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Uncertainty in spatially explicit population models

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ABSTRACT

Spatially explicit population models (SEPMs) are often used in conservation planning. However, confidence intervals around predictions of spatially explicit population models can greatly underestimate model uncertainty. This is partly because some sources of uncertainty are not amenable to the classic methods of uncertainty analysis. Here, we present a method that can be used to include multiple sources of uncertainty into more realistic confidence intervals. To illustrate our approach, we use a case study of the wood thrush (*Hylocichla mustelina*) in the fragmented forest of the North Carolina Piedmont. We examine 6 important sources of uncertainty in our spatially explicit population model: (1) the habitat map, (2) the dispersal algorithm, (3) clutch size, (4) edge effects, (5) dispersal distance, and (6) the intrinsic variability in our model. We found that uncertainty in the habitat map had the largest effect on model output, but each of the six factors had a significant effect and most had significant interactions with the other factors as well. We also found that our method of incorporating multiple sources of uncertainty created much larger confidence intervals than the projections that incorporated only sources of uncertainty included in most spatially explicit population model predictions.

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1. Introduction

Conservation scientists and practitioners often rely on spatially explicit population models (SEPMs) to predict the response of species to management schemes, assist with reserve site selection, or guide reintroduction efforts (Liu et al., 1995; Gerber and VanBlaricom, 2001; Carroll et al., 2003; Kramer-Schadt et al., 2005; Pearson and Dawson, 2005; Rushton et al., 2006; Schiegg et al., 2006; Vandel et al., 2006). These complex models typically use patches or a lattice to represent the landscape, identify the location of every object of interest, and simulate birth, mortality, and dispersal at the individual or population level (Dunning et al., 1995). In an attempt to improve the realism of model output, modelers sometimes fall prey to a natural inclination to increase the number of explanatory variables and the complexity of these

models (Gardner and Urban, 2003). However, as models grow in complexity, it becomes increasingly difficult to quantify the various sources of uncertainty, which can cloud the interpretation of model results. Even more importantly, model output that does not include an estimate of uncertainty may invoke a false sense of confidence, resulting in uninformed conservation decisions with potentially serious consequences.

There is a large literature on uncertainty analysis based in a regression framework, in which parameter values are sampled from their distributions, (e.g., Gardner et al., 1981; Gardner, 1984; Haefner, 1996; Crosetto et al., 2000; reviewed by Gardner and Urban, 2003), but all components of spatially explicit population models are not equally amenable to this procedure. Traditionally, the standard errors of the estimates of model coefficients are used to constrain Monte Carlo methods for assessing uncertainty (Gardner and Urban, 2003). In this,

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several replicate simulations are conducted, and in each simulation a different set of model parameters is selected randomly from the joint distribution of parameters. The model is then run with each parameter set, and model output (some dependent variable selected for its diagnostic value) is regressed on the input parameters. Sensitivity analysis is often conducted in the same framework, except the range of variation for each parameter is constrained to be some fraction of its nominal value (e.g., 10%) and Monte Carlo simulations are run for a large number of slightly perturbed parameter sets. By convention, a parameter's uncertainty is indexed by the amount of variation that its estimation error induces in the output, while its sensitivity is indexed as its partial regression slope (i.e., a sensitive parameter is one for which a small change in the parameter elicits a large change in model output). There are many examples of this type of analysis in the literature (Crosetto and Tarantola, 2001; Cox et al., 2003; Harmon et al., 2004), but this approach can be difficult to apply to several sources of data error that are common in spatially explicit population models (e.g., habitat maps that have different numbers of patches, or alternative algorithms for animal dispersal). As a result, uncertainty in less traditional (although increasingly common) model inputs, such as GIS habitat maps, have been largely ignored in terms of effect on spatially explicit population model output. What is needed is a way to recast these and other, non-traditional, sources of uncertainty so that they can fit into the Monte Carlo regression framework with which most modelers are familiar.

In this paper, we demonstrate a way to extend the general approach described above to a wide variety of sources of model error by simply relaxing the mechanics of the approach. The “parameter sets” can then be drawn from a collection of predefined alternatives including input maps, boundary conditions, alternative model algorithms, and conventional parameter values. To illustrate our approach, we use a case study of the wood thrush (*Hylocichla mustelina*) in the fragmented forests of the North Carolina Piedmont. We examine what we consider to be the 6 most likely sources of uncertainty in our spatially explicit population model: (1) the habitat map, (2) the dispersal algorithm, (3) clutch size, (4) edge effects, (5) dispersal distance, and (6) the intrinsic variability in our model. With little prior knowledge of their relative importance, we selected these factors because they were often associated with great uncertainty in the literature and they covered a range of sources to illustrate our approach. The results highlight model components that need to be more accurately calibrated to improve the utility of our spatially explicit population model, give a general indication of the reliability of the model predictions, and identify trends that may be meaningful to users of other models.

2. Methods

Our goal in this paper was to establish the importance of incorporating diverse sources of uncertainty into model results and to illustrate an easy approach for doing so. To accomplish this as simply as possible, we have selected six key model factors and represented the uncertainty in each

one with just two alternative values or possibilities. Five of these sources are model inputs representing aspects of avian biology, and the sixth is the intrinsic model variability that can affect any given parameter set. Of the five model inputs, two of them (the habitat map and the dispersal algorithm) do not fit obviously into the classical method of error analysis. We do not include every model component in the uncertainty analysis, nor do we explore every possible option for the model components we do include, although we acknowledge that there are probably an infinite number of model components and parameters we could have chosen to incorporate. This is not to imply that other sources of model uncertainty are unimportant, but attempting to include them all would only complicate rather than clarify the case. However, this same approach could easily be extended to explore any model in greater detail, by first identifying the sources of uncertainty that are of greatest concern and then “zooming in” and exploring them in more depth.

2.1. The focal species

We used the wood thrush as the focal species for this study for several reasons. First, it is a well-studied species and there are data in the literature for most of the parameters needed in the model. Second, it is a Neotropical migrant, somewhat of a habitat specialist, and a common host for the brood-parasitic brown-headed cowbird (*Molothrus ater*) and so may be especially sensitive to edge effects and forest fragmentation (Roth et al., 1996). Finally, while wood thrushes are fairly abundant across most of their range (the eastern US and southern Canada), they have been declining in numbers over the past several decades (Sauer et al., 2002) and so are of conservation interest. However, while the wood thrush is a compelling subject for this analysis, this was not meant to be an evaluation of wood thrush ecology but rather an illustration of a method that could be used with any simulation model or species.

2.2. The model

We used a spatially explicit, individual-based model to simulate habitat use, fecundity, dispersal, and mortality of individual birds (updated from Urban and Shugart, 1986). The spatially explicit population model (Fig. 1) simulates three kinds of birds: adult breeders, adult floaters, and juveniles. Breeders are adult birds with established territories, floaters are adults without territories, and juveniles are birds in their first year (also without territories). Juveniles and floaters do not breed. The model was initialized by randomly filling the landscape to half of its total carrying capacity with adult breeders. Although these initial conditions are not necessarily realistic, they are inconsequential because we subsequently allowed the metapopulation to reach a stochastic equilibrium. Each breeder produces offspring at a rate dictated by stochastic parameters such as clutch size, number of broods, and nest predation and parasitism rates (Table 1). Following reproduction, each individual has a probability of dying before the next time step, based on expected longevity. Adult breeders have the lowest mortality and juveniles and adult floaters have higher mortality (Table 1). If any habitat patch still has more birds than the carrying capacity allows follow-

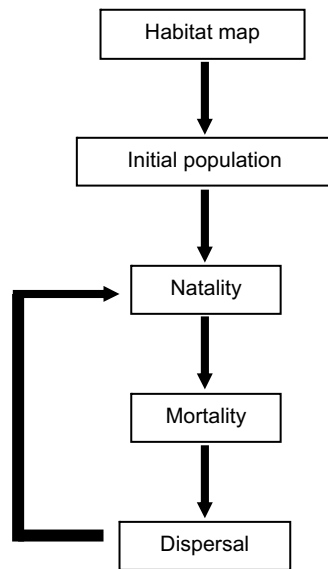


Fig. 1 – A flow diagram of the spatially explicit population model.

ing mortality, then dispersal will occur. Dispersal is a stochastic event based on the size of the patches and the distance and/or habitat between them (see below). Dispersal is the product of two species life-history parameters: the maximum distance that a bird will disperse in a single event (its *range*), and the number of total times an individual will attempt to disperse before settling (its *mobility*). If the bird reaches a patch that has an available territory, it will settle. If it does not, it will either become a floater or disperse to a new patch, depending on whether it has reached its maximum number of dispersal events. Juveniles and floaters have a much higher probability of dispersal than breeders because breeders have high site fidelity. This means that breeders tend to remain in the same patches year after year. Once dispersal has occurred, the juveniles become adults and the model begins another cycle. At any given time, the population size of a single patch is the sum of (a) surviving resident adults, (b) immigrat-

ing juveniles from other patches (or juveniles staying within the natal patch), and (c) the number of juveniles leaving the natal patch (dispersing). Floaters are not included in the population of any particular patch but are counted in the overall landscape population. The output of the model includes total population abundance, number of patches occupied on the landscape, number of birds on each patch, and the number of times each patch population goes extinct and becomes re-colonized. The model can be used to predict species abundance and potential for long-term persistence, as well as which patches may play a particularly important role in overall landscape connectedness.

We began our simulations with a landscape in which each habitat patch had a carrying capacity based on its size and the territory size of the wood thrush. Each habitat patch also had an “edge” value, calculated by averaging the distance between each cell in the patch and the closest non-forest edge. This metric incorporates patch shape, so that a compact patch would have a lower edge value than an elongated patch of the same size if both were surrounded by non-forest. We used the average edge value because we cannot predict the exact nesting location for each bird within a patch. This edge effect (rate or probability) is inversely and nonlinearly related to nest predation and parasitism rates by a modified Weibull function:

$$p(d) = b_0 + \exp[(d/b_1)^{b_2}] \quad (1)$$

where d is distance to an edge and the b 's are fitted constants, with b_1 being the functional distance of an edge (the extent of edge effects). When edge effects are turned off, each habitat patch in the landscape experiences nest predation and parasitism pressures equal to average rates for that particular species. When edge effects are turned on, patches vary in their predation and parasitism rates based on their proximity to non-forested edges.

2.3. The habitat map

There are numerous sources of uncertainty involved in making habitat maps (Scott et al., 2002), which often originate

Table 1 – Model parameters

Parameter	Range of values in the literature	Value used in model	Citation (listed in same order as values)
Nest parasitism rate	0–100%	75%	Donovan et al. (1995) and Fauth (2001)
Nest predation rate	10–82%	65%	Hoover et al. (1995) and Brawn and Robinson (1996)
Edge distance ^A	0–300 m	0 m, 200 m	Fauth (2000) and Brittingham and Temple (1983)
Annual adult survival	0.58–0.71	.65	Powell et al. (2000) and Roth et al. (1996)
Juvenile/floater survival	0.29	.3	Anders et al. (1997) (data only for juveniles)
Clutch size ^{A,B}	1.9–3.7 eggs	2.5 eggs, 3eggs	Trine (1998) and Roth et al. (1996)
Number of broods attempted	1–4	2	Roth et al. (1996)
Territory size	0.08–2.8 ha	1 ha	Twomey (1945) and Weaver (1949)
Dispersal distance ^A	0.6–3.56 km	1.5 km, 3 km	Anders et al. (1998)
Juvenile/floater site fidelity ^C	0.5	0.10	Roth et al. (1996)
Breeder site fidelity ^C	0.19–0.65	0.90	Robinson (1992) and Roth et al. (1996)

^AParameters included in uncertainty analysis.

^BEstimates of clutch size include parasitized nests.

^CValues from the literature represent return rate of all individuals from the previous year, whether they survived or not; value used in our model includes only surviving individuals.

from satellite imagery and form the spatial template upon which the population processes will play out. Most habitat maps are based on field observations of species presence or abundance, and such observations may be faulty or have imprecise spatial locations (McKelvey and Noon, 2001). The extrapolation of this information to a landscape, usually in a GIS framework, creates additional uncertainties associated with spatial imprecision and inaccuracy in base GIS layers (e.g., digital elevation models, vegetation cover maps). In binary habitat maps (consisting of only habitat and non-habitat), a somewhat arbitrary division must be drawn between what is classified as habitat and non-habitat. This process inevitably misclassifies some habitat as non-habitat and vice versa, which can be especially true for very rare or common species.

In our case study, the spatially explicit population model was run on a habitat map created from remote sensing imagery of a 51,778 ha region in the Triangle area in the North Carolina Piedmont (Fig. 2). Classified land cover types were created from Landsat TM images (30 m resolution) from May 1992 using a supervised, maximum-likelihood analysis in Erdas Imagine, with training data points taken from high-resolution aerial photographs. The image was classified into 6 discrete classes (Table 2). For forested pixels, the hardwood basal area (m^2/ha) of each pixel was calculated using a regression model that relates TM spectral characteristics with deciduous and evergreen basal area from long-term monitoring plots in the Duke Forest. A set of Duke Forest permanent

Table 2 – Land cover classification and composition for the study area

Land cover classification	Area (ha)	% of total landscape	Travel cost
Sparse vegetation	18,152	36.6	2
Highly reflective/developed	14,461	29.2	5
Hardwood forest	9297	18.8	1
Pine forest	6647	13.4	1
Water	645	1.3	2
Mixed vegetation	354	0.7	1

sample plots was used as training data, where the spectral characteristics of the TM images (excluding band 6) were regressed against the (log-transformed) total hardwood basal area. Previous bird surveys done in the area (Das, 2000) were used to determine the typical basal area of forest habitats occupied by wood thrushes. In order to account for the uncertainty involved in the process of creating habitat maps, we used two different habitat threshold values to create maps that bound the possibilities of wood thrush habitat requirements: $15 \text{ m}^2 \text{ ha}^{-1}$ of hardwood forest for a “generous map”, and $20 \text{ m}^2 \text{ ha}^{-1}$ of hardwood forest for a “strict map” (Fig. 3). Any pixel that met these requirements was considered habitat, and habitat cells were grouped into patches according to an eight-neighbor rule. Only patches greater than 1 ha (11 cells) were used because this is typically the smallest for-

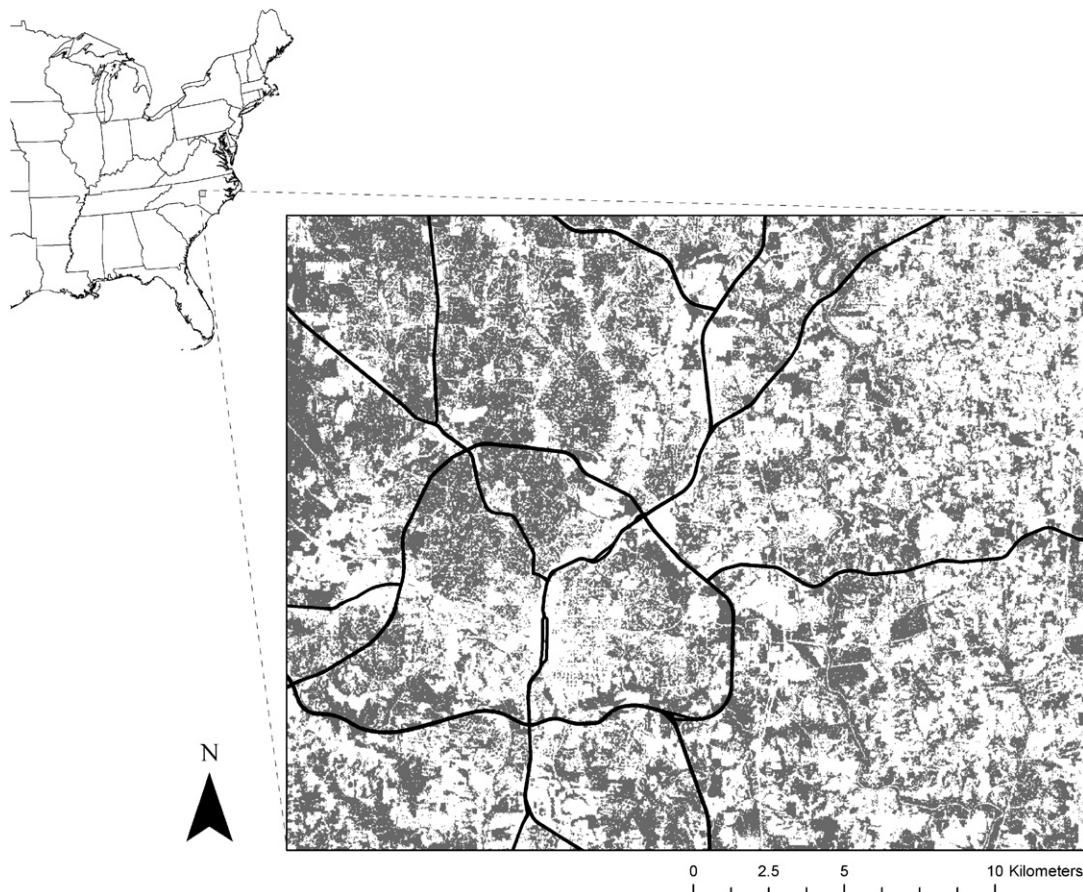


Fig. 2 – Satellite image of the study site in Raleigh, North Carolina (USA). Shaded areas are forested.

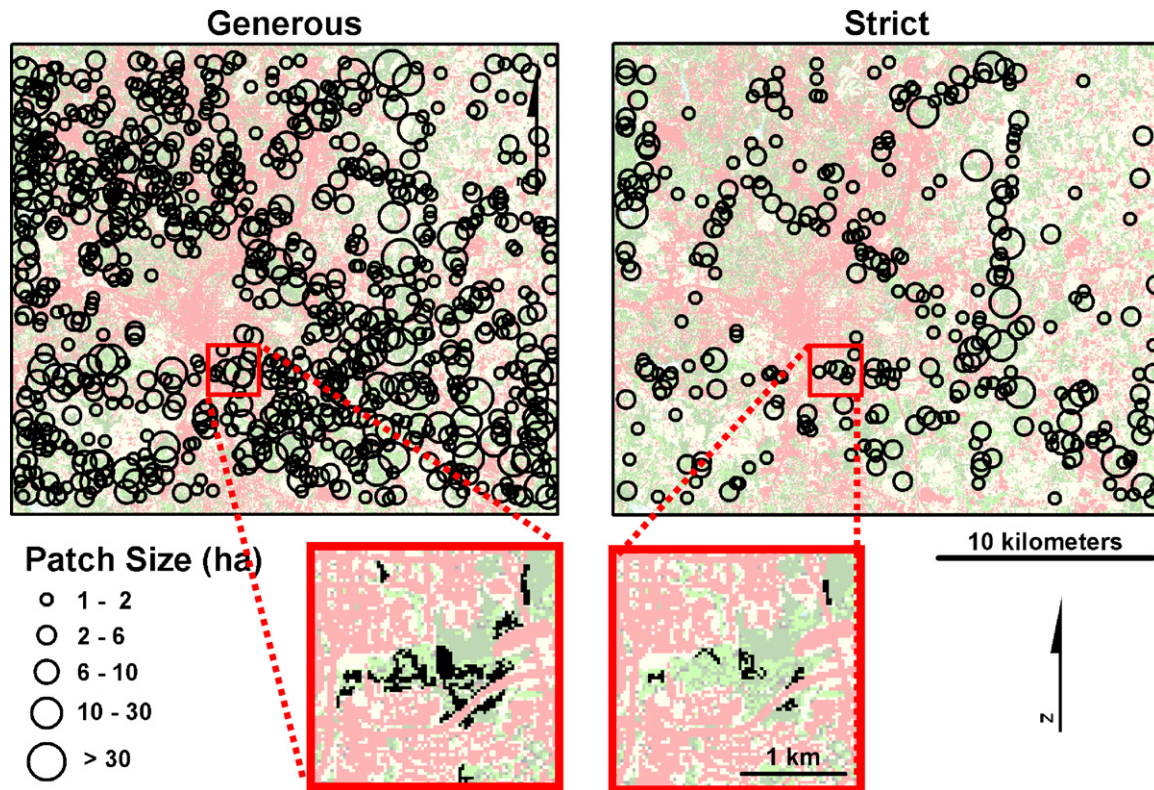


Fig. 3 – Contrasting maps of wood thrush habitat using strict and generous habitat classification thresholds. Red areas are urban development, green areas are forested. Habitat patches are shown as black circles in the larger maps and simply colored black in the close-up (smaller) maps.

est patch occupied by wood thrushes (Roth et al., 1996). The generous habitat map was made up of 823 discrete habitat patches, together representing 3230 ha of viable habitat or approximately 6% of the entire study area. The average patch size was 4 ha (std. 6 ha). The strict habitat map contained 794 ha of wood thrush habitat in 306 discrete patches, which made up 1.5% of the study area. Average patch size in the strict habitat map was 2.5 ha (std. 3 ha). About 60% of the patches in the strict map could only contain one breeding pair (<2 ha), and about 48% of the patches in the generous map could only contain one breeding pair. Distance-to-edge calculations between habitat maps (strict and generous) were similar. The average distance to non-forest edge was 56.0 m (± 19.5 m, max distance of 151 m) and 52.9 m (± 16.5 m, max distance of 219 m) for the strict and generous map, respectively. The use of “generous” and “strict” maps is a unique approach that allows us to account for the uncertainty of wood thrush habitat preferences. We opted not to include the additional uncertainty of satellite image interpretation into our analysis for simplicity’s sake, but there are several methods available for assessing this kind of uncertainty (see discussion above).

2.4. Dispersal models

Bird dispersal is a complex and somewhat mysterious phenomenon that is modeled in many different ways in the literature. Do birds disperse when their habitat patch has reached

carrying capacity or before? How does dispersal affect mortality rates? How do birds move through non-preferred habitat? All of these questions reflect differences in the way the dispersal algorithm of a spatially explicit population model can be structured. This lack of understanding could lead to very different implementations of dispersal in a model. At one level, a dispersal kernel may be used to define the probability of dispersal between two patches as a function of between-patch distance; in this case the choice of the form of the kernel (negative-exponential? Gaussian?) invites model specification errors. At another level, dispersal algorithms may operate as some kind of constrained random walk (Gustafson and Gardner, 1996) or a foray search strategy (Conradt et al., 2003) in which individual birds “disperse” in search of available habitats. The term “dispersal algorithm” should not be confused with “dispersal distance”, which we discuss in the following section. Although the distance traveled between two habitat patches always depends on the dispersal algorithm used, the reverse is not necessarily true: the algorithm used can be completely independent of the distance between any pair of patches.

In individual-based models that divide the landscape up into patches, as our model does, dispersal is stochastically modeled according to a set of probabilities of movement between patches. Our model includes two different methods of determining these probabilities. The first uses a negative-exponential function of nearest-neighbor (edge-to-edge) distance and patch size to estimate the probability of dispersal from patch i to j :

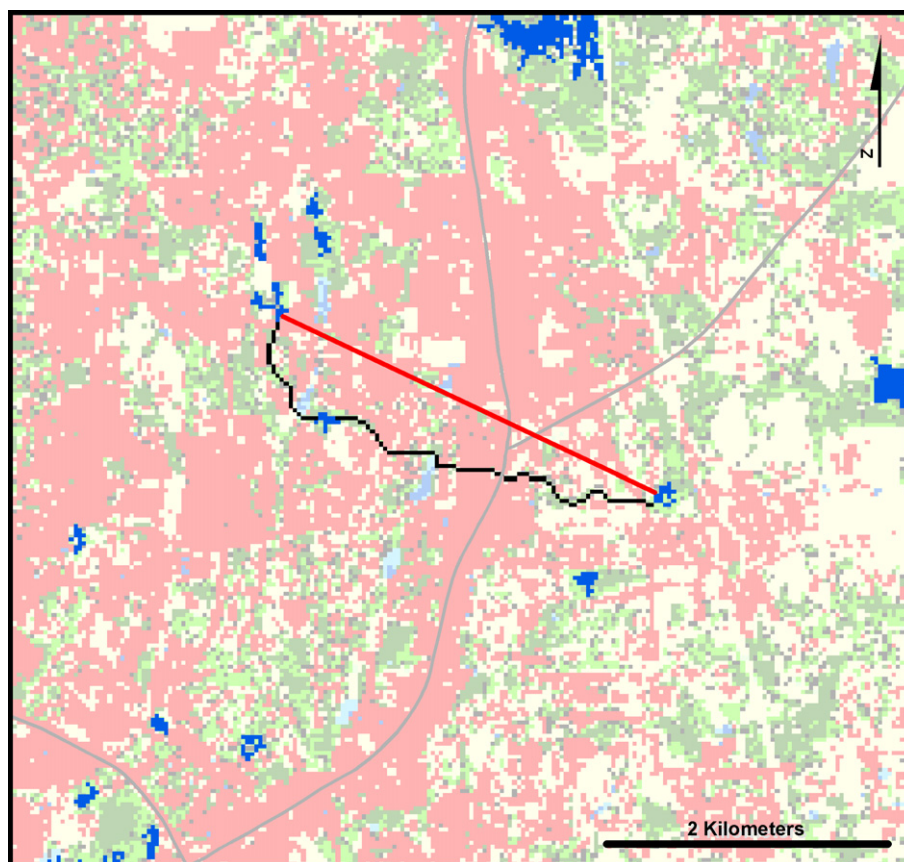


Fig. 4 – A comparison of the inter-patch distance used in the Euclidean dispersal method (red line) and the least cost method (black line). Habitat patches are shown in blue. Because the two patches of interest are separated by mostly developed land (shown in red), the least cost method follows a rather convoluted path with the minimal travel cost.

$$p_{ij} = a_j \exp(-\theta d_{ij}) \quad (2)$$

where θ is an extinction coefficient estimated from the tail distance at which $p_{ij} = 0.01$, and d_{ij} is the distance between patches i and j . Here, a_j is the area of the target patch and provides for a “target area” effect, which means that larger patches are more likely to be destinations for dispersing birds. This method of determining dispersal probabilities between patches assumes that the inter-patch habitat is homogenous and therefore traversability is the same for all intervening habitat. As a result, dispersal distance between patches is based on Euclidian distance between patches and patch size only. The second dispersal mechanism uses a least-cost path between each patch to calculate distance (Bunn et al., 2000). In general, this method determines the minimum accumulative ‘travel cost’ between every pair of patches. The cost of travel across an individual cell in the non-habitat matrix is based on the amount of effort it takes to cross the cell. This effort, although subjective, allows the model to take into effect a flight preference of the birds. For example, it may be reasonable to assume that a bird would more likely traverse the matrix through wooded corridors, rather than flying in a straight line (i.e., Euclidean distance) to a neighboring patch through developed areas and across major highways. Therefore, we assigned the following *ad hoc* cost values to the land cover classes (higher cost = more difficult to cross): all for-

ested habitat has cost of 1, sparse vegetation and shallow water has cost of 2, and highly reflective/developed has cost of 5 (Table 2). In other words, it is 5 times more costly to cross developed areas than it is to pass through preferred habitat. The fact that we computed a least-cost path for every pair of patches globally implies that the birds respond to intervening patches as well as the surrounding habitat. Both habitat patches and non-habitat forest patches (like those patches that are below the 1 ha threshold) are assigned the lowest cost (1); the underlying assumption is that the birds will follow the ‘cheapest’ path, often traversing intervening habitat patches and forested parcels in a stepping-stone manner along the way. Implementing this least-cost path approach within the dispersal sub-model effectively increases the travel distance between patches where the matrix is more developed and less desirable to the birds. This concept is shown graphically in Fig. 4. The least-cost path distance (black) between these two patches is much greater than the Euclidean distance (red) due to the highway and highly developed region between these patches. It is this greater ‘travel cost’ that is used in the least-cost path implementation, rather than the closest Euclidean distance, again using Eq. (2). Note that this approach essentially recasts a different dispersal logic into the same model framework by reparameterizing the model.

The Euclidean and least-cost path dispersal methods are not directly comparable, but this only emphasizes the impor-

tance of our approach. We currently have no way of knowing which of these equally viable methods to include in our model, and a traditional uncertainty analysis would not allow us to include this kind of uncertainty. There are also many other ways to compute dispersal paths, including a middle-ground between our two choices: it would be possible (and perhaps even biologically realistic) to calculate a Euclidean path where a bird does incur risks (costs) depending on land cover but is unable to alter course in response to the risks. However, including every possible kind of dispersal model is beyond the scope of this paper.

2.5. Model parameters

Clutch size, edge effects, and dispersal distance are the more traditional sources of uncertainty in our analysis in that there are discrete parameters defining them. Uncertainty in parameters associated with life history characteristics (e.g., mortality, fecundity) is a common concern in the creation and use of spatially explicit population models. Estimating these life history parameters is a central goal of population ecology, yet confidence in these values is often limited due to the great difficulty in obtaining empirical data. Minimizing errors in these parameters requires large sample sizes, and is complicated by the natural variability of ecological systems. In some cases, uncertainty might be entirely due to errors in observation, as in the case where a field estimate of clutch size (eggs per nest) is used as a model parameter directly. In other cases, as in this case study, these parameter values are selected from the literature. This presents a different set of issues, since the field studies in the literature might be completed in ecological and geographic settings that are unlike the ones being modeled (Gardner and Urban, 2003). Even in well-studied species, there exists a wide range of parameter values in the literature that exacerbates error within the model.

The parameters used in this model were taken from the literature (Table 1). Most of the values varied greatly from study to study, but the most inconsistent results are of the effects of edges on nest predation and parasitism rates. Two reviews of the effects of edge on nest predation even are in disagreement about the very existence of edge effects (Paton, 1994; Lahti, 2001). Additional parameters with high uncertainty are clutch size, which has a high variation in the literature, and dispersal distance, which is largely unknown. Because edge effects and clutch size vary the most in the literature and dispersal distance has a high degree of uncertainty, we varied these three factors in our spatially explicit population model in order to explore the error associated with our uncertainty of these parameters. We ran the model with edge effects turned on and off and using two different values each for clutch size (2.5 and 3 eggs per clutch) and maximum dispersal distance (1500 m and 3000 m).

2.6. Intrinsic model variability

The intrinsic variability in our model incorporates an element of chance into model parameters by drawing their values randomly from some distribution. This can be used to represent

truly stochastic processes (e.g., mortality) as well as processes not simulated explicitly (e.g., year-to-year variability in weather affecting food resources, which in turn affect clutch size; this might be modeled as stochastic variation in clutch size). In spatially explicit population models, demographic processes often are modeled as stochastic because the models operate on an individual basis. For example, each bird either lives or dies each year, and only entire birds are fledged, although the probabilities of these occurrences are not whole numbers. Likewise, the model has dispersal probabilities [0, 1] for every habitat patch, but each bird disperses ultimately to only one patch. For stochastic processes such as inter-annual variability in weather as this might affect demographic rates, ecologists commonly rely on variations of random number generators. There is a fine line separating variation in a parameter due to “natural variability” and variation due to sampling error, but the implementation is essentially the same. Separating the natural system variability from other kinds of errors can be difficult but is important in the interpretation of results. Typically, ecologists developing spatially explicit population models will run a stochastic model multiple times in Monte Carlo fashion in order to generate some measure of this variability. For each individual bird, a series of random numbers is drawn to determine the outcome of stochastic events such as dispersal, mortality, and clutch size. We included this intrinsic variability in our model by running the model 100 times for each set of conditions.

2.7. Simulations and analyses

To quantify the uncertainty related to each of the above components, we conducted a series of model simulations that varied each model component in isolation and in combination with each other component in a full factorial design for a total of 32 cases (Fig. 5). Each model simulation ran for 100 years to allow the population trend to proceed beyond any transients induced by the initial conditions. Since the model is stochastic, 100 replicates were performed for each simulation and averaged. This resulted in a total of 3200 model runs. We analyzed the model results using two ANOVAs on two response variables, considering separately the number of birds on the landscape (using the log to stabilize the variance) and the percent of carrying capacity occupied (using an arcsine-square root transformation). We considered both of these response variables because the two habitat maps had very different carrying capacities and thus populations could not be compared directly. We also examined total model error using a Monte Carlo approach in which we randomly selected three replicates from each of the 32 cases described above. In essence, by selecting the same number of replicates from each scenario, we considered all scenarios to have the same likelihood of being true, although this could easily be altered if certain scenarios were considered more likely than others. The median prediction of the model in any year is then simply the median response of all of the selected replicates, expressed as percent carrying capacity to make comparisons between generous and strict maps possible. Similarly, confidence intervals can be estimated by drawing out the appropriate quantiles from the selected replicates.

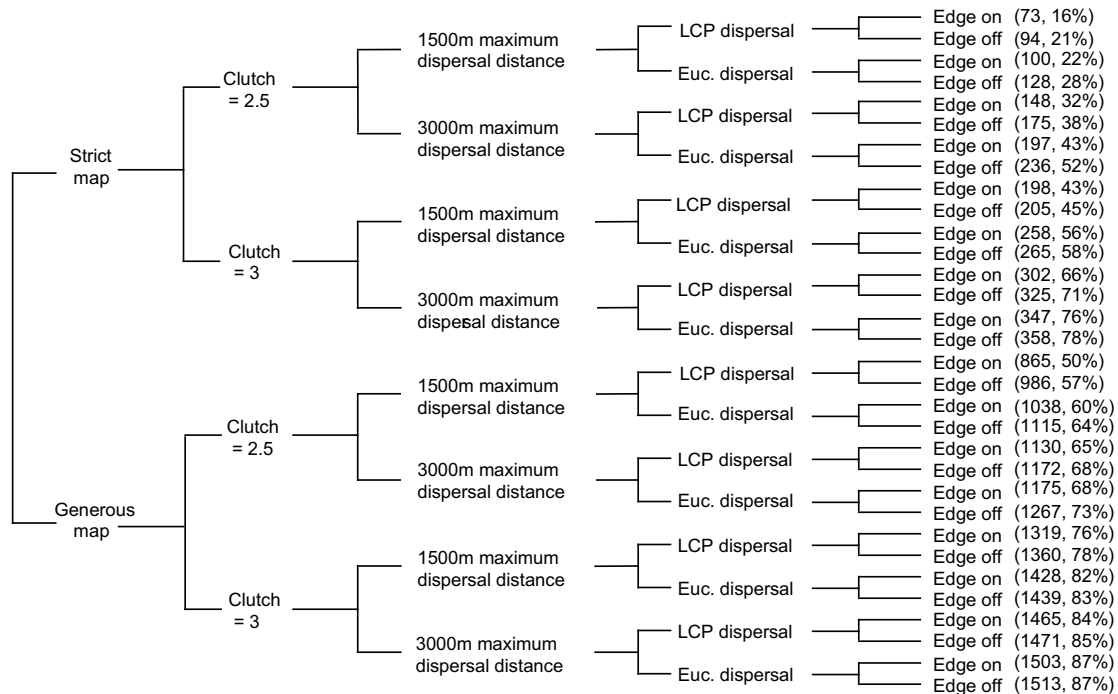


Fig. 5 – Diagram of all model simulations, to test for overall sensitivity in the spatially explicit population model. Note that there are 32 different simulations and 100 replicates for each one, and thus a total of 3200 model runs. Numbers in parentheses at the end of each branch reflect the average number of birds and the percent of the landscape carrying capacity occupied at the end of that particular simulation.

2.8. Patch level evaluation

To offer an additional viewpoint on model sensitivity, we also considered a patch-level response variable in our analysis. This was in contrast to the landscape-level response variables that we have been considering to this point, which provide an overall measure of population persistence but do not look at the significance of specific habitat patches. Patch persistence, defined here as the average number of years a patch is occupied during the last 10 years of the model run (when a stochastic equilibrium has been reached), is calculated for each habitat patch on the landscape. This metric provides some measure of the conservation value of a patch. For simplicity, we used only two combinations of model factors in this analysis: holding everything else constant with a strict habitat map, least-cost dispersal method, clutch size of 2.5 eggs, and no edge effects, we looked at patch persistence under two different dispersal distance scenarios (1500 m and 3000 m). This analysis provides a meaningful illustration of the spatial distribution of model uncertainty rather than the aggregate effect averaged over the entire study area.

3. Results

Because the model was initialized with the population at 50% of carrying capacity, the number of birds on the landscape had the potential to either increase or decrease as the simulation proceeds, depending on the set of input factors. To illustrate a typical model run, we show the mean output from one particular scenario as a time-series graph with 95% confidence intervals (Fig. 6). The confidence intervals are produced from the intrinsic model variability alone, by running the model 100 times for one particular set of input factors. This is often the only kind of uncertainty included in spatially explicit population model output. For this particular example (a 100 year model run with the generous habitat map, least-cost dispersal method, 3000 m maximum dispersal, a clutch size of 2.5, and edge effects on) the population increases fairly rapidly within the first 25 years, then reaches equilibrium and levels out at about 1100 breeding birds (63% of carrying capacity) on the landscape. This was a typical model run in that the output did not change very much after the first 25 years.

Depending on the set of input variables, the bird population at equilibrium ranged from less than 20% of carrying capacity (<100 breeding birds remain when the model is run on the strict landscape using 2.5 eggs per clutch, dispersal distance of 1500 m, and least cost dispersal method) to a landscape filled to 87% of carrying capacity (>1500 birds remain in the landscape using the generous habitat map, 3 eggs per clutch, dispersal distances of 3000 m, and Euclidean dispersal method) (Fig. 5).

3.1. Model response to each source of uncertainty

Each factor in the ANOVA had a significant main effect on population size as well as percent of carrying capacity occupied, and most of the first-order interactions were significant as well (Table 3). This significance is due, in part, to the large sample size (100 replicate runs per parameter set), which makes even relatively small effect sizes statistically significant.

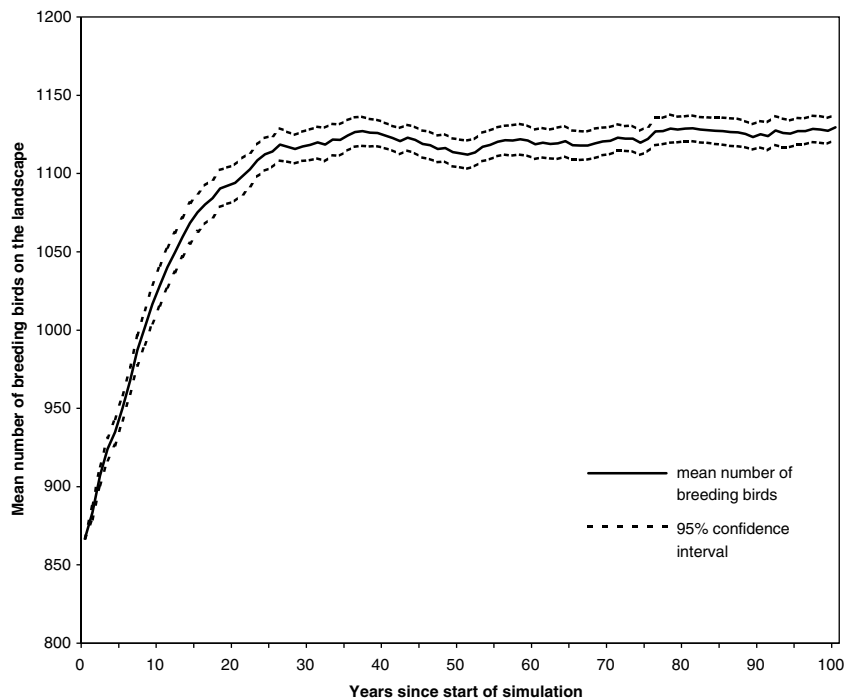


Fig. 6 – Time series showing the mean and 95% confidence intervals of 100 model simulations using the generous habitat map, the least-cost dispersal method, a 3000 m dispersal distance, a clutch size of 2.5 eggs, and edge effects on. The 95% confidence interval shows the uncertainty due only to the intrinsic variability in the model. Its maximum value in this case is ± 13 birds.

Table 3 – Analysis of variance on the effects of each source of model uncertainty on population abundance

Source of variation	Df	Sum of sq.	Mean sq.	F value	Pr (F)
Dispersal model	1	5.68	5.68	3476.25	0.00
Map	1	65.57	65.57	40150.67	0.00
Clutch size	1	60.44	60.44	37006.97	0.00
Dispersal distance	1	19.80	19.80	12121.84	0.00
Edge effects	1	1.28	1.28	786.29	0.00
Dispersal model \times map	1	0.41	0.41	251.30	0.00
Dispersal model \times clutch size	1	0.00	0.00	0.80	0.37
Dispersal model \times dispersal distance	1	0.08	0.08	51.09	0.00
Dispersal model \times edge effects	1	0.00	0.00	0.86	0.35
Map \times clutch size	1	1.60	1.60	979.97	0.00
Map \times dispersal distance	1	2.98	2.98	1827.02	0.00
Map \times edge effects	1	0.06	0.06	34.09	0.00
Clutch size \times dispersal distance	1	0.07	0.07	43.23	0.00
Clutch size \times edge effects	1	0.27	0.27	166.55	0.00
Dispersal distance \times edge effects	1	0.00	0.00	0.62	0.43

cant. When considering total population size, the choice of habitat map (strict vs. generous) had the largest effect on model output (Fig. 7), followed by clutch size, maximum dispersal distance, the intrinsic model variability, the type of dispersal model, and lastly, edge effects. When considering percent of carrying capacity occupied, the order of importance was the same except intrinsic model variability and dispersal distance switch rankings. The result is that habitat map had the largest effect, followed by clutch size, intrinsic model variability, dispersal distance, dispersal method, and finally edge effects.

The effect of the habitat map was almost 3 times as important as the other factors when considering total population size, although only slightly more important than clutch size and process error when considering the percent of carrying capacity occupied on the landscape. The strict habitat map resulted in lower total population numbers as well as a lower portion of the habitat occupied than the generous map, although the difference was greatest when comparing total population size between the maps. Every other factor had a significant interaction with habitat map as well. The difference between maps became larger when maximum dispersal

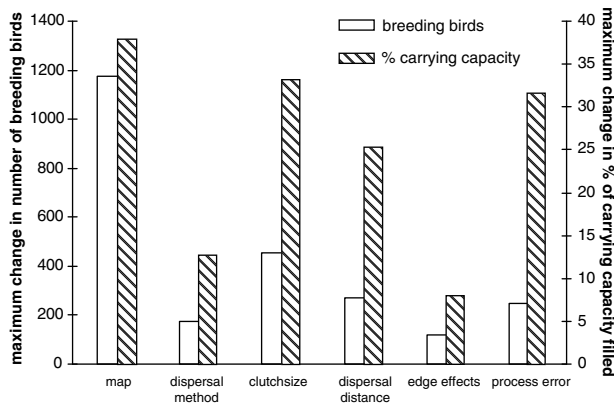


Fig. 7 – A measure of model sensitivity to each error type. The y-axis shows the maximum difference in model output for two different metrics when varying one factor and holding the others constant.

distance was decreased and when the least-cost path dispersal method was used.

The dispersal algorithm had the fifth largest (or next to last) effect on model output. The least-cost path method of dispersal consistently resulted in lower population numbers and percent of carrying capacity occupied. This result was magnified when using the strict habitat map. While statistically significant, these differences were relatively small.

Uncertainty in the life history parameters had varying degrees of importance to model output, depending on which factor was being considered. Clutch size was the second most important factor to model output. At 2.5 eggs per clutch, the population size was greatly reduced. This difference was most significant in the strict habitat map. Every other factor except the dispersal method had a significant interaction with clutch size, and these interaction effects were most noticeable when generated on the strict habitat map. Dispersal distance had the third largest effect on total number

of breeding birds and fourth largest effect on percent of carrying capacity occupied. Allotting the birds longer dispersal distances increased both total population size and percent of carrying capacity occupied. When considering the percent of carrying capacity occupied, this effect appeared to be more pronounced in the strict map. However, when considering the total population size, this effect was more pronounced in the generous map. Dispersal distance showed significant interaction terms with all other factors except edge effects. Edge effects, the final life history parameter we examined, had the smallest effect on model output, although there was still a statistical difference in the population with and without edge effects. When the edge effects were turned on, both the total population and the percent carrying capacity were consistently, although only slightly, lower than when they were turned off.

Intrinsic model variability had an intermediate effect on model output. To obtain an estimate of this effect, we left all input factors constant and examined the amount of variability generated by the stochastic processes alone. An idea of how this uncertainty affected our prediction was obtained from the 95% confidence intervals around the mean in Fig. 6. The maximum variability due to this factor in any one simulation was 249 birds or a 32% change in carrying capacity occupied. However, simulations varied widely in the size of their confidence interval, from 62 birds (for the simulation with the strict map, Euclidean dispersal method, 3 eggs/clutch, 3000 m maximum dispersal distance, and no edge effects) to 249 birds (for the simulation with the generous map, Euclidean dispersal method, 2.5 eggs per clutch, 1500 m maximum dispersal distance, and edge effects on). The most important input factor in determining the effect of the intrinsic model variability was clutch size. Holding everything else constant, simulations with a clutch size of 2.5 eggs had a smaller confidence interval than simulations with a clutch size of 3 eggs, suggesting an interaction between these two kinds of uncertainty.

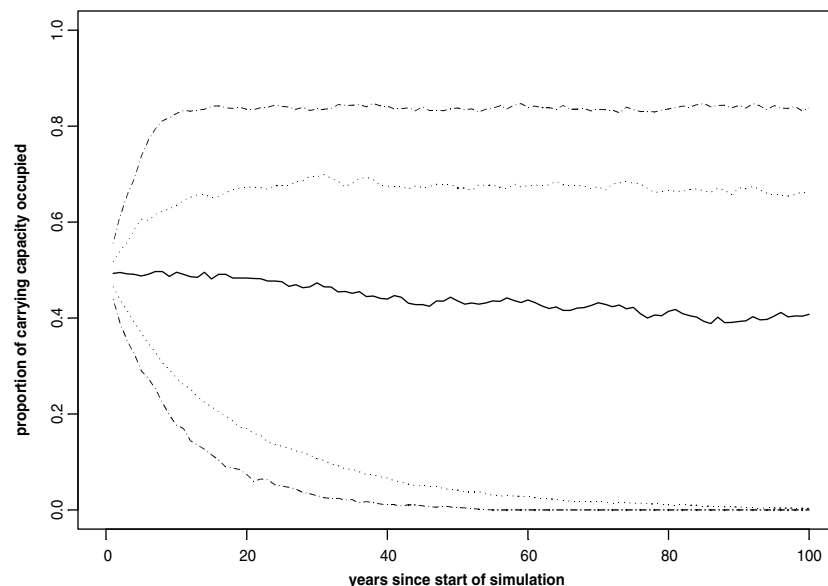


Fig. 8 – Time series showing the mean, 50%, and 95% confidence intervals when including all sources of error in model output.

Total model error was very large when all sources of error were included in the analysis (Fig. 8). The 50% confidence interval around the mean ranged from 0% to 75% of the carrying capacity occupied, and the 95% confidence interval ranged from 0% to 83%.

3.2. Patch-level evaluation

Patch persistence for each habitat patch was classified according to the average number of years the patch was occupied by a wood thrush in the last 10 years of the model simulations. We should point out that two patches with the same persistence value are not necessarily equivalent. For example, one patch may be occupied for five consecutive years during a 10-year period (i.e., sustain a population for an extended period of time), while another patch may be occupied for five alternating years (i.e., not able to sustain a population for more than one year). However, this metric still provides a useful illustration of our methods. Under both dispersal distance scenarios (maximum dispersal of 1500 m and 3000 m), it was only the larger patches that were occupied 8–10 of the last 10 years (Fig. 9, red circles). When the maximum dispersal distance was 3000 m, all of the largest patches and some of the smaller patches were occupied for 8–10 of the last 10 years. However, when the maximum dispersal distance was 1500 m, several of the patches in the largest size class were very rarely occupied (green circles). In the latter case, whether or not a large patch was occupied appeared to depend strongly on its location in the landscape. For example, patches in the high-density southeastern corner tended to remain occupied, while more isolated patches to the north and west tended to be unoccupied more frequently. In fact, for the shorter dispersal distance, only patches in the southeastern corner of the map were occupied for more than four

of the last 10 years. The remainder of the landscape contained patches that were only rarely occupied. Additionally, the majority of the patches in the smallest size classes were completely unoccupied (white circles) with the shorter dispersal distance, but there were very few unoccupied patches with the longer one.

4. Discussion

Every factor that we vary in our model has a significant effect on the output. In addition, most interaction terms are also significant. The range of output of the model is quite large when taking all these uncertainties into account. While this may be disconcerting, our results show that there are some steps that can be taken to reduce model error as much as possible. Although every factor is significant, the majority of overall model uncertainty is due to just a few factors (habitat map and clutch size). The key to reducing model uncertainty is to focus data collection efforts on those factors that are most important to model output (Dunning et al., 1995). Fortunately, the factors indicated by our model as most important are relatively easy to measure; habitat requirements and clutch size can be much more easily determined than dispersal behavior. These factors are also relatively easy for the model user to modify, which is an important issue to consider. Often, managers and conservationists are not modelers themselves and will use a model that has been created by someone else. In that case, it can be very difficult for them to change algorithms that are internal to the model, such as the dispersal algorithm. Changing the clutch size, however, can be as easy as typing in one number. Nevertheless, it is important to note that the relative importance of factors will vary according to the focal species and landscape.

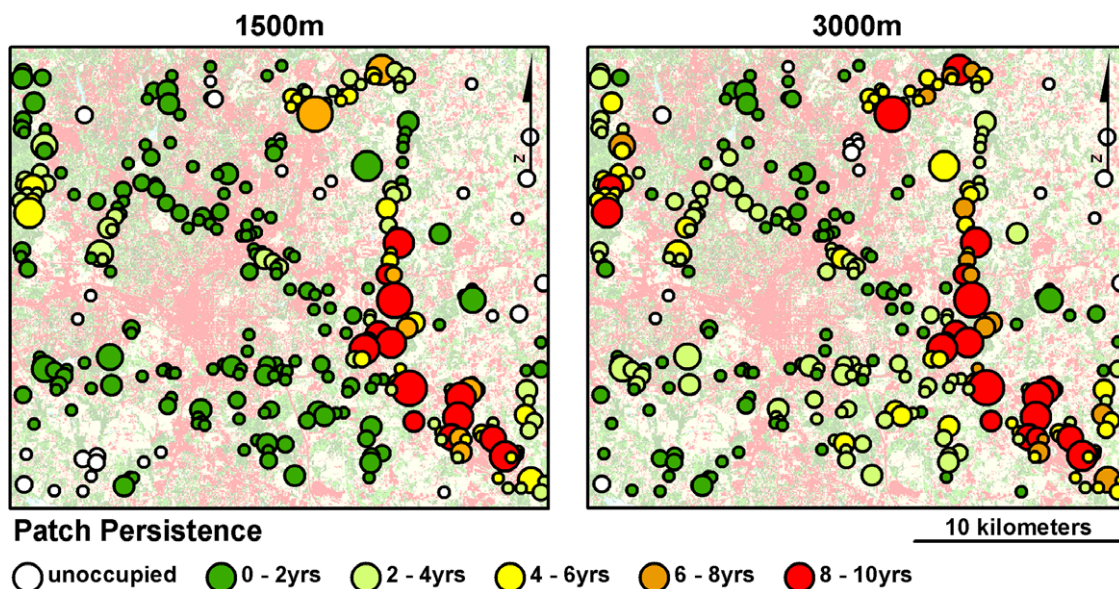


Fig. 9 – A comparison of patch persistence in simulations with 1500 m maximum dispersal distance and 3000 m maximum dispersal distance. Habitat patches are shown as circles; size of circle is relative to size of habitat patch. Patch persistence is equal to the average number of years the patch was occupied during the last 10 years of the simulation. Both simulations use the strict map, least-cost dispersal method, 2.5 eggs/clutch, and edge effects turned off.

4.1. The habitat map

The uncertainty in the habitat map is the largest source of error in our model. This finding should be stressed, since habitat map uncertainty is rarely (if ever) included in spatially explicit population model output. Several studies have looked at the importance of a hypothetical habitat map on spatially explicit model output (Ruckelshaus et al., 1997, 1999; Pulliam et al., 1992), but to our knowledge, ours is the only study that examines the uncertainty involved in an actual habitat classification into population estimates. Furthermore, our methods allow model users to incorporate this uncertainty into their predictions rather than make a choice about whether to use the “strict” or “generous” map.

In contrast to our findings, Ruckelshaus et al. (1997, 1999) found that dispersal factors were more important sources of error than the habitat map, while Pulliam et al. (1992) found that demographic parameters were more important than the habitat map. These examples illuminate the difficulty in generalizing results across studies: each study uses a different model, considers different response variables, and examines different sources of uncertainty. A potentially useful rule has been suggested by King and With (2002), who found that spatial pattern in landscapes should only be important to predicting dispersal behavior when habitat abundance is less than 40%.

In our case, the importance of the habitat map is a fairly intuitive result because the two maps we generated differ greatly in both the total amount of habitat and the arrangement of habitat; increasing the amount of habitat on our map also increased connectivity by bringing the patches closer together. While our methods do not allow us to determine the relative importance of these two map components, they do represent the reality that confronts scientists and managers attempting to define habitat for a species. In a real landscape, configuration is a fundamental attribute of the map and habitat cannot be lost or gained without also changing configuration. Partially as a result of this interaction, a small difference in the threshold value of acceptable habitat (from 15 m² ha⁻¹ of hardwood forest to 20 m² ha⁻¹) results in large differences in model output. In our model, the maximum difference between the two maps is a 40% change in percent carrying capacity occupied (Fig. 7), which means that not only does the strict map result in much less available habitat (from 3230 ha to 794 ha), but also less of the available habitat is filled. This can be attributed to the loss of connectivity described above. Therefore, simulated dispersing birds are less likely to locate suitable habitat patches, become floaters more frequently, and have a higher mortality. This highlights the capacity for model errors to propagate through other parts of the model.

It is somewhat counter-intuitive that the average distance to a non-forest edge is not very different between our two maps. To understand this, we should note that many of the habitat patches in both of our maps are embedded in a forested matrix. Although that forest matrix may not be suitable habitat, it does not qualify as edge in the way that we have used the term (i.e., an edge is a forest/non-forest edge). This is because most of the biological effects associated with edge habitats are due to the introduction of nest predators or par-

asites from non-forested habitat to forested habitat (e.g., brown-headed cowbirds, many corvid species). The habitat patches in the strict map are often a smaller portion of the patches in the generous map, and therefore are not more “edgy” since they tend to be surrounded by forest. Clearly this result could vary for landscapes with more non-forest habitat.

4.2. Dispersal models

Our uncertainty about the dispersal algorithm does not play a large role in the total model uncertainty, although it still has a significant effect. Using the least-cost path dispersal method has a similar effect to using the strict map, in that it essentially creates a landscape with larger between-patch distances. However, the least-cost path dispersal method is expected to increase between-patch distance in a very local manner. In particular, it should have a larger effect in areas of high development. Connected patches (patches that are within the maximum dispersal distance of a particular species from each other) that are separated from each other by areas of commercial development might become disconnected when using the least-cost path method, while two patches separated by other land-cover types would not be affected by changing the dispersal method. In general, changing the dispersal method does not have a large effect on the total population in our landscape because most patches are not very far apart from each other, even when using least-cost paths. Therefore, the connectivity between patches does not change very much. In a different landscape with patches separated by larger distances, or with a more inhospitable matrix between patches, we would expect using the least-cost path dispersal method to have a much larger effect. Other studies have found mixed results about the importance of dispersal behaviors (Wennergren et al., 1995; South, 1999), suggesting again that the importance of dispersal and connectivity is landscape specific and particularly might be important only in landscapes near a critical threshold in habitat area (King and With, 2002; Bender et al., 2003).

When considering the least-cost path dispersal method, the dispersal cost each land cover type is assigned could have a large effect on the model output. If we increased the dispersal resistance of each non-forest cover type, this would increase the least-cost path distance between patches, and the dispersal method might become a more important factor in the model. Furthermore, there is no reason to assume that the dispersal-cost values we assigned land cover types are even relatively correct. For example, we decided that it was five times more costly to cross developed areas than forested areas but only two times more costly to cross through sparse vegetation (usually agricultural fields) (Table 2). It is possible that the cost of crossing developed areas and sparse vegetation could be equal, or even that crossing sparse vegetation is actually more costly than crossing developed areas. Field studies, such as those by St. Clair (2003), could be used to parameterize these kinds of models more realistically in the future.

4.3. Model parameters

We found that the three sources of parameter error we examined varied considerably in their influence on overall model

uncertainty. Clutch size was the second largest source of uncertainty in our model. Every other factor except the dispersal method had a significant interaction with clutch size, and these interaction effects were most noticeable when generated on the strict habitat map. Interactions between clutch size and other model factors may not be intuitive at first. But consider that increased clutch size can produce more birds on a habitat patch than carrying capacity allows, while a reduced clutch size may result in habitat patches occupied well below carrying capacity. For example, when clutch size is high, a longer dispersal distance would allow juveniles to reach far-away habitat patches and settle down as breeders, but when clutch size is low, birds would tend to remain in their natal patch and the increased dispersal distance would not have as large of an effect.

The large effect of clutch size on model output is logical, since changing the clutch size is the most direct way to alter the number of birds on the landscape. A sensitivity analysis by Pulliam et al. (1992) also found demographic parameters to be more important than dispersal ability, although they found the greatest model sensitivity to survivorship. While survivorship/mortality has been shown to be important in other studies as well (Plissner and Haig, 2000; Wemmer et al., 2001; Letcher et al., 1998), we did not vary this parameter in our analysis because we examined clutch size instead. Since the net recruitment rate is the difference between natality (i.e., clutch size) and mortality, commensurate changes in either of these have the same effect (Urban et al., 1988).

It was surprising that edge effects had the smallest effect on model output in our analysis. This may just be an artifact of our particular landscape, since many of our patches are small and not surrounded by non-forest edge, or of the way that we implemented edge effects. It is also possible that our estimates of nest predation and parasitism rates are low, which could substantially influence results. To determine if this is the case, it would be worthwhile to run additional tests on the sensitivity of this parameter using different landscapes and values for nest predation and parasitism. While ecologists have invested a lot of time and effort into the issue of edge effects, if further tests do not reveal model sensitivity it may be appropriate to focus conservation research onto areas that have a larger impact on population dynamics.

Maximum dispersal distance is the third most important source of error for total number of birds and the fourth most important for percent of carrying capacity occupied. Increasing the maximum dispersal distance increases the total population of birds because it creates a more connected landscape and allows birds to reach patches that are farther away. This is a similar effect to creating the generous map or using the Euclidean dispersal method, although those would all likely show spatial (patch-level) differences if not overall differences in population numbers (or landscapes).

4.4. Intrinsic variability

Intrinsic model variability is probably the most common kind of uncertainty included in spatially explicit population model output. It is clear from this analysis that studies that include only this uncertainty in their confidence intervals are overes-

timating the precision of their models. While this variability has an intermediate effect on model output, that effect seems to interact with other factors in the model. Simulations with the larger clutch size also show a larger range in model output from the intrinsic variability alone, suggesting that the variance increases with the mean.

4.5. Overall uncertainty

Our representation of “total error” (Fig. 8) is not a true estimate of the total uncertainty in the model. On the one hand, we generated this figure by randomly sampling over the full range of cases simulated in model experiments. In fact, we do have some opinion of the relative likelihoods of many aspects of the model, and so could use these expectations to constrain priors used to condition the Monte Carlo simulations. This would reduce the total error in model predictions. On the other hand, in this exercise we have not considered all of the model components and parameters in our model. Furthermore, we might have considered a wider range of alternative models or algorithms (e.g., dispersal models based on correlated random walks). Such considerations would increase the total uncertainty in the model. Indeed, because all models are simplifications of reality, there is perhaps no upper limit to the amount of uncertainty that could be propagated by adding yet one more factor to any model.

In our study, the amount of total model variability is huge relative to the amount of intrinsic model variability, which is typically all that is included in illustrations of model simulations (viz., Fig. 8 versus Fig. 6). Importantly, much of this uncertainty stems from sources that are not typically included in a parametric uncertainty or sensitivity analysis (Haefner, 1996), and these sources propagate and interact through the model. For example, a decision about alternative model formulations or algorithms implies corresponding issues of estimating parameter values. In particular, errors in the underlying habitat map affect the amount and pattern of habitat, and so interact strongly with model components and parameters associated with dispersal. This, in turn, implies that errors in algorithms might have a locational bias or be nonrandom across the study area. To assess this, patch-level analysis is especially important.

4.6. Suggestions and summary

So what is a land manager or conservation practitioner to do when faced with all these uncertainties? Should spatially explicit population models be abandoned all together? We do not advocate such a dramatic approach for most situations, because managers and conservationists may actually have more knowledge about model input than we did in this case study. For example, consider a preserve manager who has been monitoring nest sites for years. In this case, habitat map, clutch size, and edge effects would be well-known for that location, although the dispersal distance and algorithm would likely still be uncertain. However, the uncertainties associated with the dispersal distance and algorithm may be small enough to provide the manager

with confidence in the model output. In situations where it is less obvious which model factors contain the most uncertainty, we would suggest an exploratory approach be used (as we have shown here) to identify the factors with the largest effect on model output. Data collection efforts can then be focused on the factors that will reduce model uncertainty the most.

Patch-level analysis can also be helpful when using a spatially explicit population model to make conservation decisions. As Fig. 9 illustrates, individual patch dynamics are unequally affected by changes in model input. When there is uncertainty in an important parameter and decisions must be made about the conservation value of habitat patches, it is useful to map the results spatially and locate patches that retain their good quality regardless of model input (i.e., patches that are insensitive to model input). The patch-level approach can also be used to refine a spatially explicit population model and develop better parameter estimates. For example, returning to Fig. 9, in order to determine whether or not the maximum dispersal distance of the wood thrush was closer to 1500 or 3000 m, it would be possible to go out to the field and look for wood thrushes in the patches that are empty (white) in the map of 1500 m dispersal but not in the map of 3000 m dispersal. If wood thrushes were found in those patches, it might be reasonable to conclude that their maximum dispersal distance was closer to 3000 than 1500 m. Similarly, a map of model discrepancies arising from varying some other factor in the model would provide a facile tool for isolating locations where these factors could be studied effectively in the field.

In summary, we examined the effects of multiple kinds of model error on the output of our spatially explicit population model, and also took a spatially explicit look at the sensitivity of one of these sources of error. Each factor that we varied had a significant effect on our model output and most had significant interactions with the other factors as well. We chose to test the sensitivity of factors that we felt were most uncertain, but given infinite time and resources it would be possible to include countless other sources of uncertainty in the analysis. While our results suggest that model uncertainty can be reduced by developing better estimates of habitat map and clutch size, it is important to recognize that these results are specific to the landscape and focal species that we used. Spatially explicit population models simulated on landscapes with more habitat or different spatial configuration might differ greatly in their ranking of important factors to model uncertainty (King and With, 2002; Bender et al., 2003). Our analysis provides an estimate of the large amount of uncertainty that goes into and comes out of most spatially explicit population models, and it is important to note that much of this uncertainty is usually unaccounted in spatially explicit population model predictions. While the results we present here are specific to our particular landscape and focal species, it is probable that the habitat map will be of utmost importance to model output in other landscapes with sparse habitat. This is especially significant because few, if any, published studies include the effect of this uncertainty in spatially explicit population model output. Fortunately, more realistic model predictions can easily be produced by using the methods presented here.

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