

Spatial relationship of resident and migratory birds and canopy openings in diseased ponderosa pine forests

Robin M. Reich ^{a,*}, John Lundquist ^b, Vanessa A. Bravo ^a

^a Department of Forest Sciences, Colorado State University, Fort Collins, CO 80523, USA

^b Rocky Mountain Research Station, USDA Forest Service, Fort Collins, CO 80526, USA

Received 20 April 1999; accepted 26 October 1999

Abstract

A method is described for predicting the spatial distribution of individual birds using presence data. The approach is demonstrated using a statistical habitat association model developed for resident and migratory birds on a 12 ha plot of ponderosa pine (*Pinus ponderosa*) heavily infested with southwestern ponderosa pine dwarf mistletoe (*Arceuthobium vasinatum* subsp. *Cryptopodum* (Englemann) Hawksworth and Weins). Bird locations and densiometer readings of canopy opening were recorded on a 5 m×5 m sampling grid. Minimum threshold theory was used to fit a logistic regression model to the presence data as a function of canopy opening. Highest occupancy of birds occurred at 61% canopy density. Higher probability of birds occurred in more dense canopy than less dense. Model validation indicated that the model adequately described the spatial distribution of the presence of individual birds with respect to canopy opening. Such a model could be used to determine stand conditions that are conducive and/or necessary for certain bird species, and to characterize and quantify the likely ecological consequences of changes to stand structure caused by diseases and other small scale disturbances. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Habitat model; Point process model; Spatial patterns; Species richness; Logistic regression; Minimum threshold theory; Kriging; Dwarf mistletoe

Software availability

Name of software: Spat99.zip and spat99.tar are a collection of Splus functions developed for analyzing spatial data.

Program Title: spat99.zip, spat99.tar

Developer: Dr. Robin M. Reich and Dr. Richard Davis

Contact Address: Department of Forest Science, Colorado State University, Fort Collins, Colorado 80523, USA

E-mail: robin@cnr.colostate.edu

Hardware Required: IBM PC compatible, UNIX workstation

Program Language: Splus 3.3 or higher

Availability and Cost: The PC and UNIX versions are free. A manual is also available for a small fee to cover printing costs. Contact Dr. Reich.

1. Introduction

Factors associated with habitat selection of birds are not well known, but it is well documented that stand structure influences the abundance and distribution of a variety of bird species (Bennetts et al., 1996; Eaton and Martin, 1998; Sharpe, 1996). Diseases that kill trees cause canopy openings with distinctive characteristics. These openings are primary units of structural heterogeneity in a forest stand. Since pathogens operate at several scales, a mosaic of habitats can develop if a forest stand is not managed for an extended period of time. MacArthur and MacArthur (1961) suggest that “patchiness (is) the principle factor affecting bird species diversity.” Little is known about the spatial relationship between tree diseases and bird abundance and distribution (Hart, 1995).

Most research on disease impact in the Rocky Mountains has focused on losses in commercial timber production and has usually been summarized with stand averages. Metrics used in these studies have been mostly adapted from timber production assessments, and almost

* Corresponding author.

always relate to reductions in volume or basal area (Stark, 1987). Not all disease impacts are negative, and the relationship between lost or foregone timber volume within a stand and the quality of bird habitat is indirect, at best. Forest disturbance is a spatial phenomenon, and a measure of the juxtaposition of disturbance/recovery events is almost entirely absent from timber assessments. Disturbance processes are probably essential for various bird species (Connell, 1978; Hart, 1995), but different types of metrics are needed to make such assessments.

The need to answer several key questions are integral to efforts to conserve resident and migratory birds in the Rocky Mountain region. What are the habitat requirements of species sensitive to small-scale disturbances? Where does suitable habitat occur for these species, and what is the spatial distribution of species with suitable habitat? What are the impacts of small-scale disturbances on individual species? A number of studies have investigated the first of these questions and have examined the direct impact of harvesting and fragmentation on bird communities (Hagan et al., 1996; Schmiegelow et al., 1997; Eaton and Martin, 1998). However, there have been few attempts to use such information to make spatial predictions of the distribution of individual birds to small-scale disturbances.

Statistical habitat association models are useful for assessing the relationship between small-scale disturbances and the abundance and diversity of individual birds (van Manen and Pelton, 1997; Ozesmi and Mitsch, 1997). These models relate the probability of occurrence of an individual species to various measures of habitat quality and have been developed using linear regression (Morrison et al., 1987), logistic regression (Lindenmayer et al., 1995; Ozesmi and Mitsch, 1997; van Manen and Pelton, 1997), discriminant analysis (Livingston et al., 1990), principle component analysis (Debinski and Brusard, 1994), canonical correlation analysis (Andries et al., 1994) and classification and regression tree (CART) (O'Connor et al., 1996).

These models generally require actual counts (i.e. 0, 1, 2, ...) of how many individuals were observed at a given location, along with one or more descriptions of habitat. It is generally assumed that the locations of all the individuals in the population are known so one can distinguish between sites being utilized by the species and sites not being used. When the data is recorded as 0 or 1, instead of actual counts, the data is referred to as presence-absence data. Many wildlife surveys, however, are not based on presence-absence data. Instead, data are collected at locations at which the species was observed. Presence data are common in surveys of highly mobile populations that might use a site when not being observed. In such cases, it is almost impossible to state that a given site is never used by a particular species.

Recently, Clark et al. (1993) and Knick and Dyer

(1997) developed a spatial habitat model specifically for presence data. Their method is based on the Mahalanobis statistic which characterizes optimal habitat as the multivariate vector of means of habitat variables calculated from the presence data. Habitat quality of a given location is based on the distance to the multivariate mean measured by the Mahalanobis statistic. Dettmers and Bart (1999) developed a procedure for using presence data to construct habitat models using data available in a GIS. Optimal ranges of habitat variables were identified by maximizing the difference between the cumulative distribution functions of habitat variables at locations in which the species was observed, and the value of habitat variables for all locations across the landscape. Using the optimal ranges of the habitat variables, a classification tree is used to classify habitat quality as being “good” or “otherwise.”

In this study, we present a procedure for using presence data to fit a logistic regression model to examine the influence on canopy structure within-stand bird distribution in a ponderosa pine (*Pinus ponderosa*) stand heavily infected with southwestern ponderosa pine dwarf mistletoe (*Arceuthobium vaginatum* subsp. *Cryptopodum* (Englemann) Hawksworth and Weins). Bennetts et al. (1996) describe a notable similar study. The specific objective of our study was to develop a method of quantifying the spatial relationship between dwarf mistletoe and the spatial distribution of resident and migratory birds.

2. Methods

2.1. Field data

This study was conducted at the Manitou Experimental Forest, located 26 miles northwest of Colorado Springs, Colorado at an elevation of 2200 m. Our site was close to Bennetts et al. (1996) original site. The dominant vegetation is primarily mixed-age ponderosa pine with an understory of Mountain muhly (*Muhlenbergia montana* (Nutt.) A. Hitchc.), Arizona fescue (*Festuca arizonica* Vasey) and true mountain mahogany (*Cercocarpus montanus* Raf.). The major tree-killing disturbance in the area is southwestern ponderosa pine dwarf mistletoe. For a more detailed description of the study site see Bennetts et al. (1996).

One 12 ha plot (600 m×200 m) was established on a 5 m×5 m grid marked with numbered flagging such that a portion of the plot was in an undisturbed area and a portion in an area severely impacted by dwarf mistletoe. At each grid coordinate, an optical densiometer was used to estimate percent canopy opening. For five consecutive days during late May 1997 (spring nesting period), bird surveys were made across the grid by spot mapping (Ralph et al., 1993). The survey was conducted by 2

observers walking four transects parallel to the longest dimension of the plot at 50 m intervals starting 25 m from the plot edge and noting what birds they saw or heard within 25 m of each side of the transect. Counts were completed within three hours after sunrise. The order in which the transects were surveyed was rotated daily to avoid confounding time-of-day effects among the transects. Once a bird was sighted, the sighting distance and sighting angle were visually estimated and used to assign the sighting to the nearest grid point. This information was recorded on field maps of the study plot.

It was possible for individual birds to be observed in one portion of the study plot, and then move elsewhere within the plot and be counted a second time. This type of movement was not considered critical since the objective was to describe the spatial relationship between canopy structure and the probability of observing a bird.

2.2. Test for randomness of bird distribution

The first step in the analysis was to test the null hypothesis that the spatial distribution of resident and migratory birds is random. Using the x - y coordinates of each bird sighting, a Monte Carlo test based on the Cramer-von Mises type statistic (Cressie, 1991)

$$k_1 = \int_0^{\infty} \{ \hat{K}(h)^{1/2} - \pi^{1/2} h \}^2 dh \quad (1)$$

was used to test the null hypothesis of complete spatial randomness (*csr*). Specifically, the goodness-of-fit was determined by Monte Carlo simulations of a spatial Poisson process. For each simulation i , $i = 2, 3, \dots, R$, we calculated the empirical K -function $\hat{K}_i(h)$, corrected for edge effect (Cressie, 1991), and the Cramer-von Mises statistic k_i . We then ranked the k_i 's from 1 to R . The significance level of the goodness-of-fit is estimated to be $(R + 1 - r)/R$, where r is the rank of k_1 . The null hypothesis of *csr* was rejected if the p -value was less than 0.05.

2.3. Habitat association model

The spatial relationship between canopy openings and the spatial distribution of resident and migratory birds was modeled using minimum threshold theory (Neter et al., 1985). Individual birds were assumed to have a threshold, T_i , such that an increase in canopy opening would be considered unsuitable. Since we could observe an individual bird for only a short period of time, it was not possible to find the actual threshold for each bird. We could only determine whether or not the threshold level was above, or below a particular level of canopy opening.

To develop the model, we assumed there was some

minimum canopy opening threshold associated with the presence of individual birds. Let $Y_i = 1$ whenever $T_i \leq X_i$, and 0 whenever $T_i > X_i$, where X_i is the level of canopy opening at spatial location s_i , and T_i is the minimum threshold of canopy opening. For a given level of canopy opening X_i , the probability of observing a bird is

$$\pi_i = P(Y_i = 1 | X_i) = P(T_i \leq X_i) \quad (2)$$

where $P(T_i \leq X_i)$ is the cumulative probability distribution of the thresholds of all locations in the population.

The logistic response function was assumed to be an appropriate descriptor of the relationship between canopy opening and the probability that an individual bird would be observed. This decision was based on theoretical and empirical considerations that suggest that when the dependent variable is binary, the shape of the response function is typically curvilinear in the form of a tilted S, with asymptotes of 0 and 1 (Hosmer and Lemeshow, 1989; Neter et al., 1985).

If we can assume the cumulative probability distribution of thresholds is logistic:

$$P(T \leq X) = \frac{\exp(\beta_0 + \beta_1 X + \dots + \beta_k X^k)}{1 + \exp(\beta_0 + \beta_1 X + \dots + \beta_k X^k)} \quad (3)$$

we can approximate this distribution using the logistic response model. The logistic model can be transformed to allow parameter estimation using least squares procedures (Neter et al., 1985):

$$\ln\left(\frac{\pi_i}{1 - \pi_i}\right) = \beta_0 + \beta_1 X_1 + \dots + \beta_k X^k \quad (4)$$

2.4. Kriging canopy opening

To validate the model it was necessary to generate a continuous surface of canopy openings for the study site. Ordinary kriging was used to spatially predict canopy opening from a 5 m to 2 m resolution. This was accomplished by first calculating the sample variogram, which describes the spatial variability in canopy openings at pairs of points separated by increasingly larger distances. Weighted non-linear least squares was used to fit various theoretical models (i.e. Gaussian, spherical, exponential, linear) to the sample variogram data as a function of distance. Akaike's (1977) corrected information criteria (AICC) was used to select a variogram model that best describes the spatial continuity in canopy opening. The variogram model with the smallest AICC was selected as the best fitting model. Using the fitted variogram model, image maps of the kriging prediction of canopy openings were developed.

2.5. Simulation model and model validation

To test the hypothesis that the distribution of resident and migratory birds were spatially related to canopy opening, we developed a spatial model combining the logistic model with the kriged response surface of canopy opening. Given a set of random numbers (realizations of the Uniform random variable U) a statistically equivalent set of realizations of canopy opening (X) can be obtained by inverting the cumulative distribution function ($P(T_i \leq X_i)$, Eq. (3)). This was accomplished by solving for the roots of the fitted polynomial given in Eq. (4). Using this approach we generate a random number, $U(0,1)$, which immediately determines the equivalent realization of canopy opening, X , that is the mid-point of the corresponding interval ΔX . The size of ΔX determines the level of precision of X . In our simulations, ΔX was set to 1%. The model then locates all possible locations on the kriged surface of canopy opening such that the canopy opening is equal to $X \pm \Delta X/2$ and the bird is randomly allocated to one of these locations. This process is repeated until the number of individual birds counted on the study plot (N) have been allocated. In simulating the spatial pattern of resident and migratory birds it was assumed there was no interspecific interactions between species.

The goodness-of-fit of the point process model for resident and migratory birds was assessed by comparing the empirical K -function, corrected for edge effect (Cressie, 1991) to K -functions from 200 realizations of the point process model. An empirical K -function that extended above or below the simulation envelopes would support the hypothesis that a mechanism other than canopy structure were involved in the spatial distribution of resident and migratory birds. An empirical distribution within the bounds would support the hypothesis of a spatial dependency between the location of individual birds and canopy distribution, for which some desired minimum threshold exists.

2.6. Statistical analysis and software

All statistical analyses were conducted using a spatial library developed by Reich and Davis (1998) for use with Splus (Mathsoft, 1997). A manual describing the use of the software is available from the authors.

3. Results

A list of bird species observed on the study plot is given in Table 1, along with their preferred habitat and migratory form. Disturbed and undisturbed areas had similar numbers of bird species and thus the bird diversity (richness) was similar, but birds were more abundant on the disturbed part of the plot. Birds in disturbed areas

were more often in gaps, and birds in the less disturbed areas were mostly between gaps. Junco species, violet-green swallows, and mountain chickadees were the most abundant species overall. All three of these bird species occurred throughout the study area, but their numbers were greater in the disturbed areas. Five species were found in the interior canopy and not in disturbed areas; these included: olive-sided flycatcher, yellow-rumped warbler, tree swallow, Hammond's flycatcher, and, warbling vireo (Table 1). Four species occurred in disturbed areas of the plot, but not in undisturbed areas; these included: turkey vulture, Steller's jay, brown-headed cowbird, and white-breasted nuthatch. No relationship was found between the migratory form (permanent resident, short distance migratory species, or neotropical migratory species) and occurrence in the disturbed or undisturbed portions of the plot ($\chi^2_{df=4} = 7.138$, p -value = 0.129).

The transformed K -function, ($\hat{L}(h) = \{\hat{K}(h)/\pi\}^{1/2}$) (Ripley, 1981) of the spatial distribution of individual birds on the sample plot is given in Fig. 1, along with 95% simulation envelopes assuming *csr*. It is evident from this figure how different the observed $\hat{L}$ is from these envelopes. This figure suggests that resident and migratory birds are clustered, since the empirical K -function extends above the upper simulation envelope for distances (h) between 0 and 30 m. At distances greater than 30 m the empirical K -function fluctuates about the upper simulation envelope. These results are supported by the Cramer-von Mises goodness-of-fit statistic ($D = 105.5$, p -value = 0.01).

The logistic transformation, while linearizing the response function (Eq. (3)), does not eliminate the unequal variances of the error terms. Hence, weighted least squares was used to fit the logistic model to the presence data (Neter et al., 1985) with weights, $\hat{w}_i = n_i \pi_i (1 - \pi_i)$. The final transformed logistic equation that minimized the AICC is a 5th degree polynomial given by:

$$\ln\left(\frac{\hat{\pi}_i}{1-\hat{\pi}_i}\right) = 10.254 + 1.896X - 0.227X^2 + 0.014X^3 - 0.4 \times 10^{-3}X^4 + 0.5 \times 10^{-5}X^5 \quad (5)$$

$$R^2 = 0.991 \quad S_{xy} = 0.498 \quad n = 112$$

All variables were significant at the 0.05 level. The response function is plotted in Fig. 2. The estimated probability density function for thresholds of canopy opening is given in Fig. 3. This curve is approximately normally distributed with a slight skewness to the left. When comparing the right tail with the left tail of the curve, there is a higher probability of birds occurring in more dense canopy than more open canopy. This indicates an increased preference for less openings in the canopy than for more. The crown density associated with the highest occupancy of birds was 61%.

Table 1

List of bird species recorded during counts on the 12 ha plot in the Manitou Experimental Forest

Common name	Scientific name	Number sightings		Forest habitat ^a	Migrant form ^b
		Dist.	Undist.		
Turkey vulture	<i>Cathartes aura</i>	2	0	w	s
Hermit thrush	<i>Catharus guttatus</i>	4	5	i	s
Common flicker	<i>Colaptes auratus</i>	2	1	ie	n
Western wood-pewee	<i>Contopus sordidulus</i>	0	3	e	n
Olive-sided flycatcher	<i>Contopus borealis</i>	0	1	e	n
Stellers jay	<i>Cyanocitta stelleri</i>	2	0	e	p
Yellow-rumped warbler	<i>Dendroica coronata</i>	0	4	ie	s
Hammond's flycatcher	<i>Empidonax hammondi</i>	0	1	i	n
Junco spp.	<i>Junco spp.</i>	12	5	ie	s
Brown-headed cowbird	<i>Molothrus ater</i>	3	0	e	s
Townsend's solitaire	<i>Myadestes townsendii</i>	5	4	ie	s
Mountain chickadee	<i>Parus gambeli</i>	7	5	i	p
Hairy woodpecker	<i>Picoides villosus</i>	2	1	I	p
Broad-tailed hummingbird	<i>Selasphorus platycercus</i>	5	3	ge	n
White-breasted nuthatch	<i>Sitta carolinensis</i>	2	0	i	p
Pygmy nuthatch	<i>Sitta pygmaea</i>	5	2	i	p
Williamson's sapsucker	<i>Sphyrapicus thyroideus</i>	2	1	i	s
Tree Swallow	<i>Tachycineta bicolor</i>	0	1	g	s
Violet-green swallow	<i>Tachycineta thalassina</i>	9	2	g	n
American robin	<i>Turdus migratorius</i>	3	4	e	s
Warbling vireo	<i>Vireo gilvus</i>	0	1	ie	n
Solitary vireo	<i>Vireo solitarius</i>	2	2	ie	n
Mourning dove	<i>Zenaida macoura</i>	5	3	ge	s

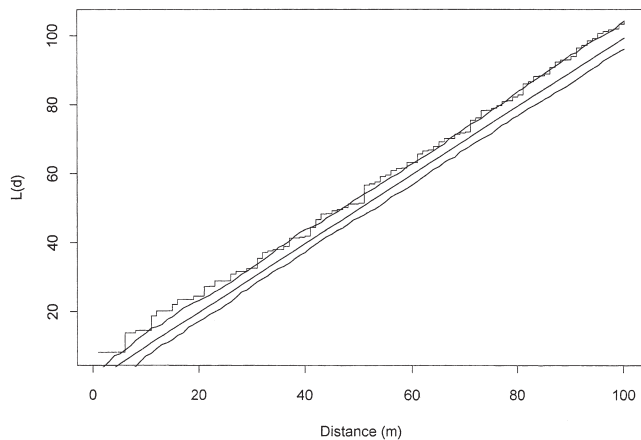
^a w = wide range, i = interior, g = gaps, and e = edges (Kaufman, 1996).^b s = short distance migrant species; p = permanent resident species; n = neotropical migrant species.

Fig. 1. Plot of transformed k -function, $L(h) = \{K(h)/\pi\}^{1/2}$ against distance h , for resident and migratory birds on the 12 ha plot in the Manitou Experimental Forest. The staircase line represents the empirical k -function calculated from the data and the continuous lines represent the upper, average, and lower simulation envelopes for 100 realizations of a spatial Poisson process.

A spherical variogram model (nugget = 56.95, sill = 88.14, range = 182.2 m) was used to krig canopy opening to a 2 m resolution using four nearest neighbors (Fig. 4). The approximate R^2 value associated with the surface was 0.574 (Kallas, 1997; Metzger, 1997). The low R^2 value is due to the large nugget effect (i.e., the nugget

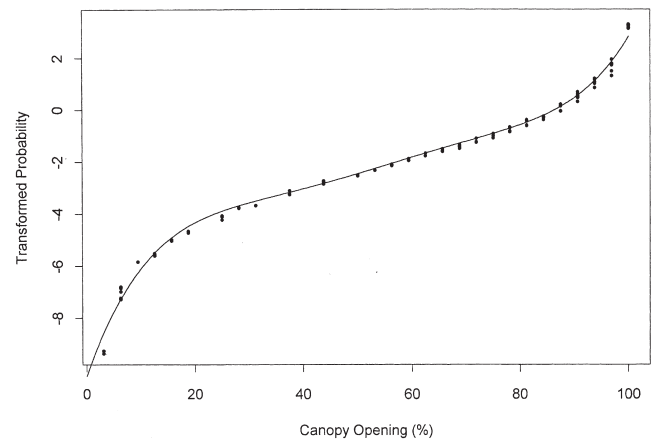


Fig. 2. Plot of the transformed cumulative probability distribution and fitted logistic response function for thresholds of canopy openings of all resident and migratory birds on the 12 ha plot in the Manitou Experimental Forest.

is 64% of the sill). As the nugget approaches the sill, the spatial distribution of canopy openings approaches that of a random condition. The large nugget effect also indicates a possible scale of pattern smaller than 5 m. At distances greater than 182 m (i.e., the range) individual observations of canopy openings are spatially independent. At distances less than this, some pattern was evident, though this relationship is very weak. Also, the

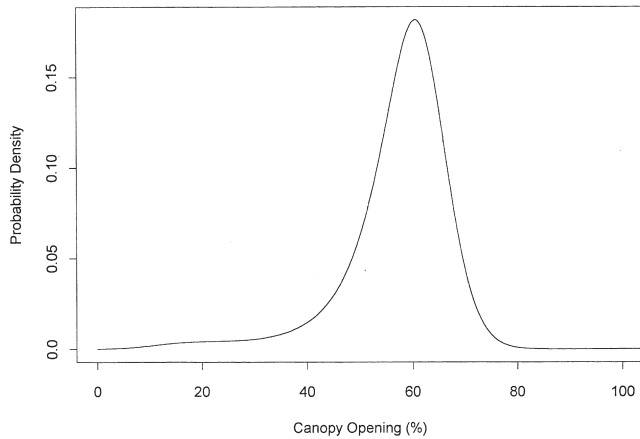


Fig. 3. Estimated probability density function for thresholds of canopy openings for all resident and migratory birds on the 12 ha plot in the Manitou Experimental Forest.

range is approximately equal to the size of the area impacted by dwarf mistletoe in the eastern part of the plot (Fig. 4).

Distribution of canopy openings on the sample plot is given in Table 2. Seventy-six percent of the plot had canopy openings less than or equal to 40% (Fig. 5a) and were located in the western two-thirds of the plot. The eastern portion of the study area, which was severely impacted by dwarf mistletoe had canopy openings between 50 and 70% (Fig. 5b), constituting the optimal range of canopy openings (Fig. 3) where abundance was greatest. This clustering of favorable habitat may be the reason why individual birds were aggregated on the study plot (Fig. 1). Six percent of the plot had canopy openings greater than or equal to 80% (Fig. 5c).

Table 2

Distribution of canopy openings on the 12 ha plot in the Manitou Experimental Forest

Percent canopy opening	Percent of plot
0–5	5.43
6–15	23.61
16–25	22.03
26–35	15.19
36–45	9.83
46–55	7.61
56–65	5.46
66–75	4.49
76–85	3.03
86–95	2.48
96–100	0.82

The transformed K -function for the canopy model is depicted in Fig. 6. The staircase line is the transformed empirical K -function for the observed point pattern, while the straight lines are the 99% simulation envelopes associated with the canopy model. The transformed empirical K -function is contained within the bounds of the simulation intervals, suggesting the canopy model adequately described the spatial relationship between presence of individual birds and canopy opening. While the model does assume independence among individual birds, this does not imply there is no behavioral attraction or repulsion between species. The model is strictly a habitat model looking at how canopy openings influences the spatial distribution of individual birds. It is not intended to capture other behavioral aspects of the individual species.

Since it was not possible to express the canopy model

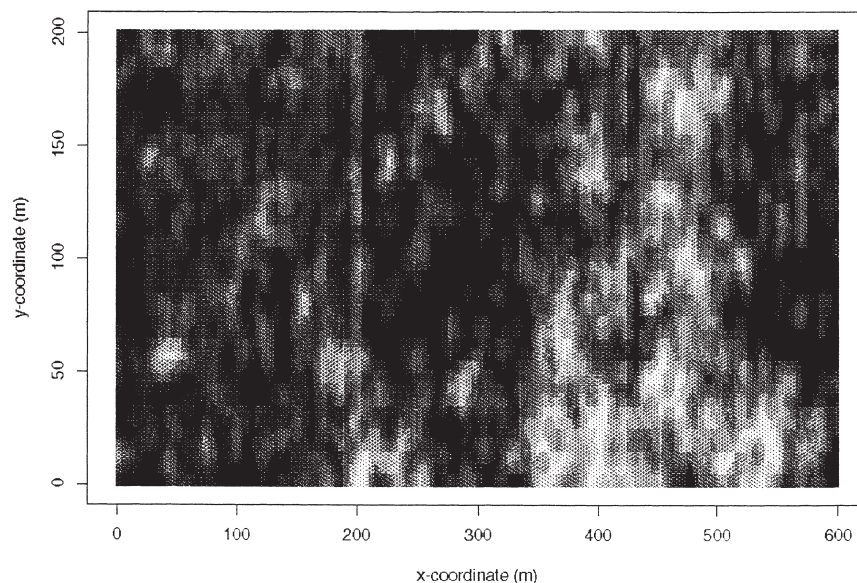


Fig. 4. Grey scale map of the kriged surface of canopy opening on the 12 ha plot in the Manitou Experimental Forest. Canopy opening decreases from white (100% open) to black (0% opening).

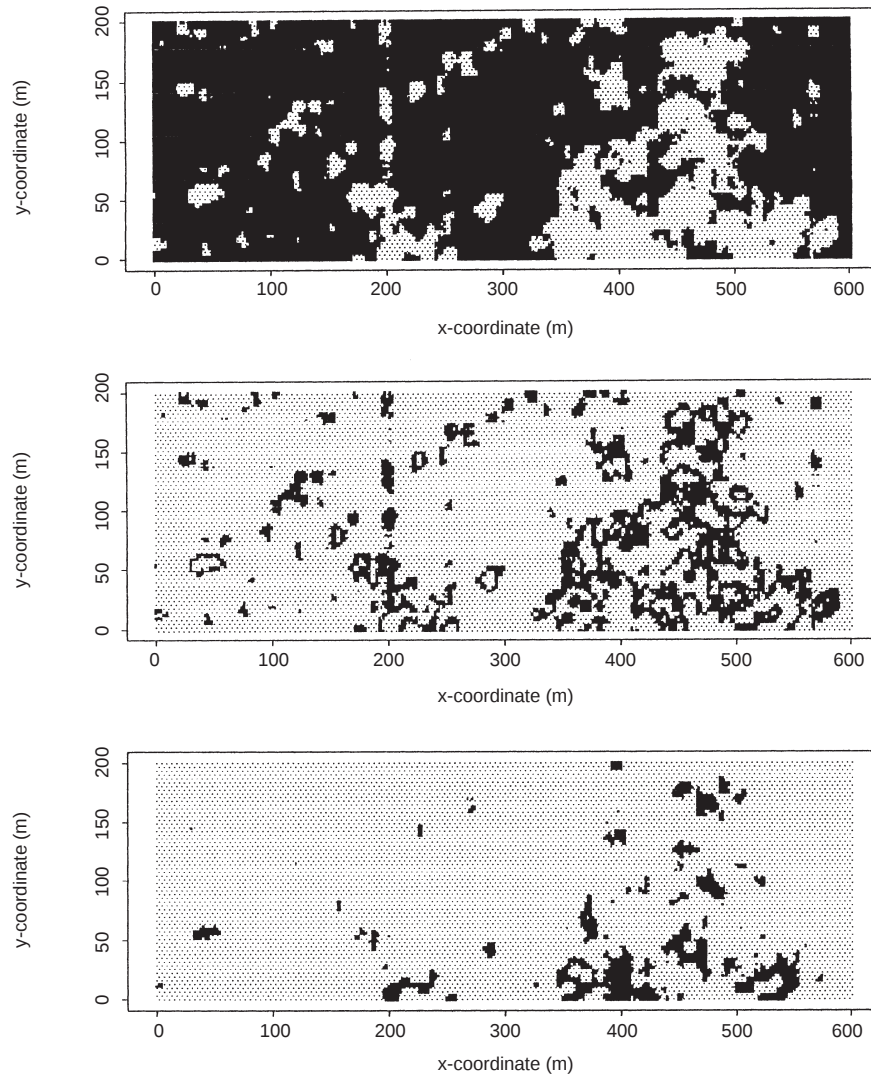


Fig. 5. Indicator maps showing the spatial location of canopy openings (black) (a) less than or equal to 40 percent, (b) 50 to 70 percent, and (c) greater than or equal to 80 percent on the 12 ha plot in the Manitou Experimental Forest. Canopy openings between 50 and 70 percent correspond to conditions in which the greatest number of birds were found.

mathematically in the form of a K -function it was not possible to assess the goodness-of-fit using an exact test such as the Cramer-von Mises statistic (Eq. (1)). Thus, we must rely on graphical procedures to assess the goodness-of-fit of the point process model. As noted by Rathburn and Cressie (1991), the method used to generate the simulation envelopes are not simultaneous confidence bounds and any departures from these envelopes only indicate departures from expectations.

4. Discussion

In this study, we developed a probability model to predict the within-stand spatial distribution of individual birds based on the spatial arrangement of canopy openings created by trees killed by dwarf mistletoe. This

model aims at determining to what extent dwarf mistletoe and other similar forest tree diseases can relate to the spatial arrangement of bird habitat. We examined this association by comparing a relatively undisturbed part of a plot with a part that had been significantly impacted by this disease. Further tests of this model could be used to determine stand conditions that are conducive and/or necessary for certain bird species, and to characterize and quantify the likely ecological consequences of changes to stand structure caused by diseases and other small scale disturbances.

Our study shows that individual bird distribution and abundance was associated with disease distribution, but it does not infer the mechanism underlying the associations. Dwarf mistletoes create a “mosaic of habitat structures” (Bennetts et al., 1996) by its effects on stem density, species and age class composition, host spatial

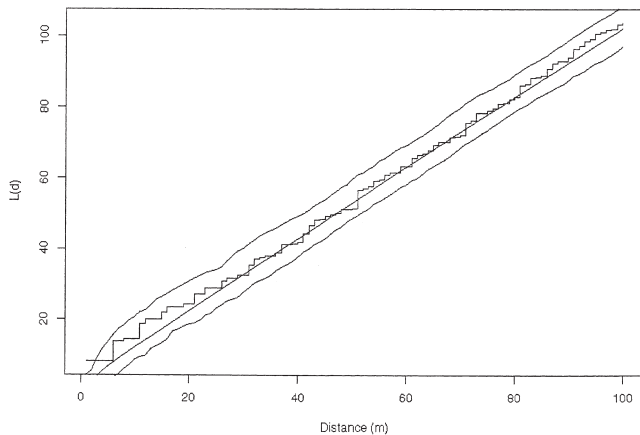


Fig. 6. Plot of transformed k -function, $L(h) = \{K(h)/\pi\}^{1/2}$ against distance h , for resident and migratory birds on the 12 ha plot in the Manitou Experimental Forest. The staircase line represents the empirical k -function calculated from the data and the continuous lines represent the upper, average, and lower simulation envelopes for 200 realizations of the canopy model.

distribution, abundance and spatial distribution of snags, coarse woody debris, recolonizing vegetation. The distribution of birds within this mosaic was not random, and these symptoms of dwarf mistletoe probably increased the number of suitable nesting, foraging, and roosting sites (Mlot, 1991) on the ponderosa pine trees within our study plot. Birds commonly nest in boles of trees putatively killed by dwarf mistletoe or in the witches brooms it creates. However, cause and effect relationships are difficult to prove in forestry, and proving that dwarf mistletoe is responsible for the bird distribution observed in this survey is not possible. However, the evidence certainly suggests that this disease has partly determined these patterns.

Small-scale disturbances, like dwarf mistletoe, alter habitat quality, amount of edge, spatial arrangement and distance between favorable habitat. Certain bird species have varying degrees of sensitivity to these changes and adjust to them in different ways; thus, impacts are positive for some birds, negative for others. Some birds prefer canopy interiors, others canopy gaps, and still others prefer edges between interiors and gaps (Table 1). According to Sharpe (1996), gaps are “typically characterized by heightened avian richness and abundance.” Bennetts et al. (1996) found that the level of southwestern ponderosa pine dwarf mistletoe infection on ponderosa pine was directly related to bird species richness. In our study, birds were more common in the disturbed areas, but not more diverse.

Characteristics of bird populations depend not only on the character of individual gaps but also on what the surrounding environment is like and the closeness of neighboring similar patches. The effect of a disturbance on one part of the stand influences other parts of the stand. Quantifying this effect has not been well

developed for forest pathogens, and spatial models for tree diseases are not well developed (Jeger, 1986). Most studies that quantify spatial variation are conducted at the watershed or landscape scale. In this study, we focus on the relatively small within-stand scale. The importance of the spatial distribution of favorable and unfavorable sites at the patch scale is not well understood (Tucker et al., 1997), but according to Wiens (1976), “if we study a system at an inappropriate scale, we may not detect its actual dynamics and patterns, but may instead identify patterns that are artifacts of scale.”

Birds occur where canopy opening or closure is suitable. Neither the absence of canopy nor the complete closure of canopy create conditions preferred by birds. The model developed here suggests that moderate level disturbances create the optimal conditions for bird abundance on our plot, which supports the intermediate disturbance hypothesis of Connell (1978).

This study was not meant to be a definitive study of forest stand characteristics that affect individual bird distribution and abundance in ponderosa pine stands along the Colorado Front Range. Rather, this study was designed to provide a description of the spatial relationship between crown structure as it relates to dwarf mistletoe and bird use. Ponderosa pine is a dominant forest type in this region, and dwarf mistletoe is the most important forest disease. The use, or lack of use by various bird species may help explain the distribution and abundance of these species across this region.

5. For Further Reading

Ripley, 1977

References

- Akaike, H., 1977. On entropy maximization principle. In: Krishnamah, P.R. (Ed.) *Applications of Statistics*. Publisher, Amsterdam, North-Holland, pp. 27–41.
- Bennetts, R.E., White, G.C., Hawksworth, F.G., Severs, S.E., 1996. The influence of dwarf mistletoe on bird communities in Colorado ponderosa pine forests. *Ecological Applications* 6, 899–909.
- Clark, J.D., Dunn, J.E., Smith, K.G., 1993. A multivariate model of female black bear habitat use for a geographic information system. *Journal of Wildlife Management* 57, 519–526.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199, 13002–13010.
- Cressie, N., 1991. *Statistics for Spatial Data*. John Wiley and Sons, New York.
- Debinski, D.M., Brussard, P.F., 1994. Using biodiversity data to assess species-habitat relationships in Glacier National Park, Montana. *Ecological Applications* 4, 833–843.
- Dettmers, R., Bart, J., 1999. A GIS modeling method applied to predicting forest songbird habitat. *Ecological Applications* 91, 152–163.
- Eaton, W.E., Martin, K., 1998. The effect of vegetation management on breeding bird communities in British Columbia. *Ecological Application* 8, 1092–1103.

- Hart, J.H. 1995. Interaction of diseases and insects with wildlife in forest ecosystems. In: Society of American Foresters. Foresters together: meeting tomorrow's challenges, Proceedings of the 1993 Society of American Foresters National Convention, Indianapolis, IN, November 7–10, pp. 107–112.
- Hosmer, D.W. Jr, Lemeshow, S., 1989. Applied Logistic Regression. John Wiley and Sons, New York.
- Jeger, M.J., 1986. The potential of analytic compared with simulation approaches in plant disease epidemiology. In: Leonard, K.J., Fry, W.E. (Eds.), Plant Disease Epidemiology: Population Dynamics and Management, vol. 1. MacMillan Publishing Co, N.Y., pp. 255–281.
- Kallas, M., 1997. Armillaria Root Disease on the Black Hills National Forest. Dept. Forest Science, Colorado State University, Fort Collins, CO.
- Kaufman, K., 1996. Lives of North American Birds. Houghton Mifflin Co, New York.
- Knick, S.T., Dyer, D.L., 1997. Distribution of black-tailed jackrabbit habitat determined by GIS in southwestern Idaho. Journal of Wildlife Management 61, 75–85.
- Lindenmayer, D.B., Ritman, K., Cunningham, R.D., Smith, J.D.B., Hurauth, D., 1995. A method for predicting the spatial distribution of arboreal marsupials. Wildlife. Research 22, 445–456.
- Livingston, S.A., Todd, C.S., Krohn, W.B., Owen, R.B. Jr, 1990. Habitat model for nesting bald eagles in Maine, USA. Journal of Wildlife Management 54, 644–653.
- MacArthur, R.H., MacArthur, J.W., 1961. On bird species diversity. Ecology 42, 594–598.
- Metzger, K., 1997. Modelling Forest Stand Structure to a Ten Meter Resolution Using Landsat TM Data. Dept. Forest Science, Colorado State University, Fort Collins, CO.
- Mlot, C., 1991. Diversity and dwarf mistletoe. Bioscience 41, 755.
- Morrison, M.L., Timossi, I.C., With, K.A., 1987. Development and testing of linear regression models predicting bird-habitat relationships. Journal of Wildlife Management 51, 247–253.
- O'Connor, R.J., Jones, M.T., White, D., Hunsaker, C., Loveland, T., Jones, B., Preston, E., 1996. Spatial partitioning of environmental correlates of avian biodiversity in the conterminous United States. Biodiversity Letter 3, 97–110.
- Neter, J., Wasserman, W., Kutner, M.H., 1985. Applied Linear Statistical Models. Irwin, Homewood, IL.
- Ozesmi, U., Mitsch, W.J., 1997. A spatial habitat model for the marsh-breeding red-winged blackbird (*Agelaius phoeniceus* L.) in coastal Lake Erie wetlands. Ecological Modeling 101, 139–152.
- Ralph, C.J., Pyle, P., Martin, T.E., DeSonte, D.F., 1993. Handbook of field methods for monitoring land birds. Gen. Tech. Rep. PSW GTR-144. Albany, CA, Pacific Southwestern Research Station, USDA Forest Service. 41p.
- Rathburn, L., Cressie, N., 1991. A space-time survival point-process for long-leaf pine forest in southern Georgia. Journal American Statistical Association 89, 1164–1174.
- Reich, R.M., Davis, R., 1998. Manual for Quantitative Spatial Analysis. Colorado State University, Fort Collins, CO 80523.
- Ripley, B.D., 1981. Spatial Statistics. John Wiley and Sons, New York.
- Sharpe, F., 1996. The biologically significant attributes of forest canopies to small birds. Northwest Science 70, 86–93.
- Splus, 1997. MathSoft, Inc. 1700 Westlake Ave. N. Suite 500, Seattle, WA 98109 USA.
- Stark, R.W., 1987. Impacts of forest insect and diseases, significances, and measurement. Critical Review in Plant Sciences 5, 161–203.
- Tucker, K., Rushton, S.P., Sanderson, R.A., Martin, E.B., Blaiklock, J., 1997. Modeling bird distributions — a combined GIS and Bayesian rule-based approach. Landscape Ecology 12, 77–93.
- van Manen, F.T., Pelton, M.R., 1997. A GIS model to predict black bear habitat use. Journal of Forestry 95, 6–12.
- Wiens, J.A., 1976. Population responses to patchy environments. Annual Review of Ecology and Systematics 7, 81–120.

Further reading

- Ripley, B.D., 1977. Modeling spatial patterns. Journal Royal Statistical Society B 396, 172–192.