Kremen 2007, Boscolo and Metzger 2009). Certainly, this is a potential problem when a study focuses on assessing the relative influence of habitat availability at multiple scales, but this issue is different from the potential violation of spatial independency resulting from overlapping landscapes.

Our analyses support the findings from other studies suggesting that non-overlapping landscapes do not necessarily ensure spatial independency (Schooley 2006), but we additionally found no evidence that even large percentages of overlap lead to greater autocorrelation in model residuals. In their study of habitat relationships for neotropical migrants in the southern Appalachian Mountains, Lichstein et al. (2002) suggested that the use of overlapping landscapes may have contributed to spatial autocorrelation in their models, but went on to suggest that their habitat variables would have been autocorrelated even if the circles were non-overlapping because of larger-scale variability in habitat composition. They presented overlap as a cause for further spatial autocorrelation, but did not suggest non-overlapping landscapes as a solution. We tested for the effect of increasing
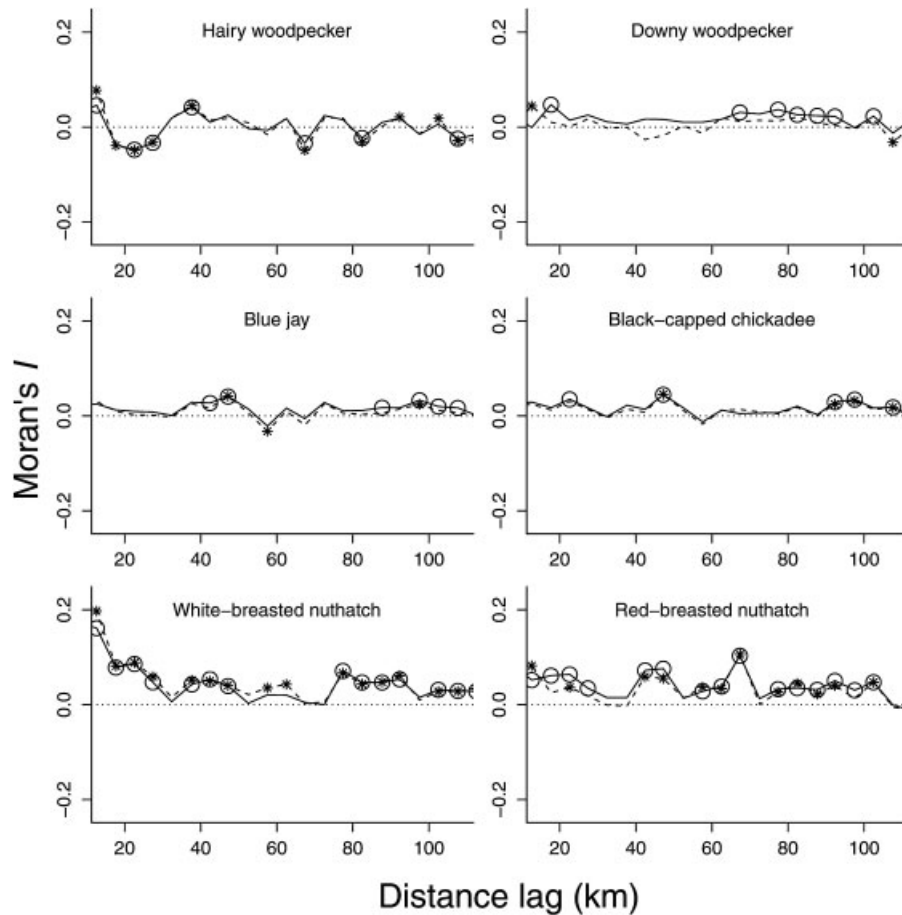
Figure 5. Spatial correlograms of model residuals from a selection of 6 species from the Ontario Forest Bird Monitoring Program. Moran's *I* values as a function of distance classes are shown from models with the smallest 100-m landscape (solid lines) and the largest 24-km landscape (dashed lines). Significant autocorrelation ($P < 0.05$) at each distance class is represented for the smallest landscapes (open circles) and largest landscapes (star).

landscape overlap and found no evidence for a consistent increase in spatial autocorrelation with increased overlap using data from 2 study areas with very different patterns of forest composition.
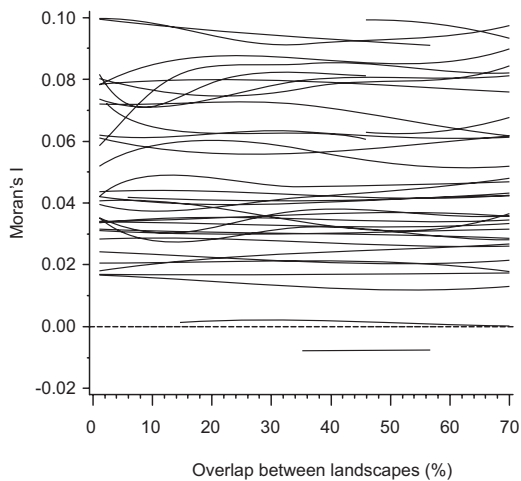
Figure 6. Relationships between spatial autocorrelation and overlap among landscapes in 37 species for which we analyzed data from the Ontario's Forest Bird Monitoring Program.

MANAGEMENT IMPLICATIONS

The issue of spatial autocorrelation and its effects on ecological modeling is an active and complex area of research. Spatial independence among sites should not be assumed by setting thresholds of similarity among regressor values, nor should researchers assume that overlapping landscapes lead to an immediate reduction in independent sample size. Instead, researchers need to use any of the number of analytical techniques available for assessing and incorporating the effects of residual spatial autocorrelation into the analysis of ecological data (Betts et al. 2006, Dormann et al. 2007, Bini et al. 2009, Beale et al. 2010). Spatial autocorrelation is only problematic when it is assumed not to exist in a data set or it is not explicitly accounted for and the results of a model are interpreted incorrectly (Lichstein et al. 2002, Dormann et al. 2007, Hawkins et al. 2007). In addition, an overemphasis on overlapping landscapes as a sole cause of spatial autocorrelation tends to ignore behavioral characteristics of wildlife species that affect the scale of spatial independence. Indeed, researchers should investigate possible sources of inherent spatial autocorrelation that could lead to spatial clustering, such as conspecific attraction. Incorporating this information can, in some cases, improve models of

habitat use (Nocera and Forbes 2010). The failure to find a significant spatial pattern in model errors does not demonstrate absence of influential autocorrelation, and even in these cases, weak autocorrelation can have substantial effects on parameter estimation and model interpretation (Beale et al. 2010). Evaluating the presence and degree of spatial autocorrelation is essential, regardless of steps taken to try to minimize spatial dependency during the design of sampling schemes or processing of data for analysis.

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LITERATURE CITED

Banerjee, S., B. P. Carlin, and A. E. Gelfand. 2004. Hierarchical modeling and analysis for spatial data. Chapman & Hall/CRC, Boca Raton, Florida, USA.

Beale, C. M., J. J. Lennon, J. M. Yearsley, M. J. Brewer, and D. A. Elston. 2010. Regression analysis of spatial data. Ecology Letters 13:246–264.

Betts, M. G., A. W. Diamond, G. J. Forbes, M. A. Villard, and J. S. Gunn. 2006. The importance of spatial autocorrelation, extent and resolution in predicting forest bird occurrence. Ecological Modelling 191:197–224.

Bini, L. M., J. A. F. Diniz-Filho, T. F. L. V. B. Rangel, T. S. B. Akre, R. G. Albaladejo, F. S. Albuquerque, A. Aparicio, M. B. Araujo, A. Baselga, J. Beck, M. I. Bellocq, K. Bohning-Gaese, P. A. V. Borges, I. Castro-Parga, V. K. Chey, S. L. Chown, P. de Marco, D. S. Dobkin, D. Ferrer-Castan, R. Field, J. Filloy, E. Fleishman, J. F. Gomez, J. Hortal, J. B. Iverson, J. T. Kerr, W. D. Kissling, I. J. Kitching, J. L. Leon-Cortes, J. M. Lobo, D. Montoya, I. Morales-Castilla, J. C. Moreno, T. Oberdorff, M. A. Olalla-Tarraga, J. G. Pausas, H. Qian, C. Rahbek, M. A. Rodriguez, M. Rueda, A. Ruggiero, P. Sackmann, N. J. Sanders, L. C. Terribile, O. R. Vetaas, and B. A. Hawkins. 2009. Coefficient shifts in geographical ecology: an empirical evaluation of spatial and non-spatial regression. Ecography 32:193–204.

Bjørnstad, O. N., and W. Falck. 2001. Nonparametric spatial covariance functions: estimation and testing. Environmental and Ecological Statistics 8:53–70.

Bjørnstad, O. N., R. A. Ims, and X. Lambin. 1999. Spatial population dynamics: analyzing patterns and processes of population synchrony. Trends in Ecology & Evolution 14:427–432.

Boscolo, D., and J. P. Metzger. 2009. Is bird incidence in Atlantic forest fragments influenced by landscape patterns at multiple scales? Landscape Ecology 24:907–918.

Brennan, J. M., D. J. Bender, T. A. Contreras, and L. Fahrig. 2002. Focal patch landscape studies for wildlife management: optimizing sampling effort across scales. Pages 68–91 in J. Lui and W. W. Taylor, editors. Integrating landscape ecology into natural resource management. Cambridge University Press, New York, New York, USA.

Buler, J. J., F. R. Moore, and S. Woltmann. 2007. A multi-scale examination of stopover habitat use by birds. Ecology 88:1789–1802.

Cadman, M. D., H. J. Dewar, and D. A. Welsh. 1998. The Ontario forest bird monitoring program (1987–1997): goals, methods and species trends observed. Technical Report 325. Canadian Wildlife Service, Ottawa, Ontario, Canada.

Campomizzi, A. J., J. A. Butcher, S. L. Farrell, A. G. Snelgrove, B. A. Collier, K. J. Gutzwiller, M. L. Morrison, and R. N. Wilkins. 2008. Conspecific attraction is a missing component in wildlife habitat modeling. Journal of Wildlife Management 72:331–336.

Cliff, A. D., and J. K. Ord. 1973. Spatial autocorrelation. Pion, London, England.

Cunningham, M. A., and D. H. Johnson. 2006. Proximate and landscape factors influence grassland bird distributions. Ecological Applications 16:1062–1075.

Desrochers, A., C. Renaud, W. M. Hochachka, and M. Cadman. 2010. Area-sensitivity by forest songbirds: theoretical and practical implications of scale-dependency. Ecography 33:921–931.

Dickinson, J. L., B. Zuckerberg, and D. N. Bonter. 2010. Citizen science as an ecological research tool: challenges and benefits. Annual Review of Ecology, Evolution, and Systematics 41:149–172.

Diniz-Filho, J. A. F., L. M. Bini, and B. A. Hawkins. 2003. Spatial autocorrelation and red herrings in geographical ecology. Global Ecology and Biogeography 12:53–64.

Diniz-Filho, J. A. F., and M. P. D. Telles. 2002. Spatial autocorrelation analysis and the identification of operational units for conservation in continuous populations. Conservation Biology 16:924–935.

Dormann, C. F., J. M. McPherson, M. B. Araujo, R. Bivand, J. Bolliger, G. Carl, R. G. Davies, A. Hirzel, W. Jetz, W. D. Kissling, I. Kuhn, R. Ohlemuller, P. R. Peres-Neto, B. Reineking, B. Schroder, F. M. Schurr, and R. Wilson. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30:609–628.

Draper, N. R., and H. Smith. 1998. Applied regression analysis. Third edition. Wiley, New York, New York, USA.

Dungan, J. L., J. N. Perry, M. R. T. Dale, P. Legendre, S. Citron-Pousty, M. J. Fortin, A. Jakomulska, M. Miriti, and M. S. Rosenberg. 2002. A balanced view of scale in spatial statistical analysis. Ecography 25:626–640.

Eigenbrod, F., S. J. Hecnar, and L. Fahrig. 2011. Sub-optimal study design has major impacts on landscape-scale inference. Biological Conservation 144:298–305.

Fahrig, L. 2005. When is a landscape perspective important? Pages 3–10 in J. Wiens and M. Moss, editors. Issues and perspectives in landscape ecology. Cambridge University Press, Cambridge, United Kingdom.

Faraway, J. J. 2006. Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models. Chapman & Hall/CRC, Boca Raton, Florida, USA.

Fortin, M.-J., and M. R. T. Dale. 2005. Spatial analysis: a guide for ecologists. Cambridge University Press, Cambridge, United Kingdom.

Graham, M. H. 2003. Confronting multicollinearity in ecological multiple regression. Ecology 84:2809–2815.

Hawkins, B. A., J. A. F. Diniz, L. M. Bini, P. De Marco, and T. M. Blackburn. 2007. Red herrings revisited: spatial autocorrelation and parameter estimation in geographical ecology. Ecography 30:375–384.

Holland, J. D., D. G. Bert, and L. Fahrig. 2004. Determining the spatial scale of species' response to habitat. Bioscience 54:227–233.

Homer, C., J. Dewitz, J. Fry, M. Coan, N. Hossain, C. Larson, N. Herold, A. McKerrow, J. N. VanDriel, and J. Wickham. 2007. Completion of the 2001 National Land Cover Database for the conterminous United States. Photogrammetric Engineering and Remote Sensing 73:337–341.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187–211.

Koper, N., and F. K. A. Schmiegelow. 2006. A multi-scaled analysis of avian response to habitat amount and fragmentation in the Canadian dry mixed-grass prairie. Landscape Ecology 21:1045–1059.

Legendre, P. 1993. Spatial autocorrelation—trouble or new paradigm. Ecology 74:1659–1673.

Lennon, J. J. 2000. Red-shifts and red herrings in geographical ecology. Ecography 23:101–113.

Lichstein, J. W., T. R. Simons, S. A. Shriner, and K. E. Franzreb. 2002. Spatial autocorrelation and autoregressive models in ecology. Ecological Monographs 72:445–463.

McCulloch, C. E., S. R. Searle, and J. M. Neuhaus. 2008. Generalized, linear, and mixed models. Second edition. Wiley, Hoboken, New Jersey, USA.

McGarigal, K., and S. A. Cushman. 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. Ecological Applications 12:335–345.

McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. Computer software program produced by the authors at the

University of Massachusetts, Amherst. <http://www.umass.edu/landeco/research/fragstats/fragstats.html>. Accessed 30 Mar 2009.

Nocera, J. J., G. J. Forbes, and L. A. Giraldeau. 2009. Aggregrations from using inadvertent social information: a form of ideal habitat selection. Ecography 32:143–152.

Nocera, J. J., and G. J. Forbes. 2010. Incorporating social information to improve the precision of models of avian habitat use. Condor 112(2):235–244.

McGarigal, K., and W. C. McComb. 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. Ecological Monographs 65:235–260.

Pan, W. 2001. Akaike's Information Criterion in generalized estimating equations. Biometrics 57:120–125.

Schaalje, G. B., J. B. McBride, and G. W. Fellingham. 2001. Approximations to distributions of test statistics in complex mixed Linear models using SAS Proc MIXED. Paper 262 *in* Proceedings of the 26th Annual SAS Users' Group International Conference. SAS Institute, Inc., Cary, North Carolina, USA.

Schooley, R. L. 2006. Spatial heterogeneity and characteristic scales of species–habitat relationships. Bioscience 56:533–537.

Spectranalysis, Inc. 1999. Ontario land cover data base. Revised user's manual. Prepared for Ontario Ministry of Natural Resources. Spectranalysis, Inc., Oakville, Ontario, Canada.

Thogmartin, W. E., and M. G. Knutson. 2007. Scaling local species–habitat relations to the larger landscape with a hierarchical spatial count model. Landscape Ecology 22:61–75.

Turner, M. G., R. H. Gardner, and R. V. O'Neill. 2001. Landscape ecology in theory and practice: pattern and process. Springer, New York, New York, USA.

Vos, C. C., J. Verboom, P. F. M. Opdam, and C. J. F. Ter Braak. 2001. Toward ecologically scaled landscape indices. American Naturalist 157:24–41.

Wagner, H. H., and M. J. Fortin. 2005. Spatial analysis of landscapes: concepts and statistics. Ecology 86:1975–1987.

Wells, J. V., K. V. Rosenberg, E. H. Dunn, D. L. Tessaglia-Hymes, and A. A. Dhondt. 1998. Feeder counts as indicators of spatial and temporal variation in winter abundance of resident birds. Journal of Field Ornithology 69:577–586.

Williams, N. M., and C. Kremen. 2007. Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. Ecological Applications 17:910–921.

Yamaura, Y., K. Katoh, and T. Takahashi. 2006. Reversing habitat loss: deciduous habitat fragmentation matters to birds in a larch plantation matrix. Ecography 29:827–834.

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