Ecography 34: 001–009, 2011
doi: 10.1111/j.1600-0587.2011.06936.x

Subject Editor: Michel Baguette. Accepted 8 July 2011

The relative contribution of local habitat and landscape context to metapopulation processes: a dynamic occupancy modeling approach

Sarah J. K. Frey, Allan M. Strong and Kent P. McFarland

S. J. K. Frey (sarah.frey@oregonstate.edu), Dept of Forest Ecosystems and Society, Oregon State Univ., Corvallis, OR 97331, USA. – A. M. Strong, Rubenstein School of Environment and Natural Resources, Univ. of Vermont, Burlington, VT 05405, USA. – K. P. McFarland, Vermont Center for Ecostudies, PO Box 420, Norwich, VT 05055, USA.

Changes in site occupancy across habitat patches have often been attributed to landscape features in fragmented systems, particularly when considering metapopulations. However, failure to include habitat quality of individual patches can mask the relative importance of local scale features in determining distributional changes. We employed dynamic occupancy modeling to compare the strength of local habitat variables and metrics of landscape patterns as drivers of metapopulation dynamics for a vulnerable, high-elevation species in a naturally fragmented landscape. Repeat surveys of Bicknell's thrush *Catharus bicknelli* presence/non-detection were conducted at 88 sites across Vermont, USA in 2006 and 2007. We used an organism-based approach, such that at each site we measured important local-scale habitat characteristics and quantified landscape-scale features using a predictive habitat model for this species. We performed a principal component analysis on both the local and landscape features to reduce dimensionality. We estimated site occupancy, colonization, and extinction probabilities while accounting for imperfect detection. Univariate, additive, and interaction models of local habitat and landscape context were ranked using AICc scores. Both local and landscape scales were important in determining changes in occupancy patterns. An interaction between scales was detected for occupancy dynamics indicating that the relationship of the parameters to local-scale habitat conditions can change depending on the landscape context and vice versa. An increase in both landscape- and local-scale habitat quality increased occupancy and colonization probability while decreasing extinction risk. Colonization and extinction were both more strongly influenced by local habitat quality relative to landscape patterns. We also identified clear, qualitative thresholds for landscape-scale features. Conservation of large habitat patches in high-cover landscapes will help ensure persistence of Bicknell's thrushes, but only if local scale habitat quality is maintained. Our results highlight the importance of incorporating information beyond landscape characteristics when investigating patch occupancy patterns in metapopulations.

Understanding distributional patterns of organisms in space and time is a fundamental question in ecology. Variations in species occurrence patterns can elucidate drivers of important population processes such as site occupancy, colonization, and local extinction (Gaston 1990). By linking these processes to environmental features we can begin to understand the ecological factors that motivate habitat selection and drive changes in species distributions. Landscape structure (MacArthur and Wilson 1967, Hanski 1998) and composition (With et al. 1997), local patch characteristics (Mortelliti et al. 2010), and species' dispersal capabilities (Thomas 2000) have all been implicated as important drivers of distribution dynamics.

Incorporation of spatial structure into population dynamics is a central concept of metapopulation models (Hanski 1998). A metapopulation is defined as a network of sub-populations that are linked by migration. Changes in occupancy state, through subpopulation extinction and colonization, depends on the size and isolation of the habitat patch (Hanski 1998). However, most landscape studies only consider features at the landscape-scale (i.e. patch size and isolation), while ignoring local habitat quality within patches (Mortelliti et al. 2010). This can be an oversimplification (Hastings and Harrison 1994), especially in heterogeneous ecosystems where distributions are likely driven by factors at multiple scales. There is increasing evidence that this variation in local habitat quality is an important factor in population dynamics and should be incorporated into metapopulation models (Thomas et al. 2001, Fleishman et al. 2002, Armstrong 2005), however, there have been few empirical tests (Mortelliti et al. 2010). Further, investigations of the influence of landscape structure on metapopulation processes are generally conducted in anthropogenically fragmented forest surrounded by an agricultural matrix (Opdam 1991), as opposed to naturally fragmented systems.

Dynamic (or multi-season) occupancy models (MacKenzie et al. 2003) can be used to assess distributional patterns at a variety of scales. Dynamic occupancy models allow estimation of the probability that a site will be occupied, as well as colonization and extinction probabilities. Occupancy modeling can be used to address an array of questions about distributional patterns through inclusion of survey- and site-specific covariates to calculate unbiased colonization and extinction rates through the incorporation of detection probabilities (MacKenzie et al. 2003). Including detection probabilities into dynamic occupancy models avoids issues associated with false absences thought to be the largest source of bias in traditional approaches to the estimation of metapopulation parameters (Moilanen 2002).

Species with spatially isolated subpopulations, especially those that occupy naturally restricted ranges, are well suited for this type of approach (Hanski 1998). Bicknell's thrush *Catharus bicknelli* is a montane fir-forest specialist that inhabits a naturally fragmented breeding range in the northeastern United States, southeastern Québec, and Maritime Canada (Rimmer et al. 2001, Lambert et al. 2005). It occupies ephemeral, disturbance-driven, mid-successional, fir-dominated forests within montane or highland regions. Bicknell's thrush is ranked as a top conservation priority among Nearctic-Neotropical migrants in the northeast (Rich et al. 2004) with a global status of vulnerable (BirdLife International 2000). A habitat model for Bicknell's thrush (Lambert et al. 2005) allowed us to define landscape elements from a species-specific perspective (Betts et al. 2006).

Here we used dynamic occupancy modeling (MacKenzie et al. 2003) and Akaike's information criterion (AIC) model selection techniques (Burnham and Anderson 2002) to test the relative importance of local-scale habitat characteristics versus landscape-scale features in determining Bicknell's thrush site occupancy patterns over time. We used this analysis to assess metapopulation processes within an existing potential habitat model (Lambert et al. 2005) in Vermont and determine how metapopulation processes relate to habitat features at multiple scales.

Methods

Field surveys

Detection/non-detection data were collected over a two-year period from 2006 to 2007 within the Bicknell's thrush breeding range across the state of Vermont, USA. We focused on the metapopulation of the Green and Taconic Mountains, and Northeastern Highlands of Vermont, where sub-populations were defined by high-elevation habitat islands delineated using an existing habitat model for this species (Lambert et al. 2005). A total of 88 sites between 733 and 1236 m elevation were surveyed (Fig. 1). Twenty-nine sites (hereafter, SF sites) were added to 59 sites surveyed in Vermont through a citizen-science program called Mountain Birdwatch (MBW, Hart and Lambert 2007). Each site consisted of a 1-km transect of five points separated by 200–250 m (seven sites contained 3–4 points due to patch size constraints). Bird sample locations covered a rectangular area of roughly ~25 ha (1 km by ~250 m), which approximates the size of five to 10 Bicknell's thrush breeding home ranges (2.33–4.53 ha, Rimmer et al. 2001).

MBW sites were selected through random selection of high-elevation forests (montane areas > 823 m, Hart and Lambert 2007). SF sites were chosen from the remaining un-surveyed MBW sites in Vermont and filled gaps in MBW sampling by surveying marginal habitat and sites without hiking trails. The 1-km transects were fit into the habitat polygons defined by Lambert et al. (2005), following a straight line wherever possible, often along ridgelines.

Surveys were conducted during the peak of the breeding season (late May–mid-July) at optimal activity times (dawn and dusk) under favorable weather conditions. A maximum of three surveys were conducted at each site each year (mean ± SD = 2.1 ± 0.9) with slight differences between MBW and SF sites (see following two paragraphs for details). In the MBW survey protocol, the first survey period occurred between 04:30 and 06:30 h EST and consisted of a 10-min point count at each point along the transect. If no Bicknell's thrush were detected during the first survey period, up to two additional surveys were conducted to increase opportunity for detection. The second survey period directly followed the first survey and consisted of a 1-min playback of Bicknell's thrush songs and calls followed by a 2-min silent listening period at each point. If no Bicknell's thrush were detected on either the first or second surveys, a third survey was conducted within two weeks following the initial surveys (or before 15 July). The third survey occurred between either 04:30 and 06:30 h or 20:00 and 21:00 h and was done by broadcasting the 1-min playback and listening for 2 min every 100 m along the transect.

For SF sites, the three surveys were almost always conducted during a single visit to the site, weather permitting. This was achieved by conducting an evening survey followed by two morning surveys. During the evening survey a 5-min point count was conducted followed by broadcasting a 1-min playback and a 2-min listening period. Both morning surveys followed the same protocol as MBW. Detections were categorized as within or outside a 50-m radius around the survey point, although all observations were counted assuming an approximate detection limit of 125 m. For each survey at a given site (MBW and SF), either 1 (detection) or 0 (non-detection) was recorded based on whether a Bicknell's thrush was heard or seen anywhere along the transect. We tested for an effect of survey technique on detection probability during the modeling process and found little support for survey type to influence detection probability (Table 1).

Local-scale habitat measurements

Local habitat conditions were quantified once in either 2006 or 2007 and were assumed to be constant within this time period. Because within-site variation was negligible, local habitat measurements were averaged across all points to obtain a single site value. We measured site variables representative of habitat quality for Bicknell's thrush based on the species' natural history (Table 2, Rimmer et al. 2001), assuming these variables are linked to resource availability (Strong et al. 2004). To quantify coniferous shrub density at each point, we used the point-centered quarter method (Cottam and Curtis 1956). We measured basal area of snags (using a wedge prism), as snags are a useful structural indicator of the two main causes of natural disturbance in montane ecosystems in the northeastern US: severe weather and fir waves (Sprugel 1976), both of which result in areas of forest

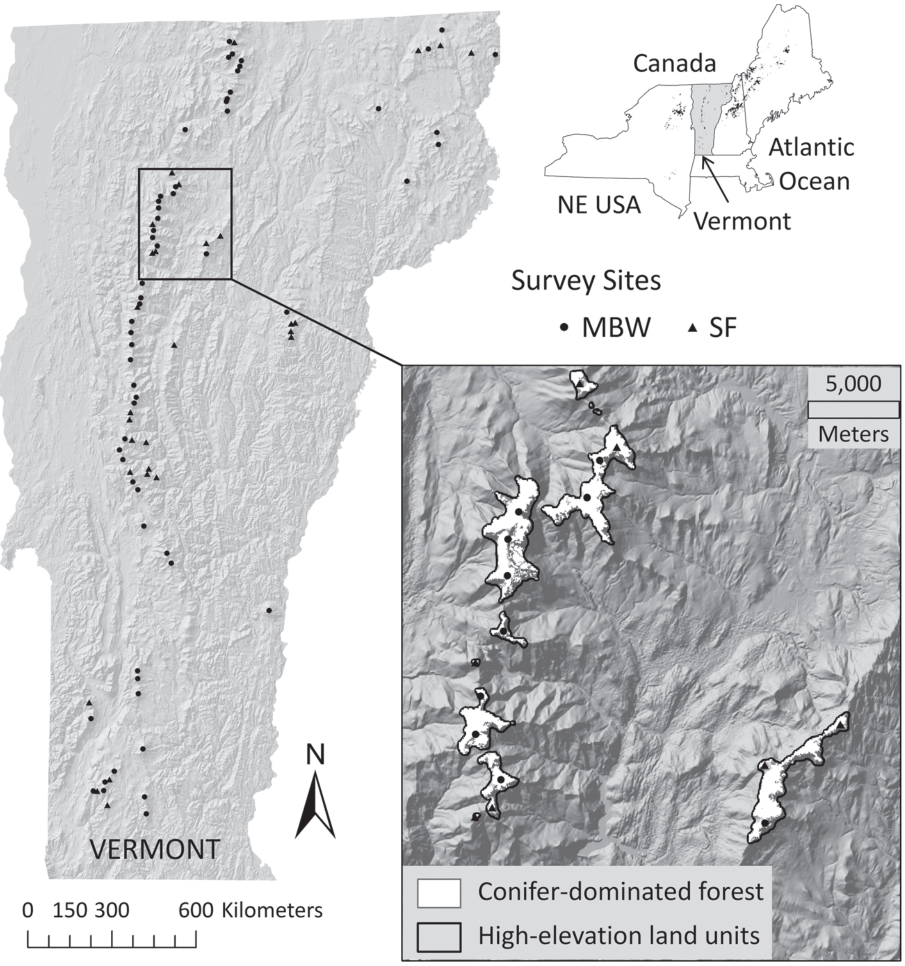

Figure 1. Area of study and survey sites in Vermont located within a Bicknell's thrush predicted habitat model (Lambert et al. 2005). Suitable habitat was identified as conifer-dominated forest (white pixels) within high elevation land units (outlined in black) delineated by an elevational-latitudinal threshold.

regeneration. Bicknell's thrush tend to select dense regenerating patches for nesting sites (Rimmer et al. 2001). Canopy species composition was classified as coniferous, deciduous, or mixed to determine the proportion of conifer-dominated points along the transect. Average canopy height (m) was also measured at each point.

Table 1. AICc model selection results for detection probability (p). Each model is ranked by its AICc score, which represents how well the model fit the data. A lower ΔAICc value is indicative of a better model. The probability that the model (of the models tested) would best explain the data is indicated by the AICc weight (ω_i). K is the number of parameters each model estimates. Initial occupancy (ψ), colonization (γ), and local extinction (ε) probabilities are constant in all models.

Model	AICc	ΔAICc	ω_i	K
$\psi \times \gamma \times \varepsilon \times p$ (survey + ps)	362.19	0	0.77	7
$\psi \times \gamma \times \varepsilon \times p$ (survey)	366.92	4.73	0.07	6
$\psi \times \gamma \times \varepsilon \times p$ (ps)	367.58	5.39	0.05	5
$\psi \times \gamma \times \varepsilon \times p$ (type)	367.93	5.74	0.04	6
$\psi \times \gamma \times \varepsilon \times p$ (playback)	368.02	5.83	0.04	5
$\psi \times \gamma \times \varepsilon \times p$ (morning v. evening)	370.88	8.69	0.01	5
$\psi \times \gamma \times \varepsilon \times p$ (time)	371.64	9.45	0.01	5
$\psi \times \gamma \times \varepsilon \times p$	372.16	9.98	0.01	4
$\psi \times \gamma \times \varepsilon \times p$ (date)	374.28	12.09	0.00	5

ps = patch size, survey = survey number (1–3), type = survey type.

Due to the complexity inherent in incorporating four local habitat covariates (Table 2) in the modeling process, we collapsed them into a single variable using a principal component analysis. We used principal component one (PC1) in the analysis. This value was termed local in the modeling process and is the sum of the products of each variable's factor coefficient and standardized value.

Landscape features

Landscape features were quantified using GIS software (ESRI 2005). Lambert et al. (2005) created a habitat model for Bicknell's thrush by delineating high-elevation land units with an elevational-latitudinal threshold based on breeding season presence-absence data. Within this range, conifer-dominated forest (based on forest composition from National Land Cover Data [Vogelmann et al. 2001]) was considered potential habitat (Fig. 1). We included two of the most common metrics of landscape structure that captured both landscape configuration and composition of Bicknell's thrush habitat (Table 2). We defined patch size as the total area of conifer-dominated forest (30 × 30 m pixels) within a

Table 2. Local- and landscape-scale habitat variables used in this study. The factor coefficients for each variable are listed for principal component one (PC1) for the local and landscape variables. The proportion of variance explained by PC1 for each scale is shown in parentheses. Sites scoring high for local were conifer-dominated, had a high coniferous shrub density, greater basal area of dead trees, and shorter canopies. Low local scores were associated with open understories, more deciduous vegetation, and taller canopies. Sites with high landscape scores were located within larger patches surrounded by higher amounts of habitat (conifer-dominated forest). A low landscape score represents a site situated in a small patch in a low-cover landscape.

Variable	PC1 factor coefficient
Local (0.51)	
Coniferous shrub density (stems m^{-2})	0.500
Dead basal area (m^{2} ha^{-1})	0.400
Proportion of coniferous dominated forest points along the transect	0.614
Average canopy height (m)	−0.462
Landscape (0.82)	
Patch size (ha)	0.511
Amount of habitat within 2 km (ha)	0.500
Amount of habitat within 5 km (ha)	0.531
Amount of habitat within 10 km (ha)	0.456

given high-elevation land unit and used this as our measure of configuration (Betts et al. 2006). For landscape composition, we used patch isolation measured as the amount of potential habitat surrounding the survey point (Fahrig 2003) at three spatial extents (2-, 5-, and 10-km radii). While habitat amount is not a direct measure of connectivity, such as distance to nearest patch, habitat isolation is thought to be best predicted by amount of surrounding habitat, which is also more meaningful for conservation (Fahrig 2003). To create one variable that captured the landscape-scale features around each site (hereafter termed landscape) we used PC1 from a second principal component analysis of the four landscape-scale variables (as described above for local).

Dynamic occupancy modeling and parameter estimation

Site encounter histories were created by compiling detections (1) and non-detections (0) from surveys conducted in 2006 and 2007. Missed surveys were not used in parameter estimation (MacKenzie et al. 2003). Model input consisted of encounter histories and the two covariates describing local and landscape habitat characteristics.

A multi-season dynamic occupancy model framework was used following MacKenzie et al. (2003). The dynamic model estimates four parameters: 1) probability of detection (p), 2) probability of initial site occupancy (ψ), 3) probability of site colonization (γ), and 4) probability of local site extinction (ε). Sites that were vacant in year t could become colonized in year t + 1 or remain vacant. Sites that were occupied in year t could become locally extinct in year t + 1 or remain occupied.

Dynamic occupancy models incorporate primary and secondary time periods. In this study, the primary sampling period was defined as a Bicknell's thrush breeding season. Between primary sampling periods movement could occur in and out of the populations causing local extinction or colonization events. This determined the occupancy status of a site the following year. Within a primary sampling period are surveys, or secondary sampling periods. Between surveys (or within a season), the population is assumed to be closed. Two additional assumptions are no false detections and detections at one site are independent of another (MacKenzie et al. 2003). These assumptions are reasonable for this species as adults display high breeding site fidelity (Rimmer et al. 2001), Bicknell's thrushes are easily identified by sound (majority of detections), and sampling locations were spaced a minimum of 8 km apart.

We conducted the modeling analyses using the program Presence (Hines 2006). Covariates relating to site-specific characteristics, at the local and landscape scale, were included to test the strength of their relationship to probability of initial site occupancy (ψ), colonization (γ), and extinction (ε). Although not the primary parameter of interest, detection probability (p) was included to correct for imperfect detection. We tested for the effect of survey type, number (first, second, or third), time, date, and patch size on detection probability. Maximum likelihood techniques were used to estimate the four parameters (p, ψ, γ, and ε) based on site detection histories with the following likelihood equation (MacKenzie et al. 2003):

$$L\left(\psi_1, \varepsilon, \gamma, p \middle| X_1, \ldots X_n\right) = \prod_{i=1}^{N} \Pr(X_i)$$

Here, ψ_1 refers to the initial occupancy in the first primary period, where thereafter ε and γ determine occupancy in the following seasons. This is a Marcovian process in which occupancy in a particular time step depends on occupancy in the previous time step. X_i are the data in the form of detection histories.

A total of 66 models were compared using AIC model selection procedures (Burnham and Anderson 2002). The models consisted of all possible combinations of 1) local, 2) landscape, 3) local + landscape, and 4) local × landscape for occupancy, colonization, and extinction. Models were ranked based on their AICc score (a small sample size adjustment of AIC) and models with ΔAICc of ≤ 2 were considered plausible. A test for model goodness-of-fit was not performed because no such test exists for dynamic occupancy models or models that have missing surveys (D. MacKenzie pers. comm.). We calculated relative variable importance for 1) landscape, 2) local, 3) landscape + local, and 4) landscape × local for occupancy, colonization, and extinction by summing the weights (AICcω_i) of the models in which they appeared for the particular parameter in question (Burnham and Anderson 2002).

Results

We found both landscape context and local habitat quality to be important in determining Bicknell's thrush occupancy patterns with both being included in the top eight most plausible models (Table 3). The additive relationship of landscape and local was the most supported model and had the highest relative importance for all population parameters (Table 3, Fig. 2). Landscape-scale characteristics alone had little support (Table 3, Fig. 2). We detected a cross-scale interaction and potential thresholds for both local and landscape variables (see Thresholds below).

Table 3. AICc model selection results for determining the effects of landscape and local-scale habitat covariates on initial occupancy (ψ), colonization (γ), and local extinction (ε). K is the number of parameters estimated in the model. Each model is ranked by its AICc score, which represents how well the model fit the data. A lower ΔAICc value is indicative of a better model. Only models within 2 AICc points of the top model were considered plausible and are displayed. The probability that the model (of the models tested) would best explain the data is indicated by the AICc weight (ω_i).

Model	AICc	Δ AICc	ω_i	K
ψ (local + landscape) γ (local + landscape) ε (local + landscape) p (survey + ps)	297.17	0	0.14	13
ψ (local × landscape) γ (local + landscape) ε (local + landscape) p (survey + ps)	297.72	0.55	0.11	14
ψ (local + landscape) γ (local + landscape) ε (local) p (survey + ps)	298.06	0.89	0.09	12
ψ (local + landscape) γ (local) ε (local + landscape) p (survey + ps)	298.40	1.23	0.08	12
ψ (local × landscape) γ (local + landscape) ε (local) p (survey + ps)	298.53	1.36	0.07	13
ψ (local + landscape) γ (local + landscape) ε (local × landscape) p (survey + ps)	298.55	1.38	0.07	14
ψ (local + landscape) γ (local × landscape) ε (local + landscape) p (survey + ps)	299.14	1.97	0.05	14
ψ (local × landscape) γ (local + landscape) ε (local × landscape) p (survey + ps)	299.17	2.00	0.05	15

Occupancy

There was strong support for occupancy probability to be driven by an interaction between scales. Specifically, if a site contained moderate quality local habitat, an ideal landscape context was necessary (i.e. large patches within high-cover landscapes, Fig. 3a) for it to be occupied. Conversely, a site situated in a poor landscape context (i.e. small patches within low-cover landscapes) would only be occupied if the local habitat quality was high (Fig. 3b). The average site occupancy probability (± 1SD) was 0.58 (± 0.31) in 2006 and 0.61 (± 0.38) in 2007 based on estimates from the top model (2007 occupancy estimate was calculated using Eq. 7 in MacKenzie et al. 2003).

Colonization and extinction

Local and landscape covariates were both important drivers of site colonization and extinction (Table 3). However, the effect of local-scale habitat was stronger relative to landscape structure in driving changes in patch occupancy (Table 4, Fig. 4). Both landscape- and local-scale habitat features positively influenced colonization and had negative effects on extinction (Fig. 4, Table 4). Compared to occupancy and colonization, the influence both of landscape- and local-scale habitat features on extinction was greater (Table 4). This resulted in a narrow range of covariate values in which extinction went from zero to one (Fig. 4c–d). Average colonization and extinction probabilities (± 1SD) across all sites were 0.52 (± 0.4) and 0.27 (± 0.33), respectively. Note the difference in rates compared to those based on the raw detections (see Raw occurrences below) not accounting for variation in detection probability (i.e. assuming $p = 1$).

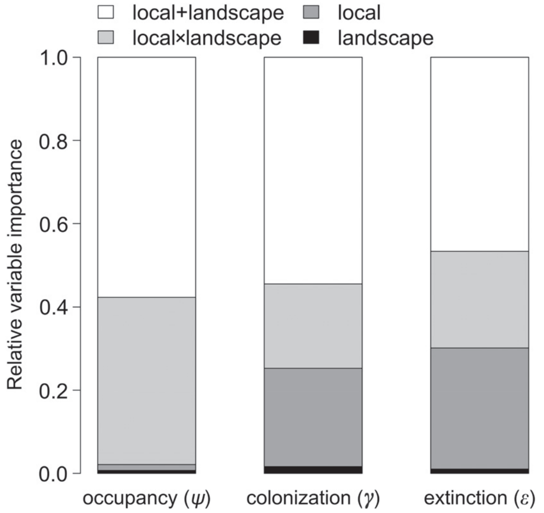

Figure 2. Relative variable importance (determined by summing the AICc ω_i for the models in which each covariate was present) for 1) local + landscape, 2) local × landscape, 3) local, and 4) landscape by parameter (probability of initial occupancy, site colonization and local site extinction).

Thresholds

All parameters, (with the exception of occupancy for local), indicated a potential threshold value beyond which an increase in local or landscape quality did not translate to an increased probability of a site becoming or remaining occupied (Fig. 3, 4). Although we did not explicitly test for threshold values, there are clear qualitative delineations seen in the relationships between the parameters and the individual landscape-scale variables (Supplementary material Appendix 1–3). Occupancy and colonization probabilities are ~1.0 and extinction rates are essentially 0 when patch size approaches ~600 ha. When the proportion of suitable habitat in the surrounding landscape within 2 km reaches 0.35 (and reaches 0.10 within 5 km) occupancy and colonization rates are ~1.0. Extinction probability drops to 0 when the proportion of habitat reaches 0.25 and 0.08 within 2 and 5 km, respectively.

Detection probability

Detection probability (p) was best explained by survey number and patch size (Table 1). Probability of detection decreased with increasing number of surveys and increased with patch size. Patch size had an equal positive effect on detection probability across all surveys (Table 4). In the first two surveys, usually done during the same visit to the site, detection probability varied little (0.77 to 0.95) and in large patches (> 850 ha), probability of detection was > 0.75,

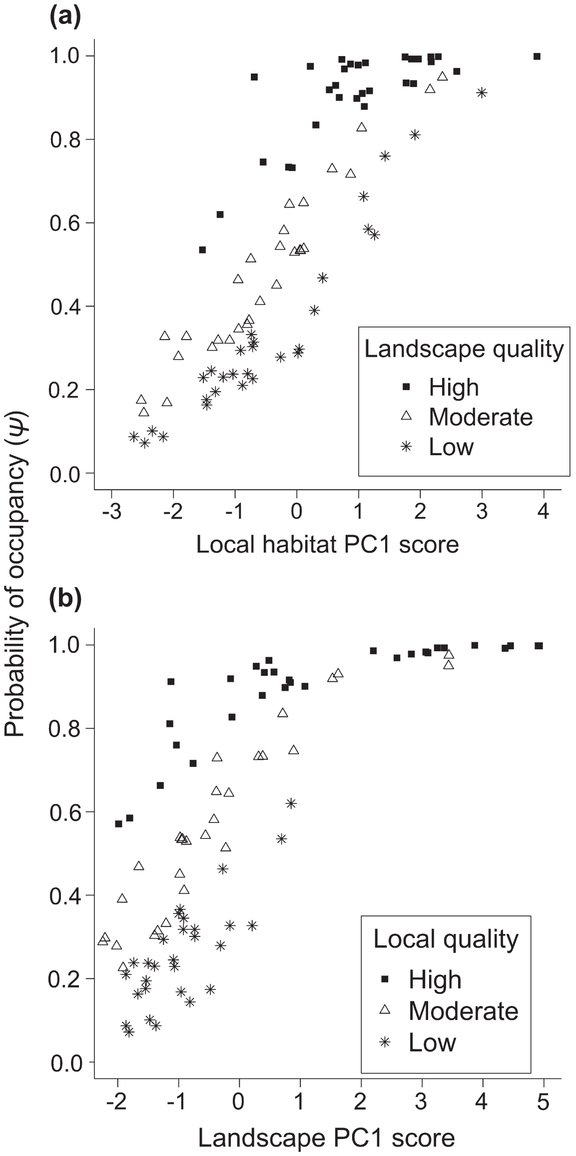

Figure 3. Estimated probability of initial site occupancy (adjusted for imperfect detection) as a function of (a) local habitat PC1 score and (b) landscape PC1 score at each site from the top ranked model: ψ (local + landscape) γ (local + landscape) ε (local + landscape) p (survey + ps). Parameter estimates were categorized as low, moderate, and high quality landscape context (a) or local habitat quality (b) to facilitate visualization of the interaction between the local and landscape scales in determining site occupancy by Bicknell's thrush in Vermont. Quality categories for both local and landscape were delineated by dividing the data range into thirds. This figure shows that in order for a site with moderate quality local habitat to be occupied, the landscape context must be ideal (i.e. large patches within high-cover landscapes). On the other hand, for sites located in poor landscape contexts to be occupied, they must contain very high quality local habitat.

regardless of the survey number. The third survey was generally done either at a later date in the breeding season or later in the morning (after an earlier survey), which may explain the lower detection probability. Essentially, if a Bicknell's thrush occupied a site, the chances of detecting it on the first survey were 83% or greater, regardless of patch size.

Table 4. Parameter estimates (β) and 95% confidence intervals (lower = LCI and upper = UCI) for probability of initial site occupancy (ψ), site colonization (γ), local site extinction (ε) and detection probability (p) for the most supported model (ψ (local + landscape) γ (local + landscape) ε (local + landscape) p (survey + ps)). Bicknell's thrush occupancy patterns were estimated as a function of local habitat and landscape context. Detection probability was modeled as a function of survey number and patch size.

Variable	β	LCI	UCI
ψ intercept	0.822	0.057	1.587
local	0.797	0.270	1.324
landscape	0.776	0.164	1.388
γ intercept	0.798	−1.289	2.885
local	1.693	0.322	3.063
landscape	1.057	−0.270	2.385
ε intercept	−3.519	−6.307	−0.732
local	−1.979	−3.791	−0.167
landscape	−1.440	−3.345	0.465
p intercept survey 1	1.874	1.234	2.514
intercept survey 2	1.459	0.733	2.185
intercept survey 3	0.177	−0.618	0.972
patch size	0.375	−0.131	0.880

Raw occurrences and principal components analyses

Bicknell's thrush overall patch occupancy remained relatively consistent during the study period. Based on raw detection data, 28 sites remained vacant (31.8%) and 38 remained occupied (43.2%), whereas nine sites were colonized (raw colonization rate = 24.3%) and six sites showed local extinction (raw extinction rate = 13.6%) between years (Fig. 5). Landscape and local habitat scores were generally higher for sites that remained occupied or became colonized than those that stayed vacant or went extinct (Fig. 5).

Discussion

We found differential site occupancy by Bicknell's thrush due to an interaction between local and landscape scales. A site with high-quality local habitat could be occupied even if the landscape context was marginal (i.e. smaller patch and/or low-cover landscape), suggesting that local site characteristics can compensate for poor landscape context. Similarly, if local habitat quality is low, it may be necessary for the site to be in a large patch and/or surrounded by a high proportion of suitable habitat to be occupied. There is some evidence that these cross-scale interactions may be common in birds (Betts et al. 2006, Renfrew and Ribic 2008) and perhaps in other taxa. A similar study in a naturally fragmented wetland system (Schooley and Branch 2007) identified cross-scale interactions between patch size, spatial connectivity, and wetland quality as determinants of patch occupancy of round-tailed muskrats *Neofiber alleni*.

We found little support for effects of landscape-scale features in driving metapopulation processes independent of local habitat quality; both local habitat characteristics and landscape-scale features played important roles in explaining Bicknell's thrush occupancy patterns in Vermont. In our system, local habitat is of equal or greater importance than landscape patterns for colonization and extinction rates.

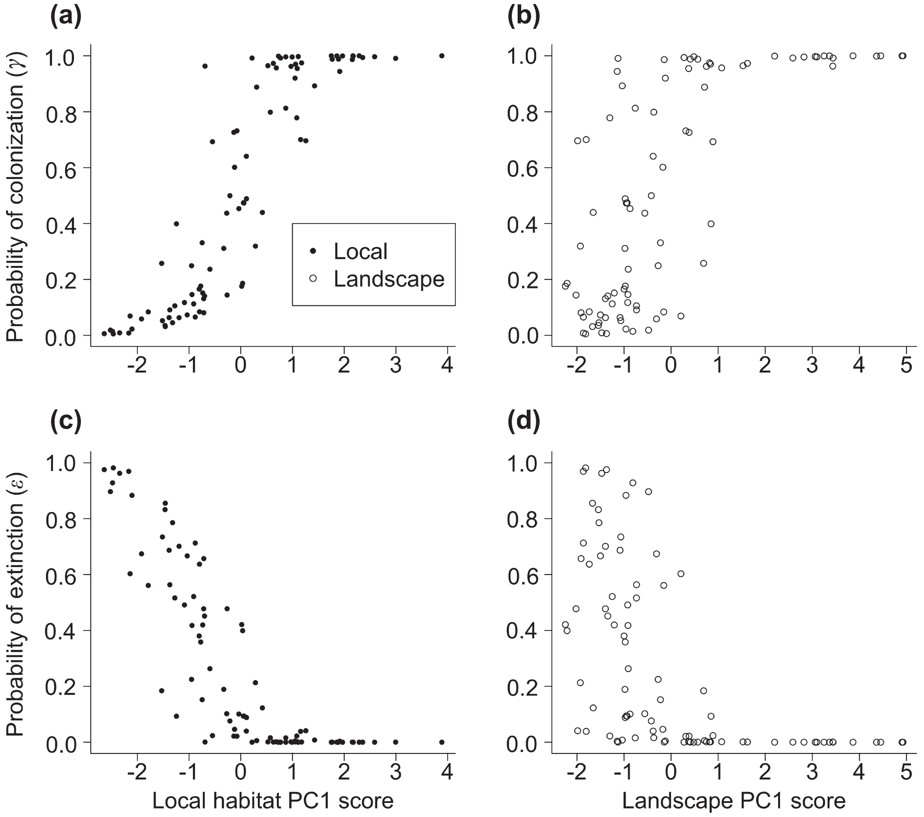

Figure 4. Predicted probability of site colonization (a and b) and local extinction (c and d) as a function of a site's local habitat PC1 score (a and c, filled circles) and landscape PC1 score (b and d, open circles) for Bicknell's thrush in Vermont. All estimates were derived from the top ranked model (ψ (local + landscape) γ (local + landscape) ε (local + landscape) p (survey + ps)) and were adjusted for imperfect detection.

Patch size and habitat amount play a key role in changes in patch occupancy, but persistence at a site requires that the proper local habitat conditions exist. These results suggest that local and landscape scales act together to influence occupancy patterns and motivate habitat selection for this vulnerable species.

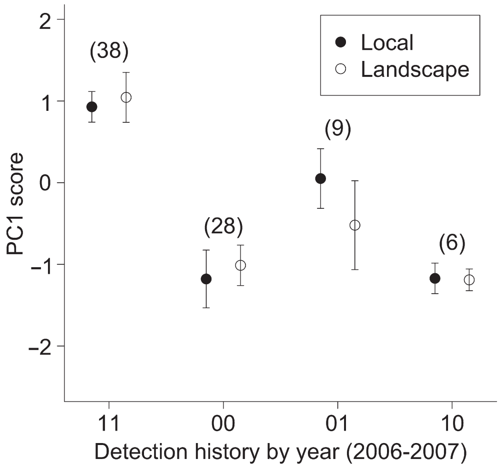

Figure 5. Comparison of means (± 1 SE) for local and landscape principal component one (PC1) scores for sites that remained occupied (11), remained vacant (00), were colonized (01), or went extinct (10) during the 2006 and 2007 Bicknell's thrush breeding seasons. Sample sizes are displayed in brackets above mean values for each detection history. The landscape and local habitat PC1 scores were significantly, positively correlated ($r = 0.51$, $p < 0.001$). However, we considered this correlation to be moderate and therefore acceptable (Ott and Longnecker 2001) for including both in the model set to test for effects of scale and to explore interactions.

Theoretical work states that landscape structure is of primary importance in driving metapopulation dynamics in patchy environments (MacArthur and Wilson 1967, Hanski and Ovaskainen 2003), although it has also been suggested that habitat quality of a patch likely influences extinction probability through birth and death rates of a subpopulation (Opdam 1991). However, incorporating local habitat quality does not always improve model fit (Moilanen and Hanski 1998) and landscape features may be more important in some systems (Vogeli et al. 2010). Our study contributes to the growing body of literature highlighting the importance of incorporating both the local patch scale and landscape context when modeling species distributions (Mortelliti et al. 2010). Collectively, both local and landscape scales have been found to be important in metapopulation dynamics for a variety of taxa including insects (Thomas et al. 2001), mammals (Schooley and Branch 2009), and birds (Verboom et al. 1991).

Identifying thresholds in landscape context at which immigration rates are no longer sufficient to maintain connectivity is useful when making conservation decisions. From a landscape perspective, Bicknell's thrush appears to be able to persist in landscapes with relatively low proportions of suitable habitat (0.10–0.35), depending on landscape extent. These findings are similar to thresholds determined for songbirds in anthropogenically-fragmented landscapes

(Andren 1994, Betts et al. 2007). Thresholds in local habitat conditions (Guenette and Villard 2005) also likely exist for Bicknell's thrush (Fig. 4, 5).

Many studies assessing the effect of forest patch size and isolation on bird population processes have been conducted within predominantly human-modified landscapes (Andren 1994, Prugh et al. 2008). In these landscapes, connectivity may be much more significant for population persistence or occupancy of small patches (Donovan et al. 1995) because species that occupy these areas have been recently separated by habitat fragmentation and may not have the capabilities to move between fragmented habitat patches or persist in small fragments. It is possible that the degree of patch isolation may be less important to birds with strong dispersal capabilities (With et al. 2006) and naturally fragmented ranges such as the Bicknell's thrush (Rimmer et al. 2001). Consequently, this may explain why our results show that landscape context is less important than local habitat quality for colonization and extinction dynamics for this species.

To ensure persistence of Bicknell's thrush, our results indicate that it is imperative that local-scale habitat characteristics are considered in addition to landscape context. Small, isolated patches are only likely to be occupied when they contain optimal local conditions, while large, connected patches without sufficient local habitat quality may be unsuitable.

Dynamic occupancy modeling provides an effective approach to incorporate the quality of both local habitat and landscape features into metapopulation dynamics for species with populations in heterogeneous environments. These methods provide unbiased estimates of colonization and extinction rates through the incorporation of detection probabilities. Simple detection/non-detection information can be easily gathered over large spatial scales making this an efficient and useful method for assessing distributional changes with respect to land use or climate change. For example, Mustin et al. (2009) showed through simulation that patch colonization and extinction rates influenced the rate at which populations shift their ranges in order to track changes in climate. Our study also points out that range changes are unlikely to be constant throughout the range due to uneven colonization and extinction rates across gradients, such as in habitat quality or landscape pattern. Information regarding the responses of species to factors at multiple scales is useful for parameterizing dynamic models aimed at predicting a species response to environmental change (Midgley et al. 2010) and will likely result in more accurate predictions of distributional changes.

Acknowledgements – We are grateful to the Mountain Birdwatch coordinators, J. Hart and D. Lambert, and all of the MBW volunteers who headed to the mountains in their free time to survey for Bicknell's thrush. We highly appreciate field assistance provided by J. Juillerat, H. Slongo, J. Klavins, and K. Pindell and recognize the demanding nature of the work. A. S. Hadley provided insightful and thoughtful comments that greatly improved this manuscript. Financial support was provided by a grant from the USDA Forest Service McIntire-Stennis Cooperative Forestry Research Program.

References

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. – Oikos 71: 355–366.

Armstrong, D. P. 2005. Integrating the metapopulation and habitat paradigms for understanding broad-scale declines of species. – Conserv. Biol. 19: 1402–1410.

Betts, M. G. et al. 2006. Independent effects of fragmentation on forest songbirds: an organism-based approach. – Ecol. Appl. 16: 1076–1089.

Betts, M. G. et al. 2007. Thresholds in songbird occurrence in relation to landscape structure. – Conserv. Biol. 21: 1046–1058.

BirdLife International 2000. Threatened birds of the world. – Cambridge and Lynx Editcions.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. – Springer.

Cottam, G. and Curtis, J. 1956. The use of distance measures in phytosociological sampling. – Ecology 37: 451–460.

Donovan, T. et al. 1995. Reproductive success of migratory birds in habitat sources and sinks. – Conserv. Biol. 9: 1380–1395.

ESRI 2005. ArcGIS, ver. 9.1. – Environmental Systems Research Inst., Redlands, CA.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. – Annu. Rev. Ecol. Evol. Syst. 34: 487–515.

Fleishman, E. et al. 2002. Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. – Conserv. Biol. 16: 706–716.

Gaston, K. J. 1990. Patterns in geographical ranges in species. – Biol. Rev. Camb. Philos. Soc. 65: 105–129.

Guenette, J. S. and Villard, M. A. 2005. Thresholds in forest bird response to habitat alteration as quantitative targets for conservation. – Conserv. Biol. 19: 1168–1180.

Hanski, I. 1998. Metapopulation dynamics. – Nature 396: 41–49.

Hanski, K. and Ovaskainen, O. 2003. Metapopulation theory for fragmented landscapes. – Theor. Popul. Biol. 64: 119–127.

Hart, J. A. and Lambert, J. D. 2007. Mountian birdwatch 2006: final report to the US Fish and Wildlife Service. – Vermont Inst. of Natural Science Technical Report 07-03.

Hastings, A. and Harrison, S. 1994. Metapopulation dynamics and genetics. – Annu. Rev. Ecol. Syst. 25: 167–188.

Hines, J. E. 2006. Presence2 – software to estimate patch occupancy and related parameters. – USGS, Patuxent Wildlife Research Center, Laurel, MD, USA.

Lambert, J. D. et al. 2005. A practical model of Bicknell's thrush distribution in the northeastern United States. – Wilson Bull. 117: 1–11.

MacArthur, R. H. and Wilson, E. O. 1967. The theory of island biogeography. – Princeton Univ. Press.

MacKenzie, D. et al. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. – Ecology 84: 2200–2207.

Midgley, G. F. et al. 2010. BioMove – an integrated platform simulating the dynamic response of species to environmental change. – Ecography 33: 612–616.

Moilanen, A. 2002. Implications of empirical data quality to metapopulation model parameter estimation and application. – Oikos 96: 516–530.

Moilanen, A. and Hanski, I. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. – Ecology 79: 2503–2515.

Mortelliti, A. et al. 2010. The role of habitat quality in fragmented landscapes: a conceptual overview and prospectus for future research. – Oecologia 163: 535–547.

Mustin, K. et al. 2009. The dynamics of climate-induced range shifting; perspectives from simulation modelling. – Oikos 118: 131–137.

Opdam, P. 1991. Metapopulation theory and habitat fragmentation: a review of holarctic breeding bird studies. – Landscape Ecol. 5: 93–106.

Ott, R. L. and Longnecker, M. 2001. An introduction to statistical methods and data analysis. – Duxbury.

Prugh, L. R. et al. 2008. Effect of habitat area and isolation on fragmented animal populations. – Proc. Natl Acad. Sci. USA 105: 20770–20775.

Renfrew, R. B. and Ribic, C. A. 2008. Multi-scale models of grassland passerine abundance in a fragmented system in Wisconsin. – Landscape Ecol. 23: 181–193.

Rich, T. D. et al. 2004. Partners in Flight North American Landbird Conservation Plan. – Cornell Lab of Ornithology.

Rimmer, C. C. et al. 2001. Bicknell's thrush (*Catharus bicknelli*). – In: Poole, A. and Gill, F. (eds), The Birds of North America. The Birds of North America.

Schooley, R. L. and Branch, L. C. 2007. Spatial heterogeneity in habitat quality and cross-scale interactions in metapopulations. – Ecosystems 10: 846–853.

Schooley, R. L. and Branch, L. C. 2009. Enhancing the area-isolation paradigm: habitat heterogeneity and metapopulation dynamics of a rare wetland mammal. – Ecol. Appl. 19: 1708–1722.

Sprugel, D. G. 1976. Dynamic structure of wave-regenerated *Abies balsamea* forests in the north-eastern United States. – J. Ecol. 64: 889–911.

Supplementary material (Appendix E6936 at <www.oikosoffice.lu.se/appendix>). Appendix 1–3.

Strong, A. M. et al. 2004. Effect of prey biomass on reproductive success and mating strategy of Bicknell's thrush (*Catharus bicknelli*), a polygynandrous songbird. – Auk 121: 446–451.

Thomas, C. D. 2000. Dispersal and extinction in fragmented landscapes. – Proc. R. Soc. B 267: 139–145.

Thomas, J. A. et al. 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. – Proc. R. Soc. B 268: 1791–1796.

Verboom, J. et al. 1991. European nuthatch metapopulations in a fragmented agricultural landscape. – Oikos 61: 149–156.

Vogeli, M. et al. 2010. The relative importance of patch habitat quality and landscape attributes on a declining steppe-bird metapopulation. – Biol. Conserv. 143: 1057–1067.

Vogelmann, J. E. et al. 2001. Completion of the 1990s National Land Cover Data set for the conterminous United States from Landsat Thematic Mapper data and ancillary data sources. – Photogramm. Eng. Remote Sens. 67: 650–662.

With, K. et al. 2006. The implications of metalandscape connectivity for population viability in migratory songbirds. – Landscape Ecol. 21: 157–167.

With, K. A. et al. 1997. Landscape connectivity and population distributions in heterogeneous environments. – Oikos 78: 151–169.