Forest Ecology and Management 258 (2009) 1093–1101

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Male Kirtland's Warblers' patch-level response to landscape structure during periods of varying population size and habitat amounts

Deahn M. Donner [a,*], Christine A. Ribic [b], John R. Probst [a]

[a] USDA Forest Service, Northern Research Station, 5985 Highway K, Rhinelander, WI 54529, United States
[b] US Geological Survey, Wisconsin Cooperative Wildlife Research Unit, Department of Forest and Wildlife Ecology, University of Wisconsin, Madison, WI 53706, United States

ARTICLE INFO

Article history:
Received 5 March 2009
Received in revised form 20 May 2009
Accepted 25 May 2009

Keywords:
Kirtlands Warbler
Habitat loss and fragmentation
Landscape structure
Temporal variability
Population dynamics
Landscape ecology
Habitat amount threshold

ABSTRACT

Forest planners must evaluate how spatiotemporal changes in habitat amount and configuration across the landscape as a result of timber management will affect species' persistence. However, there are few long-term programs available for evaluation. We investigated the response of male Kirtland's Warbler (*Dendroica kirtlandii*) to 26 years of changing patch and landscape structure during a large, 26-year forestry-habitat restoration program within the warbler's primary breeding range. We found that the average density of male Kirtland's Warblers was related to a different combination of patch and landscape attributes depending on the species' regional population level and habitat amounts on the landscape (early succession jack pine (*Pinus banksiana*) forests; 15–42% habitat cover). Specifically, patch age and habitat regeneration type were important at low male population and total habitat amounts, while patch age and distance to an occupied patch were important at relatively high population and habitat amounts. Patch age and size were more important at increasing population levels and an intermediate amount of habitat. The importance of patch age to average male density during all periods reflects the temporal buildup and decline of male numbers as habitat suitability within the patch changed with succession. Habitat selection (i.e., preference for wildfire-regenerated habitat) and availability may explain the importance of habitat type and patch size during lower population and habitat levels. The relationship between male density and distance when there was the most habitat on the landscape and the male population was large and still increasing may be explained by the widening spatial dispersion of the increasing male population at the regional scale. Because creating or preserving habitat is not a random process, management efforts would benefit from more investigations of managed population responses to changes in spatial structure that occur through habitat gain rather than habitat loss to further our empirical understanding of general principles of the fragmentation process and habitat cover threshold effects within dynamic landscapes.

Published by Elsevier B.V.

1. Introduction

Forest planners must evaluate how spatiotemporal changes in habitat amount and configuration across the landscape as a result of timber management, natural disturbance, and other factors will affect species' persistence, especially for small, habitat-limited populations. Conservation concepts are often used as a guide despite the lack of empirical support at the broad spatial and temporal scales at which forest management is conducted (Harrison and Bruna, 1999; Schulte et al., 2006). Of particular value have been concepts derived from the process of habitat loss and fragmentation (Boutin and Hebert, 2002). Theories suggest that species' response to habitat loss is nonlinear where below a critical amount of habitat remaining in the landscape, populations of individual species decline more rapidly (Andren, 1994; With and King, 1999; Fahrig, 2003; Flather and Bevers, 2002). Below a threshold amount of 10–30% of original habitat remaining in a landscape, the abrupt changes in spatial configuration (e.g., decreasing patch size and increasing patch isolation; reduced connectivity) contributes to the decline in patch occupancy and abundance beyond what is expected from habitat loss alone (Andren, 1994; With and Crist, 1995; Fahrig, 2001; Flather and Bevers, 2002).

However, empirical evidence for the existence of a habitat amount threshold is weak (Fahrig, 2003). Further, the threshold in habitat amount can vary depending on the scale of the investigation (Mönkkoönen and Reunanen, 1999); the dispersal ability, habitat affinity, and reproductive rate of the species under consideration (With and Crist, 1995; Fahrig, 1998; With and King, 2001; Lindenmayer et al., 2005; Betts et al., 2007); landscape matrix quality (Mönkkoönen and Reunanen, 1999; Fahrig, 2001; Wiegand et al., 2005); and spatially across a species' geographical

---

[*] Corresponding author. Tel.: +1 715 362 1146.
E-mail address: ddonnerwright@fs.fed.us (D.M. Donner).

0378-1127/$ – see front matter. Published by Elsevier B.V.
doi:10.1016/j.foreco.2009.05.029

range (Rhodes et al., 2008). We have little understanding of how the temporal rate of habitat change (Keymer et al., 2000), and the regional population level (i.e., whether habitat is saturated or not) influences critical habitat threshold levels and habitat occupancy. Hence, it may be impossible to delineate clear or universal threshold responses for practical use (Lindenmayer and Luck, 2005; Groffman et al., 2006; Radford et al., 2005). Examining the qualitative pattern and form of population responses across a continuum of landscape structures rather that focusing on an exact habitat amount threshold would help planners apply the threshold concept to different landscapes and more species (Radford et al., 2005).

In the 1970s, forest managers were trying to reverse the population decline of the federally endangered Kirtland's Warbler (*Dendroica kirtlandii*). This long-distance migrant winters in the Bahama archipelago, and arrives on its breeding grounds throughout May and remains there until August–September. After controlling brood parasitism by Brown-Headed Cowbirds (*Molothrus ater*), the male population stabilized but failed to increase. Researchers determined that the breeding population was habitat limited (Probst, 1986; Probst and Weinrich, 1993). Fire suppression had greatly reduced the amount and extent of dense, young (5–23-year-old) jack pine (*Pinus banksiana*) forests found on the glacial outwash ecosystems in northern Michigan (USA) that the warbler almost exclusively uses for nesting. Using past research and island biogeography theory at the time, forest planners implemented a variety of management guidelines within 23 designated Kirtland's Warbler Management Areas (KWMAs; Probst, 1988; Byelich et al., 1976) including: (1) using large jack pine plantations to increase the amount of early succession jack pine forest by improving within-stand quality by increasing stem density, and the number and size of openings to more closely mimic wildfire-regenerated habitat, (2) reducing the isolation of small habitat patches by placing new, larger plantations near existing occupied habitat to enlarge blocks of habitat composed of stands of various ages within KWMAs, (3) clustering projects and staggering stand regeneration to encourage overlap in an area's use, and (4) maintaining 20% of each KWMA in each 10-year age class under a 50-year stand rotation base.

These forest management activities as well as naturally occurring wildfires over the last two decades have spatially and temporally changed the amount and spatial configuration of suitable habitat across the warbler's primary breeding range (Probst and Weinrich, 1993; Bocetti, 1994; Probst et al., 2003; Donner et al., 2008). The warbler's population size and the species' regional spatiotemporal distribution across its breeding range in response to these dynamics has been described (Probst and Weinrich, 1993; Probst et al., 2003; Donner et al., 2008). However, the long-term management of Kirtland's Warbler also presents the opportunity to explore how changing landscape structure influences patch-scale responses.

In this paper, we investigate how the density of Kirtland's Warbler singing males changes in response to changes in patch and landscape structure related to forest management. Our specific objectives are to: (1) define past time periods that differed in the proportion of suitable habitat in the landscape and also differed in regional male population levels, and (2) determine if the relationship between average male density at the patch scale to patch attributes was similar across defined periods.

2. Methods

2.1. Study area

This study was conducted on 23 KWMAs, lands specifically managed for breeding Kirtland's Warblers in northern Lower Michigan by the United State Department of Agriculture, Huron-Manistee National Forests, Michigan Department of Natural Resources, and the United State Department of Fish and Wildlife Service. Management areas varied in size from approximately 1400 to 13,000 ha totaling 71,610 ha, and are dispersed across an area approximately 137 km × 130 km (Fig. 1). This area experiences large fluctuations in temperature because of its inland location and relatively high elevation; late spring and early fall freezes are common (see Kashian et al., 2003). KWMAs are primarily surrounded by public or commercial forested lands that are managed for forest products, wildlife, and recreation.

Kirtland's Warbler's historical breeding range and KWMAs are located mostly in the Grayling outwash plains characterized by landforms of outwash sands deposited by fast moving glacial meltwaters (Grayling Outwash Plain sub-subsection of the High-plains subsection; USDA Forest Service, Ecological Classification System) (Fig. 1). The dominant soils classify as Grayling sand at the series level, and are composed of well-washed coarse sands with less than 5% silt plus clay, generally lack weatherable minerals, and are well-drained. These poor quality soils facilitate jack pine dominance, and maintain a mixture of low shrubs [e.g., blueberry (*Vaccinium angustifolium*), juneberry (*Amelanchier* spp.), sweetfern (*Comptonia peregrina*)], grasses, sedges, and forbs that are important forage and nesting cover (Walkinshaw, 1983; Bocetti, 1994; Kashian et al., 2003; Probst and DonnerWright, 2003). The low shrub cover and the lower live branches of jack pine provide shelter and concealment for the warblers' ground nest, provide foraging places, and conceal nest access (Probst, 1988). Ground cover density varies from sparse areas with bare ground to dense patches (Bocetti, 1994; Probst and DonnerWright, 2003).

Historically, large fires perpetuated the jack pine ecosystem over the relatively flat topographic terrain (Kashian et al., 2003). Fire continues to be an important factor regenerating jack pines in this area, but due to fire suppression, the modern fire rotation interval is many times longer than in historical times, and less area is burned (Cleland et al., 2004). Managers use whole-tree harvesting followed by plantations, and unburned, natural regeneration to help maintain young jack pine forests on a short rotation throughout the KWMAs (Probst, 1988; Donner et al., 2008). Northern pin oak (*Quercus ellipsoidalis*), trembling and bigtooth aspen (*Populus tremuloides* and *P. grandidentata*), black cherry (*Prunus serotina*), and choke cherry (*P. virginiana*) are often scattered within the jack pine stands (Walkinshaw, 1983; Probst, 1988). Other major species on the outwash plains are red pine (*Pinus resinosa*), and white pine (*Pinus strobus*). Northern hardwood forests of sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*), American basswood (*Tilia americana*), and white pine dominate surrounding moraines.

2.2. Suitable breeding habitat and patch attributes

Breeding habitat for the Kirtland's Warbler consists of primarily pure, even-aged stands of young jack pine trees typically 1.7–5.0 m in height, at least 20–25% tree canopy cover, and a minimum of 2000 stems/ha (Walkinshaw, 1983; Probst and Weinrich, 1993). Preferred habitat (i.e., those stands with the highest density of warblers) has more than 7500 stems/ha, between 35 and 65% canopy cover, and was historically regenerated after wildfires (Probst, 1988; Probst and Weinrich, 1993).

The suitability of a habitat patch is a function of age and the associated changes in sapling height, canopy cover, lower live branch height, and the development of understory plants required for nesting and fledgling cover. Specifically, self-pruning of the lower branches and the elimination of small openings as trees grow diminishes cover (Probst, 1988; Probst and Weinrich, 1993). In addition, the decline in the number of males with patch age may

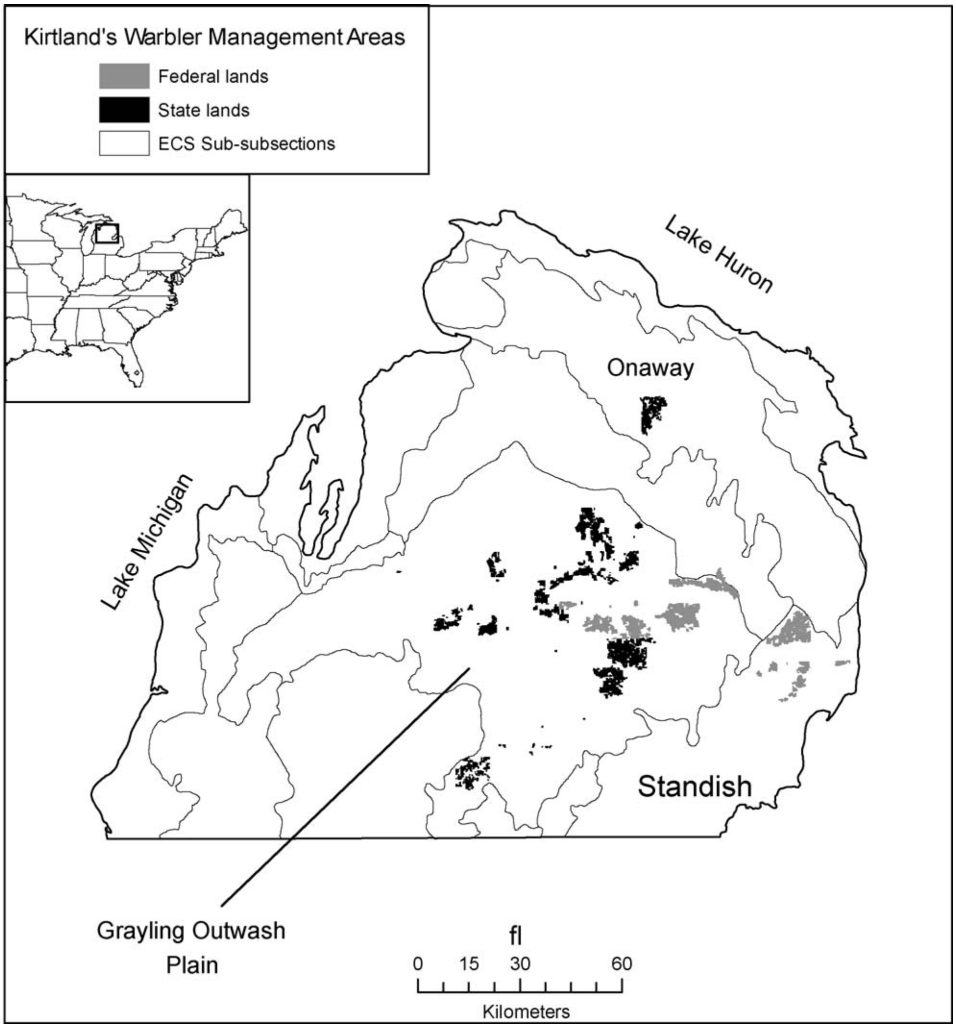

Fig. 1. Location of Kirtland's Warbler Management Areas and corresponding sub-subsections (USDA Forest Service, Ecological Classification System) in northern Lower Michigan.

be from the low recruitment of yearlings due to their innate tendency to disperse to younger habitat, especially when their natal breeding area was in aging habitat (Walkinshaw, 1983). Thus, a patch suitable for breeding by Kirtland's Warblers persists in the landscape for a limited time, and the amount of suitable habitat in a given year is a function of the rate at which new habitat becomes suitable and aging habitat becomes unsuitable. For each year, we defined suitable habitat as patches 5–23 years old and 12 ha or larger. This definition for suitable habitat was the broadest possible one based on the historical use of jack pine habitat by males (Probst and Weinrich, 1993), and reanalysis of male use from 1979 to 2004 (Donner et al., 2008). Male use of patches smaller than previously reported for the Kirtland's Warblers (32 ha; Mayfield, 1960; Walkinshaw, 1983; Probst and Weinrich, 1993) may be due to the smaller patches being positioned within larger complexes of suitably aged jack pine habitat or younger clearcuts making them more attractive to the warblers.

The annual proportion of suitable breeding habitat was calculated as the amount of 5–23-year-old jack pine divided by the previously defined landscape extent (i.e., KWMAs totaling 71,610 ha). Landscape extent included all jack pine covertype within KWMAs regardless of age, and areas used for 2 or more years by 2 or more males if outside KWMAs. Few Kirtland's Warblers nest on lands outside of KWMAs (Donner et al., 2008) because jack pine is not dense enough to provide adequate canopy cover for nesting, patch area is too small, or it is not located on well-drained soils required by this species. We assumed use of areas for only 1 year by a single male indicated inadequate cover and stem densities required for breeding. Accordingly, 22 patches totaling approximately 1000 ha (1.6% of the landscape) and containing 35 males (0.2% of the cumulative total males from 1979 to 2004) were excluded as potential suitable breeding habitat. Included areas were on public lands created by wildfires or forestry plantations that had a large component of volunteer jack pine regeneration. Federal and state stand management maps and 1992 digital orthoquads were used to recreate and digitize patch boundaries for areas outside KWMAs.

At the patch-level, area, year of origin (i.e., year planted or burned or harvested and left to naturally regenerate), and regeneration type (plantation, wildfire, and unburned, natural regeneration) were obtained from the federal and state habitat management program records. Because 2-year-old stock was used for planting, we adjusted the year of origin for plantations by 2 years to make the age structural components more similar between plantation and the other regeneration types (Donner et al., 2008). Adjacent management stands of the same regeneration type that had year of origin within 1 year were merged to form patches of similar age. The large Mack Lake Fire (24,000 ha) was separated into five patches with adjusted year of origins based on jack pine growth rate and topography (after Walker et al., 2003).

2.3. Regional population and patch-level male density

To determine the annual breeding population of male Kirtland's Warblers, we used the results from the 1979–2004 Kirtland's Warbler official census, which is coordinated under the direction of the Kirtland's Warbler Recovery Team. Jack pine stands of suitable size, site quality, and age within their primary breeding range in northern Lower Michigan (i.e., KWMAs) and a few scattered locations in the eastern and central Upper Peninsula of Michigan are surveyed annually for Kirtland's Warblers. We used only the population census results from Lower Michigan, which encompasses all of the patches within the defined study area. Methods for conducting the Kirtland's Warbler official census are standardized to minimize sources of variation important to monitoring programs (Ryel, 1981). The official census was found to be a reliable index of the regional male population trend (Probst et al., 2005).

We used patch-level results from the official census to obtain the number of males per patch annually. Federal and state forest management stands 3–23 years old are identified and surveyed for singing males from June 6 to 15 (Ryel, 1981; Probst et al., 2005). Management stands are readily discernible from each other because stands often are surrounded by roads, adjacent stands are a different age (i.e., height), or surrounding vegetation is not jack pine. The location of males is recorded along parallel routes spaced 320–400 m apart along the long axis of a stand and results combined to obtain number of males per stand (Ryel, 1981; Probst et al., 2005). The males' song is loud and can be heard for up to 400 m (Ryel, 1981; Probst et al., 2005). Bias due to variable detection rate was low because a single covertype with similar structure across regeneration types was censused and multiple observers are involved. In addition, all observers were trained in Kirtland's Warbler identification and the data collection protocol prior to the census to reduce observer bias.

2.4. Analyses

To define different time periods, we first fit linear and nonlinear models to the proportion of suitable habitat on the landscape as a function of year. Models were fit using generalized additive models (GAM) (Wood, 2006). In GAMs, the response is modeled as the additive sum of smoothed functions of covariates (i.e., nonparametric functions) allowing the response to follow any smooth curve rather than being constrained to a parametric form (Wood, 2006). However, parametric relationships (such as linear relationships) can also be modeled in this framework. The model from Donner et al. (2008) was used for the relationship between the population of singing males and year. Time periods of different habitat amounts and male population levels were determined visually from overlaying the two model curves. Time periods were based on relative levels (e.g., high, medium, low) of habitat amount and population size, and their association to each other. Significant points of change in the population trend curve were determined to be 1987 and 1994 (Donner et al., 2008), which corresponded approximately to theoretical ranges of critical habitat amount threshold levels (i.e., 10–30%).

Within each time period, the number of males counted annually for each patch was pooled and converted to density estimates (number of males per hectare). Explanatory variables were patch size, mean distance to the nearest occupied patch (i.e., isolation), mean patch age, and habitat regeneration types (wildfire, plantation, or unburned, natural regeneration). Mean patch age estimated for each time period was included to account for the reported temporal buildup and decline of males as a function of patch age (Probst, 1988; Bocetti, 1994). Patch size was log-transformed for analysis. Habitat regeneration type was included because of the known historical preference of the warblers for wildfire-regenerated habitats (Probst and Weinrich, 1993; Bocetti, 1994). For each patch within a time period, we used average Euclidean distance to the nearest occupied patch as a measure of patch isolation. Specifically, we measured distance between patch centroids for each year the patch was suitably aged (i.e., between 5 and 23 years old) over the time period. Then, mean distance to the nearest occupied patch for the time period was calculated. From a biological view, an individual male Kirtland's Warbler territory ranges from 1 to 12 ha in size, much smaller than a patch and can be located anywhere in the patch. Therefore, a territory may actually be nearer or farther from the nearest neighboring patch than the patch centroid. Because we did not measure male breeding territories, we believe that using the centroid was a reasonable and consistent way to measure distances between patches.

We used generalized additive mixed models to determine the relationship between average male densities and the explanatory variables. Mixed-effects models were used to account for the covariance structure induced by the grouping of data into KWMAs (i.e., random effects). Average male density was modeled as a Gaussian-distributed response variable. Because average male density was highly right-skewed, values were log-transformed to better meet normality assumptions. In all cases, models were fit using the 'mgcv' package in the R software environment (R, 2008) using a penalized thin plate regression spline basis to represent the smooth functions (Wood, 2006). Empirical semivariograms of the residuals from the individual time-period models showed no spatial autocorrelation in the residual spatial structure (Fortin and Dale, 2005).

Nineteen *a priori* candidate models that incorporated all factors and an interaction between patch size and habitat regeneration type were compared using Akaike's Information Criteria corrected for sample size ($\mathrm{AIC_c}$) to determine which model fit the data best for each time period. Models within 2 AIC units of the minimum were considered competitive models. We report the model with the fewest parameters that fell within the set of competitive models to avoid overfitting the data; this model was generally the model with the minimum $\mathrm{AIC_c}$ value. We also report adjusted R^2 values. Akaike weights (w_i) are presented to indicate the relative likelihood of the model given the data and candidate set of models tested (Burnham and Anderson, 2002). The relative importance of each explanatory factor was determined by summing the Akaike weights over the subset of models that included each variable (Burnham and Anderson, 2002). Factor significance was assessed at 0.05.

3. Results

3.1. Partitioning of time periods

Proportion of suitable habitat on the landscape increased monotonically from 1979 to 2001 (Fig. 2), spanning the theoretical habitat threshold estimates of 10–30%. Suitable habitat amount declined slightly in 2001, but remained near 40% of the total landscape through 2004 (Fig. 2). The regional male population trend increased during this time as well with significant points of change in 1987 and 1994 determined by a piecewise-regression model (Donner et al., 2008; Fig. 2). The following three time periods were defined based on the observed pattern between the regional male population level and the proportion of habitat on the landscape: (1) 1979–1991 (13 years), proportion of habitat on the landscape increased but remained below 30% while the regional population size remained stable at low levels, (2) 1992–1999 (8 years), proportion of habitat on the landscape was 30–40% and the regional population size increased fourfold, and (3) 2000–2004 (5 years),

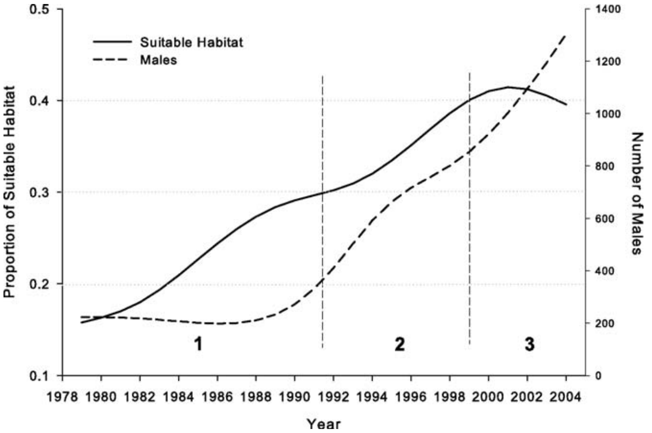

Fig. 2. Smooth functions from a generalized additive model on the proportion of suitable habitat cover (solid line) and Kirtland's Warbler male population (dashed line) using 26 years of census and habitat monitoring data collected within their primary breeding range, northern Lower Michigan, 1979–2004. Periods of population size in relation to proportion of suitable habitat are denoted by the vertical dashed lines and numbers. Period definitions are: (1) low, stable population: low, increasing habitat amount (<30% of landscape), (2) increasing population: increasing habitat amount (30–40% of landscape), and (3) high, increasing population: high, stable habitat amount (40% of landscape).

proportion of habitat on the landscape was relatively stable near 40% while the regional population size continued to increase.

The second period included 67% ($n = 288$) of the patches within the first period ($n = 424$). The third period included 45% ($n = 205$) and 76% ($n = 348$) of the patches used in the first and second periods, respectively. Mean patch size and mean patch age were comparable across time periods for suitable habitat (not all of which was occupied) and occupied habitat (Table 1). As a result of management, the number of suitable and occupied patches increased across time periods, while the mean distance to an occupied patch declined across periods as the population grew and dispersed into more habitats (Table 1; Donner et al., 2008).

3.2. Time period male density-patch relationships

In period 1, when the population was low but stable and the amount of suitable habitat was less than 30% of total habitat, average male density in a patch was related to patch age and habitat regeneration type (Table 2). This model has a probability of 0.50 of being the best model out of all models considered. Among habitat types in period 1, wildfire-regenerated habitat had the greatest male density (0.57 ± 0.62 S.D., $n = 28$) compared to plantation and unburned, natural regeneration (0.14 ± 0.21 S.D., $n = 46$; 0.12 ± 0.09 S.D., $n = 20$, respectively). The only competitive model was this model plus patch size. Patch age and habitat type were clearly the important variables with variable importance weights of 1; patch size and average distance to an occupied patch had lower importance weights of 0.40 and 0.15, respectively.

In period 2, when male population and habitat amounts were increasing from relatively low to high levels, average male density was related to patch age and patch size (Table 2). There was a nonlinear relationship between average male density and patch size; this was due to average male densities being greater in the smaller and larger patches compared to those in the middle of the patch size range (Fig. 3). Average male density in patches <40 ha was 0.35 males/ha (0.27 S.D.) and 0.26 males/ha (0.21 S.D.) in patches larger than 150 ha; in contrast, male density averaged 0.18 males/ha (0.23 S.D.) in patches between 40 and 150 ha. The competitive models were this simpler model plus either average distance to an occupied patch or habitat regeneration type. Patch age and patch size were important variables with weights of 1 and 0.92, respectively. Distance to an occupied patch and habitat regeneration types had lower weights of 0.42 and 0.33, respectively.

In period 3, when the population was increasing but suitable habitat was stable and about 40% of the landscape, average male density was related to patch age and average distance to an occupied patch (Table 2). This model had a probability of 0.29 of being the best model. Average male density declined linearly and was lower in patches that, on average, were farther from occupied patches. Male density was 0.40 males/ha (0.39 S.D.) in patches that were farther than 2.5 km from an occupied patch compared to 0.49 males/ha (0.51 S.D.) in patches that on average, were within 1.0 km of an occupied patch. There was a larger set of competitive models including combinations of the best model with patch size and habitat regeneration type. Patch age was clearly an important variable with a weight of 1.0 but average distance to an occupied patch had a lower weight of 0.63. Patch size and habitat regeneration type had importance weights of 0.57 and 0.40 due to their inclusion in the competitive model set.

Table 1
Summary of landscape metrics for suitable and occupied habitat measured within Kirtland's Warbler Management Areas in northern Lower Michigan, 1979–2004. Years delineate periods that varied in regional population levels and proportion of suitable habitat on the landscape. Habitat types are wildfire (W), plantation (P), and unburned, natural regeneration (NR).

Habitat type	Suitable habitat					Occupied habitat				
	Number patches (%)	Area (ha) (%)	Mean patch size (ha)	Mean patch age	Mean distance to occupied patch (km)	Number patches (%)	Area (ha) (%)	Mean patch size (ha)	Mean patch age	Mean distance to occupied patch (km)
Low, stable population; low, increasing habitat amount (<30% of landscape), 1979–1991										
W	51 (12)	8,333 (32)	163.4	12.7	4.4	30 (59)	6,460 (54)	230.7	12.4	4.5
P	282 (67)	13,250 (51)	47.0	11.9	10.7	88 (31)	3,790 (32)	82.4	9.4	5.7
NR	91 (21)	4,512 (17)	49.6	14.8	8.8	29 (32)	1,614 (14)	80.7	14.9	6.7
Total	424	26,094	61.5	12.6	9.5	147 (35)	11,864 (45)	126.2	11.4	5.6
Increasing population; increasing habitat amount (30–40% of landscape), 1992–1998										
W	47 (11)	7,959 (27)	169.4	14.2	3.4	22 (13)	6,694 (63)	304.3	11.5	2.9
P	329 (77)	18,565 (63)	56.4	11.7	4.9	131 (80)	10,706 (58)	81.7	10.5	3.5
NR	52 (12)	2,857 (10)	55.0	17.3	6.0	11 (7)	1,138 (6)	103.4	12.1	5.4
Total	428	29,381	68.7	12.7	4.9	164 (38)	18,538 (63)	113.0	10.8	3.6
High, increasing population: high, stable habitat amount (40% of landscape), 1999–2004										
W	35 (8)	7,051 (21)	201.4	14.7	2.5	18 (10)	894 (4)	321.1	12.9	2.3
P	392 (85)	24,812 (74)	63.3	13.5	3.0	151 (83)	14,269 (68)	94.5	11.7	2.3
NR	32 (7)	1,580 (5)	49.4	16.9	4.3	14 (7)	5,779 (28)	63.9	12.0	4.1
Total	459	33,443	72.9	13.9	3.0	183 (40)	20,943 (63)	114.4	11.8	2.4

Table 2
The selected best model using generalized additive mixed models relating average male density to patch explanatory variables in northern Lower Michigan, 1979–2004, as determined by AICc. The model-averaged estimate of regression coefficients (β) and unconditional sampling variation (SE) are presented. w_i = Akaike weight for the model.

Predictor variable	Estimated degrees of freedom	β (SE)	*F*-value/*t*-value	Approx. *P*-value	Adjusted R^2	w_i
Period 1: low, stable population: low, increasing suitable habitat amount (<30% of landscape)						
Mean patch age	2.20	0.70 (0.38)	9.17	0.00	0.37	0.51
Habitat						
Wildfire		1.68 (1.24)	5.06	0.00		
Plantation		0.65 (0.28)	1.94	0.06		
Period 2: increasing population: increasing suitable habitat amount (30–40% of landscape)						
Patch size	2.61	−0.30 (0.14)	5.66	0.00	0.25	0.37
Mean patch age	4.73	0.65 (1.03)	8.38	0.00		
Period 3: high, increasing population: high, stable suitable habitat amount (40% of landscape)						
Mean distance	1.00	−0.21 (0.05)	−3.44	0.00	0.43	0.29
Mean patch age	5.50	1.98 (3.19)	17.59	0.00		

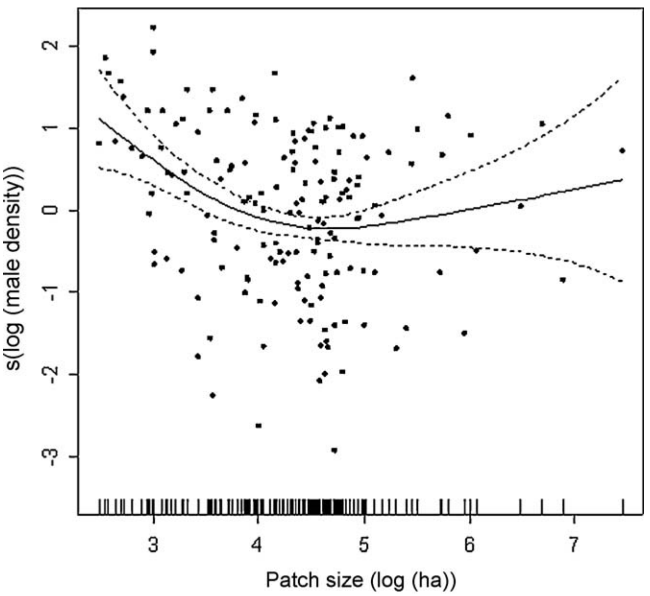

Fig. 3. Smooth functions for Kirtland's Warbler male density (s(log male density)) fit to patch size during period 2 when the male population was increasing and habitat amount was 30–40% of the defined landscape. Partial residuals and approximate 95% confidence intervals are shown. The number on the *y*-axis represents the degree of smoothing during fit using generalized additive mixed models.

Patch age was the only consistent significant predictor variable explaining male density across all three periods (Table 2). The relationship between average male density and patch age was nonlinear in all time periods (Fig. 4). The pattern detected in periods 2 and 3 reflected the buildup and decline in males numbers within aging habitat as previously reported (Probst and Weinrich, 1993; Bocetti, 1994); peak average male densities occurring within the 8–12-year-old range. However, during the first period, average male density leveled off near 15 years old instead of declining.

4. Discussion

Despite the broad focus on habitat fragmentation throughout ecology and management (Lindenmayer and Fishcher, 2006), there continues to be a lack of synthesis between general principles of the fragmentation process and field evidence (Harrison and Bruna, 1999; Huggett, 2005; Radford et al., 2005). Because theory suggests the spatial configuration of patches (i.e., patch size and distance) will have more pronounced effects on abundance patterns at low proportions of suitable habitat in the landscape (i.e., below a threshold value; Andren, 1994; With and King, 1999; see review in Huggett, 2005), many fragmentation studies have focused on examining the relative importance of total habitat amount compared to habitat configuration on populations using modeling or statistical methods to control for the effects of total habitat (see reviews in Fahrig, 2003; Koper et al., 2007). Findings from these studies are applied to real landscapes, but often in the absence of information on the regional context of total habitat amount and population level, and without the ability to isolate the co-varying components of the fragmentation process. In this study, the average density of male Kirtland's Warblers was related to a different combination of patch and landscape attributes depending on the regional amount of habitat in the landscape (covering 15–42% of management area) and corresponding population level across time.

Forest age composition has been shown to create peak abundances of different bird species at different forest ages thereby affecting density through time observations at the patch scale (Edenius and Elmberg, 1996; Holmes and Sherry, 2001). For our study species, within a breeding area, it is known that male warbler numbers increase rapidly for 3–5 years after initial colonization at 5–8 years old, then level off for the next 4–7 years before declining rapidly (Probst, 1986; Probst and Weinrich, 1993; Bocetti, 1994). This temporal pattern in male occupancy explains the importance of patch age to male density in all time periods in our study. The average patch age during each time period in our study was 12–14 years old, the optimal age when typically the highest densities of males are found. However, we found male warbler density did not decline in the older patches during the first period. We believe this pattern may be a result of the population being habitat limited due to a shortage of optimally aged regenerating habitat to replace the occupied maturing wildfire patches (Probst, 1986). Thus, males remained in older patches.

Theories of habitat selection predict individuals will use the habitat of highest suitability at low populations, and move into lesser quality sites as higher quality sites are filled through various mechanisms (Fretwell and Lucas, 1970; Pulliam and Danielson, 1991; Rosenzweig, 1991; Brown et al., 1995; Morris, 2003). In our study, habitat type was most important to male density when the regional population was low, consistent with these theories. Research during this period reported higher pairing success (i.e., more nests initiated; Probst and Hayes, 1987; Bocetti, 1994), and slightly higher mean clutch size compared to plantation habitat (Bocetti, 1994) suggesting wildfire-regenerated habitat was higher quality habitat for the Kirtland's Warbler at this time. During the first period, males were found almost entirely within six wildfire areas (70–80% of the males) even though wildfire habitat composed only 32% of suitably aged habitat in the landscape (Donner et al., 2008). As the regional male population and habitat amounts increased, however, habitat type was no longer an important predictor of male density.

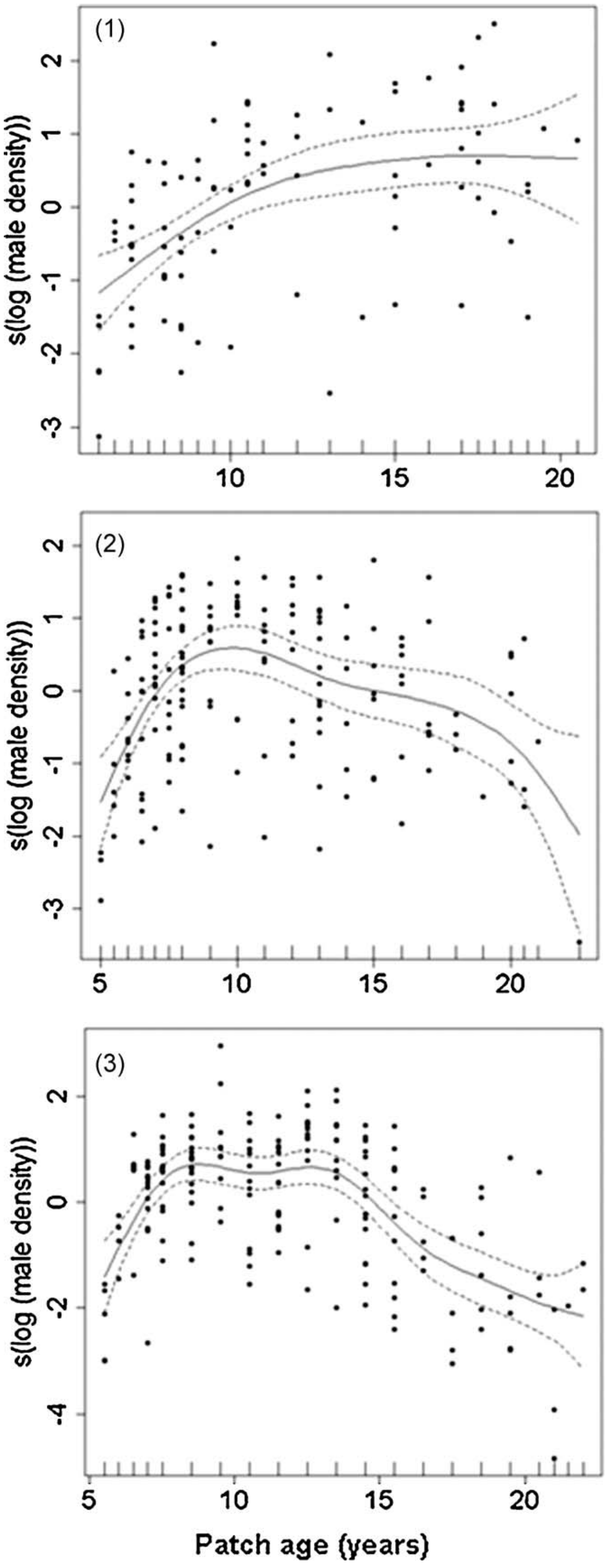

Fig. 4. Comparison of the smooth functions for Kirtland's Warbler male density (s(log male density)) fit to mean patch age during three time periods using generalized additive mixed models with a penalized thin plate regression spline fit. Partial residuals and approximate 95% confidence intervals are shown. The number on the *y*-axis represents the degree of smoothing during fit using generalized additive mixed models. Note axis scales are not uniform across periods. Period definitions are: (1) low, stable population: low, increasing habitat amount (<30% of landscape), (2) increasing population: increasing habitat amount (30–40% of landscape), and (3) high, increasing population: high, stable habitat amount (40% of landscape).

Theoretically, one would expect habitat type to remain an important predictor of male density during the second period because the male population remained at relatively low numbers, and males continued to use primarily wildfire-regenerated habitat. Approximately 75% of males were found in wildfire habitat that comprised only 27% of the suitable habitat available (Donner et al., 2008). However, patch size became an important predictor of male density. We suggest that the documented shift of males moving into plantations after filling wildfire-regenerated habitat, specifically the optimally aged 1980 Mack Lake Burn (Donner et al., 2008) during the later part of the time period may explain this relationship. Greater male densities were recorded in the large wildfire patches from the Mack Lake Burn and the smaller plantation patches that were at peak ages (10–14 years old) for occupancy, leading to the nonlinear relationship of male density and patch size.

Simulation modeling used to investigate the response of populations to spatial and temporal variability simultaneously are typically couched under the assumption that habitat is nearly saturated (i.e., near carrying capacity). Thus, temporal fluctuations in density driven primarily by variation in habitat availability are nearly instantaneous. But small populations do not always occupy all available habitats (Boone and Krohn, 2000), with the number of occupied sites being positively linked to regional population abundance (Gaston et al., 2000). Our results support this abundance-occupancy relationship. Specifically, as the population grew, more males dispersed into habitat in the peripheral KWMAs across their breeding range (Donner et al., 2008). Patches within these areas were being colonized by few males resulting in low male densities within these distant patches, and the negative relationship of male density and distance to an occupied patch. We suggest the importance of distance to an occupied patch when the population and habitat amounts were at their highest levels is the result of the population's broader spatial dispersion across the primary breeding range with increasing abundance.

The observed average male density patterns occurred in the absence of significant Brown-Headed Cowbird nest parasitism, which severely limited the population before this 26-year study period. An interagency cowbird control effort was implemented in 1972 to control nest parasitism after productivity was reportedly reduced by 60% to only 0.8 fledglings per nest (cf. Kepler et al., 1996). The impact of reduced or eliminated cowbird control on productivity between habitat types or at different patch ages is unknown. Male densities at the patch scale may be quite different without cowbird control, which may affect the relationship between male densities and patch attributes found in this study.

From 2005 to 2007, the Kirtland's Warbler breeding population continued expanding into Michigan's Upper Peninsula (Probst et al., 2005), and for the first time, breeding was documented in Wisconsin (2008 unpublished census data). Together, these areas outside the Lower Peninsula core population currently have approximately 3% of the total male population (2008 unpublished census data). This breeding range expansion was not unexpected because the amount of suitable habitat in the core breeding area was stabilizing and the male population was increasing by the end of this study. From 2007 to 2008, the male population showed signs of slowing as numbers increased by approximately 100 males (1701–1808 males) compared to previous years (http://www.fws.gov/midwest/endangered/birds/kirtland/Kwpop.html). The amount of suitable habitat in northern Lower Michigan, however, has remained fairly stable during this period suggesting that the habitat may be near saturation or carrying capacity. It is unknown how male density at the patch scale will be influenced by this population and habitat area stability. Males continue to primarily use plantation habitat, which is well dispersed throughout the KWMAs across the primary breeding range and tend to be of more uniform size (P. Huber, personal communication). Productivity studies comparing habitat regeneration types within this higher regional male population and habitat amount context would provide important information on the success of these large-complex plantations as a broad-scale forest restoration program.

5. Conclusion

Few studies examine how populations respond after increasing habitat amount even though creating reserves or protected areas is a fundamental conservation and management strategy (Huxel and Hastings, 1999; George and Zack, 2001). We show how temporal increases in both regional population size and total habitat amounts coupled with changing local patch suitability due to succession (i.e., patch age) affected the relationship between patch and landscape attributes to average male densities of Kirtland's Warblers. These results are important because too often forest managers must rely upon study results from local scales and short time periods, or simulation modeling to help determine how much habitat and what spatial configuration (e.g., patch size, isolation) is best to mitigate large-scale habitat loss or fragmentation effects. If we consider species management along a continuum of management intervention or stages of recovery (Scott et al., 2005) within the context of regional habitat amount and population level changes that will occur based on the level of intervention, managers may need to shift practices to focus on different patch and landscape attributes during the habitat management planning process.

We recognize that for many species, population size and total suitable habitat available is unknown. However, many species of management concern have variable population and habitat amount contexts that could be defined broadly and refined through time. Because creating or preserving habitat is not a random process, forest management efforts would benefit from more investigations on the response of managed populations to changes in spatial structure that occur through habitat gain rather than habitat loss. Such studies would further our empirical understanding of general principles of the fragmentation process and habitat cover threshold effects within dynamic landscapes.

Acknowledgements

This study was supported by the Institute for Applied Ecosystem Studies, U.S. Forest Service Northern Research Station. We thank Eric Gustafson, Dan Kashian, Rolff Koford, Anna Pidgeon, Jerry Weinrich, and two anonymous reviewers for reviews of earlier versions of the manuscript. We are also indebted to Elaine Carlson and Keith Kintigh with the Michigan Department of Natural Resources, and Phil Huber with the Huron-Manistee National Forest for their guidance and assistance with historical data. Mention of trade names does not imply endorsement by the U.S. Government.

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.

Betts, M.G., Forbes, G.J., Diamond, A.W., 2007. Thresholds in songbird occurrence in relation to landscape structure. Conservation Biology 21, 1046–1058.

Bocetti, C., 1994. Density, demography, and mating success of Kirtland's Warblers in managed and natural habitats. PhD Dissertation. Ohio State University, Columbus, OH.

Boone, R.B., Krohn, W.B., 2000. Predicting broad-scale occurrences of vertebrates in patchy landscapes. Landscape Ecology 15, 63–74.

Boutin, S., Hebert, D., 2002. Landscape ecology and forest management: developing an effective partnership. Ecological Applications 12, 390–397.

Brown, J.H., Mehlman, D.W., Stevens, G.C., 1995. Spatial variation in abundance. Ecology 76, 2028–2043.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodal Inference: A Practical Information-Theoretic Approach, 2nd ed. Springer, New York.

Byelich, J., DeCapita, M.E., Irvine, G.W., Radtke, R.E., Johnson, N.I., Jones, W.R., Mayfield, H., Mahalak, W.J., 1976. Kirtland's Warbler Recovery Plan. U.S. Fish and Wildlife Service, Twin Cities, MN (revised 1985).

Cleland, D.T., Crow, T.R., Saunders, S.C., Dickmann, D.I., Maclean, A.L., Jordan, J.K., Watson, R.L., Soan, A.M., Brosofske, K.D., 2004. Characterizing historical and modern fire regimes in Michigan (USA): a landscape ecosystem approach. Landscape Ecology 19, 311–325.

Donner, D.M., Probst, J.R., Ribic, C.A., 2008. Influence of habitat amount, arrangement, and use on population trend estimates of male Kirtland's warblers. Landscape Ecology 23, 467–480.

Edenius, L., Elmberg, J., 1996. Landscape level effects of modern forestry on bird communities in North Swedish boreal forests. Landscape Ecology 11, 325–338.

Fahrig, L., 1998. When does fragmentation of breeding habitat affect population survival? Ecological Modeling 105, 273–292.

Fahrig, L., 2001. How much habitat is enough? Biological Conservation 100, 65–74.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34, 487–515.

Flather, C.H., Bevers, M., 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. American Naturalist 159, 40–56.

Fortin, M.J., Dale, M.R.T., 2005. Spatial Analysis: A Guide for Ecologists. Cambridge University Press, New York.

Fretwell, S.D., Lucas, H.L., 1970. On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheoretica 19, 16–36.

Gaston, K.J., Blackburn, T.M., Greenwood, J.J.D., Gregory, R.D., Quinn, R.M., Lawton, J.H., 2000. Abundance-occupancy relationships. Journal of Applied Ecology 37 (Suppl. 1), 39–59.

George, T.L., Zack, S., 2001. Spatial and temporal considerations in restoring habitat for wildlife. Restoration Ecology 9, 272–279.

Groffman, P.M., Baron, J.S., Blett, T., gold, A.J., Goodman, I., Gunderson, L.H., Levinson, B.M., Palmer, M.A., Pearl, H.W., Peterson, G.D., Poff, N.L., Rejeski, D.W., Reynolds, J.F., Turner, M.G., Weathers, K.C., Wiens, J., 2006. Ecological thresholds: the key to successful environmental management or an important concept with no practical application? Ecosystems 9, 1–13.

Harrison, S., Bruna, E., 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? Ecography 22, 225–232.

Holmes, R.T., Sherry, T.W., 2001. Thirty-year bird population trends in an unfragmented temperate deciduous forest: importance of habitat change. The Auk 118, 589–609.

Huggett, A.J., 2005. The concept and utility of 'ecological thresholds' in biodiversity conservation. Biological Conservation 124, 301–310.

Huxel, G.R., Hastings, A., 1999. Habitat loss, fragmentation, and restoration. Restoration Ecology 7, 309–315.

Kashian, D.M., Barnes, B., Walker, W.S., 2003. Landscape ecosystems of northern Lower Michigan and the occurrence and management of the Kirtland's Warbler. Forest Science 49, 140–159.

Kepler, C.B., Irvine, G.W., DeCapita, M.E., Weinrich, J., 1996. The conservation management of Kirtland's Warbler *Dendroica kirtlandii*. Bird Conservation International 6, 11–22.

Keymer, J.E., Marquet, P.A., Velasco-Hernandez, J.X., Levin, S.A., 2000. Extinction thresholds and metapopulation persistence in dynamic landscapes. The American Naturalist 156, 478–494.

Koper, N., Schmiegelow, F.K.A., Merrill, E.H., 2007. Residuals cannot distinguish between ecological effects of habitat amount and fragmentation: implications for the debate. Landscape Ecology 22, 811–820.

Lindenmayer, D.B., Luck, G., 2005. Synthesis: thresholds in conservation and management. Biological Conservation 124, 351–354.

Lindenmayer, D.B., Fischer, J., Cunningham, R.B., 2005. Native vegetation cover thresholds associated with species responses. Biological Conservation 124, 311–316.

Lindenmayer, D.B., Fishcher, J., 2006. Tackling the habitat fragmentation panchreston. Trends in Ecology and Evolution 22, 127–132.

Mayfield, H.F., 1960. The Kirtland's Warbler. Cranbrook Institute of Science, Bloomfield Hills, Michigan.

Mönkkoönen, M., Reunanen, P., 1999. On critical thresholds in landscape connectivity: a management perspective. Oikos 84, 302–306.

Morris, D.W., 2003. Toward an ecological synthesis: a case for habitat selection. Oecologia 136, 1–13.

Probst, J.R., 1986. A review of factors limiting the Kirtland's Warbler on its breeding grounds. American Midland Naturalist 116, 87–100.

Probst, J.R., 1988. Kirtland's Warbler breeding biology and habitat management. In: Hoekstra, J.W., Capp, J. (Eds.), Integrating Forest Management for Wildlife and Fish. USDA General Technical Report NC-122. North Central Research Station, St. Paul, MN, pp. 28–35.

Probst, J.R., DonnerWright, D.M., 2003. Fire and shade effects on ground cover structure in Kirtland's warbler habitat. American Midland Naturalist 149, 320–334.

Probst, J.R., Hayes, J.P., 1987. Pairing success of Kirtland's warblers in marginal vs. suitable habitat. Auk 104, 234–241.

Probst, J.R., Weinrich, J., 1993. Relating Kirtland's Warbler population to changing landscape composition and structure. Landscape Ecology 8, 257–271.

Probst, J.R., Donner, D.M., Bocetti, C., Sjogren, S., 2003. Population increase in Kirtland's warbler and summer range expansion to Wisconsin and Michigan's Upper Peninsula, USA. Oryx 37, 365–373.

Probst, J.R., Donner, D.M., Worland, M., Weinrich, J., Huber, P., Ennis, K.R., 2005. Comparing census methods for the endangered Kirtland's Warbler. Journal of Field Ornithology 76, 50–60.

Pulliam, H.R., Danielson, B.J., 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. American Naturalists 132, S50–S66.

R: A language environment for statistical computing, R Development Core Team, 2008. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. http://www.R-project.org.

Radford, J.Q., Bennett, A.F., Cheers, G.J., 2005. Landscape-level thresholds of habitat cover for woodland-dependent birds. Biological Conservation 124, 317–337.

Rhodes, J.R., Callaghan, J.G., McAlpine, C.A., de Jong, C., Bowen, M.E., Mitchell, D.L., Lunney, D., Possingham, H.P., 2008. Regional variation in habitat-occupancy thresholds: a warning for conservation planning. Journal of Applied Ecology 45, 549–557.

Rosenzweig, M.L., 1991. Habitat selection and population interactions: the search for mechanism. American Naturalist 137, S5–S28.

Ryel, L.A., 1981. The fourth decennial census of Kirtland's Warbler, 1981. Jack-Pine Warbler 59, 93–95.

Schulte, L.A., Mitchell, R.J., Hunter Jr., M.L., Franklin, J.F., McIntyre, R.K., Palik, B.J., 2006. Evaluating the conceptual tools for forest biodiversity conservation and their implementation in the U.S. Forest Ecology and Management 232, 1–11.

Scott, J.M., Goble, D.D., Wiens, J.A., Wilcove, D.S., Bean, M., Male, T., 2005. Recovery of imperiled species under the Endangered Species Act: the need for a new approach. Frontiers in Ecology and the Environment 3, 383–389.

Walker, W.S., Barnes, B.V., Kashian, D.M., 2003. Landscape ecosystems of the Mack Lake burn, northern Lower Michigan, and the occurrence of the Kirtland's Warbler. Forest Science 49, 119–139.

Walkinshaw, L.H., 1983. Kirtland's Warbler: the natural history of an endangered species. Cranbrook Institute of Science Bulletin, 58. Bloomfield Hill, Michigan.

Wiegand, T., Revilla, E., Moloney, K.A., 2005. Effects of habitat loss and fragmentation on population dynamics. Conservation Biology 19, 108–121.

With, K.A., Crist, T.O., 1995. Critical thresholds in species' responses to landscape structure. Ecology 76, 2446–2459.

With, K.A., King, A.W., 1999. Extinction thresholds for species in fractal landscapes. Conservation Biology 13, 314–326.

With, K.A., King, A.W., 2001. Analysis of landscape sources and sinks: the effect of spatial pattern on avian demography. Biological Conservation 100, 75–88.

Wood, S., 2006. Generalized Additive Models: An Introduction with R. Chapman and Hall/CRC, Boca Raton, FL.