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Landscape and Habitat Predictors of Canada Warbler (*Wilsonia Canadensis*) and Northern Waterthrush (*Seiurus noveboracensis*) Occurrence in Rhode Island Swamps

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LANDSCAPE AND HABITAT PREDICTORS OF CANADA WARBLER

WILSONIA CANADENSIS) AND NORTHERN WATERTHRUSH

(*SEIURUS NOVEBORACENSIS*) OCCURRENCE

IN RHODE ISLAND SWAMPS

BY

NICHOLAS A. MILLER

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MASTER OF SCIENCE THESIS

OF

NICHOLAS A. MILLER

APPROVED:

Thesis Committee

Major Professor

DEAN OF THE GRADUATE SCHOOL

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1999

ABSTRACT

Canada Warblers (*Wilsonia canadensis*) and Northern Waterthrushes (*Seiurus noveboracensis*)—both forest-interior, neotropical migrants—are the only breeding bird species in Rhode Island restricted to forested wetlands. Despite continuing alterations of wetlands and surrounding upland landscapes, primarily as a result of urbanization, the factors affecting the distribution of these two species have not previously been investigated. The need for such research is urgent, especially given the long-term decline in Canada Warbler populations in the Northeast. I examined the relative influence of forest habitat characteristics and landscape context on the presence of both species in 80 survey plots located in 44 Rhode Island forested swamps during 1997 and 1998. I used both univariate and forward stepwise logistic regression analysis to create models for predicting the probability of occurrence, or incidence, of each species. Canada Warbler presence was more strongly linked to landscape features than to habitat characteristics. Incidence of this species was > 0.5 at points > 300 m from paved roads, in swamps > 6 ha, where forest covered $> 50\%$ of the land within 2 km, and where that forest contained < 22 km of paved roads. Swamps were unlikely to support Canada Warblers where the regional cover of urban and agricultural land was unusually high. At the habitat scale, Canada Warbler incidence exceeded 0.5 when *Sphagnum* moss cover exceeded 6% and when there was $< 30\%$ deciduous foliage cover within 0.5 m of the ground. Incidence of the Northern Waterthrush exceeded 0.5 in swamps > 1.5 ha and increased with the abundance of additional swamp habitat nearby. Waterthrushes seemed to prefer swamps with $> 10\%$ cover of saturated substrates, with high foliage cover in all strata below 4 m,

and with high *Sphagnum* moss cover. The probability of occurrence of this species generally increased with increasing evergreen canopy cover, tree diversity, and basal area of snags. Multivariate models suggested that the occurrence of Canada Warblers in forested wetlands may be predicted accurately from landscape characteristics alone. To accurately predict Northern Waterthrush occurrence, landscape and swamp habitat characteristics must be considered in combination. Current state and Federal laws regulate land use in forested wetlands, but they do not adequately address cumulative permitted losses; nor do they consistently consider the impacts of land use changes in surrounding uplands. Landscape context must be considered in any attempts to conserve these swamp-dependent species.

ACKNOWLEDGEMENTS

DEDICATION

I dedicate this thesis to Kristin Rogne Miller, my wife and my best friend, for her patience, help, and encouragement throughout this study. I also dedicate this thesis to my parents, James and Sylvia Miller, who taught me to appreciate forests and landscapes for all they contain.

PREFACE

This thesis was written in manuscript format in accordance with the requirements of the Graduate School of the University of Rhode Island. It adheres to the style of the journal *Conservation Biology*.

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Introduction

Forested wetland is the most abundant of all wetland types in the glaciated northeastern United States (Golet et al. 1993); it comprises 78% of the total area of inland wetlands in the State of Rhode Island (Rhode Island Geographic Information System [RIGIS] data, University of Rhode Island, Kingston). This habitat type supports a diversity of wildlife, including more than 60 species of breeding birds (Golet et al. 1993). Most of the species in this bird community are facultative; i.e., they nest and forage in both wetland and upland habitats (Swift et al. 1984; Golet et al. 1993). In Rhode Island, the only species restricted to forested wetlands are the Northern Waterthrush (*Seiurus noveboracensis*) and the Canada Warbler (*Wilsonia canadensis*). Northern Waterthrushes breed only in forested wetlands throughout their range (Bent 1953; Craig 1985). In some regions, Canada Warblers breed in forested upland containing dense shrub cover and streams or wet, mossy areas (Bent 1953; Dunn and Garrett 1997), but in Rhode Island they breed only in swamps (Enser 1992; F.C. Golet, University of Rhode Island Department of Natural Resources Science, pers. comm.). Because Northern Waterthrushes and Canada Warblers breed only in forested wetlands in Rhode Island, and because their breeding habitat continues to be altered by human land use (Golet et al. 1993), the life requisites of these species merit further investigation.

The Canada Warbler and the Northern Waterthrush are neotropical migrants that have been classified as area-sensitive, forest-interior species (Robbins et al. 1989; Freemark and Collins 1992). Forest fragmentation has been identified as a probable cause of the decline of such populations (Robbins et al. 1979; Lynch and Whigham 1984; Robbins et al. 1989). It results in the direct loss of suitable habitat, increased isolation of

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remnant habitat patches, and increased edge effects (Faaborg et al. 1993). The relative

amount of edge in a habitat patch increases as patch size decreases, causing forest-interior

birds to experience higher rates of nest predation (Wilcove 1985; Paton 1994), brood

parasitism (Brittingham and Temple 1983; Paton 1994), and interspecific competition

(Ambuel and Temple 1983). Pairing success also decreases near edges (Van Horn et al.

1995). Flather and Sauer (1996) found neotropical migrants to be more sensitive to

changes in landscape structure than other groups of birds.

Much of the literature addressing fragmentation impacts is based on studies

conducted in regions where forest patches are discrete units embedded in an agricultural

or urban matrix (e.g., Ambuel and Temple 1983). In the mid-Atlantic states, Robbins et

al. (1989) calculated minimum breeding area requirements based on the incidence of

individual bird species in forest patches of varying size. They concluded that Northern

Waterthrushes require at least 200 ha of contiguous forest, and Canada Warblers require

at least 400 ha. In the extensively forested landscapes of the northeastern United States,

forests often constitute the matrix, while agricultural and urban land uses comprise a

network of patches. Because Canada Warblers and Northern Waterthrushes are habitat

specialists in much of southern New England, it may be necessary to redefine minimum

breeding area requirements in terms of patches of suitable forest habitat (i.e., forested

wetland). Both species have been observed during the breeding season in swamps as

small as 0.5 ha (Merrow 1990). The question then arises whether it is the size of swamp

patches or the total abundance of forest in a geographic area that determines the presence

of either species. Previous research (Whitcomb et al. 1981; Lynch and Whigham 1984;

Askins et al. 1987; Robbins et al. 1989; Freemark and Collins 1992) has indicated that

the regional abundance of forest can influence both presence and abundance of neotropical migrants.

Landscape context is not the sole determinant of the presence and abundance of forest bird species. Forest habitat characteristics, such as vegetation structure and floristic diversity, also might have a major impact (Freemark and Merriam 1986; Blake and Karr 1987; Robbins et al. 1989), and may be even more important than landscape features (Lynch and Whigham 1984). Similarly, Litwin and Smith (1992) concluded that changes in forest vegetation structure may better explain population changes in selected bird species than changes in surrounding land use patterns.

Knowledge of the relative importance of internal forest habitat characteristics and landscape features in selection of breeding areas by forest birds may be critical to interpreting species-specific population trends. Analyses of Breeding Bird Survey (BBS) data have detected steady declines in Canada Warbler populations both range-wide and in southern New England since the mid-1960's (Sauer et al. 1997), but no trends are apparent for the Northern Waterthrush. These species co-occur in a diversity of forested wetland habitats; therefore, disparate population trends may result primarily from differing sensitivities to landscape-scale processes such as urbanization.

In this study, I examined the relative influence of internal forest habitat characteristics and landscape context on the presence of Canada Warblers and Northern Waterthrushes in Rhode Island forested swamps. Relative effects of the regional abundance of forest, human activity, and swamp area were investigated, and logistic regression models were developed to calculate the probability that an individual swamp would support either species.

Methods

Study Area

The study area comprises the mainland of Rhode Island west of Narragansett Bay (Fig. 1); it encompasses 2,374 km^2. Prior to European settlement the Rhode Island landscape was heavily forested; by 1850, over 80% of the State had been converted to agriculture (Griffiths 1965). Today, roughly 57% of the State is covered by forest (RIGIS data), and this forest is once again being fragmented, mainly as a result of urbanization. Forest cover is most extensive in the western half of the study area; it is least extensive in the Providence metropolitan area, at the north end of the Bay. Forested wetlands cover approximately 7% of the study area (RIGIS data), and are scattered throughout (Fig. 1). Most forested wetlands > 50 ha are found in the southern one-third of the study area.

Study Sites and Survey Plots

I selected 44 forested wetland study sites from a statewide GIS coverage using a stratified random sampling scheme. The coverage was created by merging the RIGIS wetlands data set with the RIGIS soils data set. All forested wetlands at least 0.5 ha in size and with a very poorly drained soil drainage class (Wright and Sautter 1979) were considered for selection. Site selection was random, but stratified according to a 21-cell matrix including seven wetland size classes and three forest cover classes (Table 1). Forest cover classes represented the percentage of land within 2 km of the center of each potential study site that was covered by forest (upland and wetland), as determined by a moving window analysis in the GRID module of ARC/INFO (ESRI 1998a). No forest

cover data were available for adjacent states; thus, potential sites within 2 km of the State line were excluded from the selection process. The number of potential study sites was approximately equal among the three forest cover classes. Where possible, 50% of the sites for each cell in the matrix were selected from the northern half of the study area, and 50% from the southern half. All randomly selected sites that were within 1 km of a previously selected site were excluded from consideration.

Birds were surveyed at the center of 80 50-m-radius circular plots. The number of plots per study site varied according to the size of the site (Table 1). Sites between 0.5 and 10 ha contained one plot; sites between 10 and 50 ha contained two plots; and sites > 50 ha contained four plots. To minimize the possibility of detecting the same birds in more than one plot within a site, a minimum distance of 220 m was maintained between plot centers. Where possible, plot boundaries were located at least 20 m from upland habitats. Within each plot, four perpendicular radii were flagged, with one 11-m-radius subplot centered halfway (25 m) out along each radius. Nine sites were too small or too irregularly shaped to contain an entire survey plot; at these sites I established the survey point and at least two entire subplots. Habitat characteristics were sampled in all subplots.

Bird Surveys

I surveyed birds in 44 of the plots during mid-May through June in 1997; 36 plots were surveyed during late May through early July in 1998. During these 6-week periods, I made two visits to each site between 0520 and 0930 hours. I visited each site once during the first 3 weeks and once during the second 3 weeks. The order of visitation among

plots surveyed on the same day was reversed during the second visit in an attempt to minimize the influence of time of day on results. I used a fixed-radius, point-count survey technique (Ralph et al. 1995, with modifications). On each visit, I tallied all Northern Waterthrushes and Canada Warblers that were seen or heard during a 10-minute period. Following this, I played Northern Waterthrush songs and calls for 1 minute, followed by 1 minute of observation. Then I played Canada Warbler songs and calls for 1 minute, followed by 1 minute of observation. The order of playback was reversed during the second visit to each survey point. These final 4 minutes of song playback and observation were to enhance detection of territorial birds that did not vocalize during the initial 10 minutes of the survey.

Habitat Quantification

The areal extent of surface moisture in each subplot was measured during the first 3 weeks of each bird survey period. At 50-cm intervals along each of four 11-m subplot radii, the substrate condition was categorized as surface water, saturated, or dry. Values were combined to estimate the percent cover of each moisture class in each subplot.

All other habitat characteristics were measured in July and August of the survey year. Percent cover of combined herb and shrub foliage was determined for four vertical strata along each of the four subplot radii. The four strata were 0 to 0.5 m, 0.5 to 1 m, 1 to 2 m, and 2 to 4 m. Percent cover was determined in each vertical stratum by noting presence or absence of foliage at 30-cm horizontal intervals. Foliage at each point was recorded as predominantly evergreen or predominantly deciduous. The presence of moss was also recorded at 30-cm intervals and identified as either *Sphagnum* or "other" moss.

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Tree density, diameter at breast height (dbh), canopy height, and canopy cover were recorded. All trees and saplings within 3 m of each subplot radius were measured, counted, and identified to species. Trees were defined as woody plants with a dbh of at least 7.6 cm. Saplings were defined as woody plants of tree form with a dbh between 3.0 and 7.6 cm. A clinometer was used to measure the height of one tree near the subplot center that represented the average canopy height for the subplot. A GRS densitometer (Geographic Resource Solutions, Arcata, CA) was used to determine presence or absence of evergreen or deciduous canopy foliage at 1-m intervals along each subplot radius; values were combined to estimate percent canopy cover per subplot. Thickness of the peat layer was measured with a 3-m metal rod at the center of each subplot. All habitat data obtained in subplots were combined to produce average values for each plot.

An index of tree diversity was calculated based on average subplot basal area of individual species within each plot, using the Shannon-Wiener formula (Krebs 1989). An index of foliage evenness, derived from the same formula, was calculated from cover estimates from the four foliage strata.

Landscape Quantification

Using GIS software (i.e., ARC/INFO [ESRI 1998a] and ArcView [ESRI 1998b]) and RIGIS datasets of wetlands, soils, roads, and land use-land cover, I measured characteristics of each study site and of the surrounding landscape within 2 km of each bird survey point. The wetlands dataset was produced from 1988 1:24,000-scale panchromatic aerial photographs; wetlands were classified using a modified version of Cowardin et al. (1979). The same set of aerial photos was used to develop the land use-

land cover dataset. The soils dataset was created from the Soil Survey of Rhode Island (Rector 1981). Roads were digitized from U.S. Geological Survey 7.5-minute topographic maps and Rhode Island Department of Transportation county maps.

Using the GRID module in ARC/INFO (ESRI 1998a), I calculated total forest cover (upland and wetland) within 2 km, and the amount of very poorly drained forested wetland within 2 km, of each survey point. I used the ARC module to compute the area of each study site and the distance from each bird survey point to the nearest paved road. Buffer and clip commands were used in ARC/INFO and ArcView (1998b) to calculate the total length of paved roads in forested areas within 2 km.

There was a strong linear correlation ($r = -0.883$) between the area of forest land within 2 km and the combined area of urban and agricultural land uses within 2 km. The residuals (RZ_URB) from a regression of these two variables were used as a measure of the relative amount of urban and agricultural land use for a given amount of forest. Negative values indicated lower than expected amounts of urban and agricultural land, and positive values indicated higher than expected amounts. There was also a strong linear correlation between the amount of very poorly drained forested wetland within 2 km and the size of the study site ($r = 0.926$). I used residuals (RZ_VFW) from a regression of these two variables as a measure of the relative availability of similar habitat within 2 km given a swamp of a certain size. Negative values of this new variable indicated lower than expected amounts of very poorly drained forested wetland within 2 km, and positive values indicated higher than expected amounts.

Logistic Regression Analyses

I used both univariate logistic regression analysis and forward stepwise logistic regression analysis to create models for predicting the presence of Northern Waterthrushes and Canada Warblers from certain characteristics of forested swamps and surrounding landscapes. These models may also be used to estimate the probability that either species will be present in an individual very poorly drained forested wetland.

I followed suggestions of Hosmer and Lemeshow (1989) in selecting variables to be used in the logistic regression analyses. Out of 120 landscape variables and 67 habitat variables originally considered for analysis, 6 landscape variables and 10 habitat variables were ultimately selected (Table 2). For each species, the selection was based on (1) ecological relevance, (2) low collinearity (Spearman $r < 0.50$; Table 3), and (3) the results of Mann-Whitney U tests (Table 4). Those variables that differed ($p < 0.20$) between plots containing and plots not containing each species were considered. To facilitate model comparisons between species, variables selected for both species were entered into each stepwise logistic regression analysis.

Patterns in landscapes occur at a variety of scales (Qi and Wu 1996). Because points closer together may be more similar, the assumption of independence inherent to most statistical tests may be compromised. As a result, variance estimates may be too small and the power of statistical tests may then be artificially inflated, thereby influencing the identification of significant trends (Pendleton 1995). I performed Moran's I analyses using GS^+ (Gamma Design Software 1999), and found that some variables were spatially correlated at certain distances (see Appendix). I decided that, in this study, some degree of spatial correlation could be tolerated because (1) survey points

were located at least 220 m apart, which is similar to the minimum distance recommended for avian point count surveys (Ralph et al. 1995); (2) the potentially higher Type I error rate, which may result from autocorrelation, is acceptable for proactive conservation research (Underwood 1997); and (3) the residuals of my multivariate logistic regression models were generally not spatially correlated ($p > 0.05$).

Three multivariate models were developed for each species: one including only landscape variables, one including only habitat variables, and one including both landscape and habitat variables. Variable selection in each of these models was based on log-likelihood change and chi-square tests. Differences in classification accuracy between models were assessed by conducting Pearson chi-square tests on contingency matrices. These matrices contained the number of plots correctly and incorrectly classified for each pair of models compared.

Univariate logistic regression analyses were conducted for both species using each of the 16 variables. These analyses generated probabilities of occurrence, or incidence, for each species over the observed range of values for each variable. The models provided a means of assessing the potential importance of each of the 16 variables to Canada Warblers and Northern Waterthrushes. To determine minimum requirements of either species for each variable, 50% incidence was used as a cutoff point (see Vickery et al. [1994] for rationale). These univariate graphs should be interpreted with caution because of collinearity among variables (see Table 3 for correlation coefficients). Mann-Whitney U tests were conducted using STATISTICA software (Statsoft, Inc. 1998); all other analyses were performed using SYSTAT software (SPSS, Inc. 1998).

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Results

Canada Warblers were observed in 53 (66.3%) of the 80 plots surveyed; Northern

Waterthrushes were observed in 56 (70.0%) of the plots. The species co-occurred in 42

(52.5%) of the plots, and 13 plots (16.3%) contained neither species. Individual plots

contained up to three Canada Warblers (mean = 0.95, SD = 0.825) and as many as four

Northern Waterthrushes (mean = 1.24, SD = 1.06).

Univariate Models

Canada Warbler

With only one exception, the incidence of Canada Warblers was strongly related to

landscape characteristics (Figs. 2A - 2F). The occurrence of this species was positively

related to the distance from a bird survey point to the nearest paved road (Fig. 2A), the

area of a study site (Fig. 2B), and the amount of forest within 2 km of a survey point (Fig.

2C). In general, Canada Warblers occurred more often than not in habitat distant (> 300

m) from paved roads. They rarely occurred within 100 m, and they were almost always

present when roads were at least 1 km away. The size of the forested wetland study site

was also positively related to incidence (p = 0.001). Canada Warblers occurred more

often than not in swamps > 6 ha in area, but were rarely found in swamps < 1 ha;

incidence exceeded 0.8 in forested wetlands > 100 ha. The local abundance of forest also

appeared to be important to this species. Incidence exceeded 0.5 only when forest cover

within 2 km exceeded 50%. A steady, almost linear increase in incidence occurred as the

landscape became increasingly forested.

Occurrence of Canada Warblers was negatively related to two other landscape variables: the length of paved forest roads within 2 km (Fig. 2D) and the residual amount of urban and agricultural land in that area (Fig. 2E). Although the birds responded positively to an increase in forest cover (Fig. 2C), incidence declined as those forests became increasingly dissected by roads ($p = 0.006$). Canada Warbler incidence dropped below 0.5 when the length of paved forest roads within 2 km exceeded about 22 km. Incidence was similarly affected by the residual amount of urban and agricultural land within the local region ($p = 0.010$). In this case, it dropped below 0.5 when the amount of urban and agricultural land within 2 km exceeded the expected amount by about 7%. Plots surrounded by lower than expected amounts of these land use types were likely to support Canada Warblers. The residual amount of very poorly drained forested wetland within 2 km (Fig. 2F) had no impact on Canada Warbler occurrence.

Habitat variables influenced Canada Warbler incidence to a lesser degree than landscape variables. Of the 10 habitat variables examined, only 2—*Sphagnum* moss cover and deciduous foliage cover within 0.5 m of the ground—were significantly related to incidence (Figs. 2G and 2H). The probability of occurrence was > 0.5 whenever *Sphagnum* cover exceeded about 6%; incidence was > 0.8 in swamps where *Sphagnum* covered at least 40% of the forest floor. Incidence was 0.7 - 0.8 when the cover of low deciduous foliage was < 30%; when cover was > 70%, Canada Warblers were more likely to be absent than present.

For certain habitat variables, the probability of occurrence of Canada Warblers was > 0.5 over the entire range of values observed. Evergreen canopy cover (Fig 2I), tree diversity (Fig. 2J), basal area of snags (Fig. 2K), percent cover of saturated substrate (Fig.

2L), and peat thickness (Fig. 2M) were examples. None of these variables were significantly related to incidence, but the data suggest a trend toward increasing incidence with increasing values of the variables in each case.

No significant relationship existed between Canada Warbler incidence and either total foliage cover in the 2- to 4-m stratum (Fig. 2N) or the foliage evenness index (Fig. 2O). However, upward trends in probability of occurrence were evident as values of these variables increased. Canada Warbler incidence exceeded 0.5 only when total foliage cover in the 2- to 4-m stratum was > 22%. The vast majority of plots surveyed had foliage evenness index values in excess of 0.9 (Table 4); such high values generally indicated high foliage cover in all strata. Fig. 2O suggests that foliage evenness was favorable for Canada Warblers in most of the plots surveyed.

Although the relationship was not significant, Canada Warbler incidence appeared to decrease as surface water cover increased. Figure 2P suggests that Canada Warblers were more likely to be absent than present in survey plots with > 45% surface water cover.

Northern Waterthrush

Only two landscape variables were clearly related to Northern Waterthrush presence: the area of the study site (Fig. 3B) and the residual amount of very poorly drained forested wetland within 2 km (Fig. 3F). Sites smaller than about 1.5 ha were unlikely to support Northern Waterthrushes. Where the residual amount of very poorly drained forested wetland habitat within 2 km was > 70 ha below expected values, the probability of occurrence was also < 0.5. The distance to the nearest paved road (Fig. 3A), the length of

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paved forest roads within 2 km (Fig. 3D), and the residual amount of urban and agricultural land within 2 km (Fig. 3E) had no detectable impact on Northern Waterthrush presence. There was a trend toward higher incidence with increasing amounts of forest within 2 km (Fig. 3C), but incidence values never fell below 0.5. Waterthrushes were likely to be present even when regional forest cover values were as low as 25%.

The two habitat variables that were most strongly related to Northern Waterthrush occurrence were foliage evenness (Fig. 3O; $p = 0.006$) and the percentage cover of saturated substrate (Fig. 3L; $p = 0.006$). Northern Waterthrushes appeared to require extensive foliage cover in all strata, and plots with evenness values below 0.91 were unlikely to support this species. The steep slope of this relationship (Fig. 3O) underscores the potential importance of this variable. Saturated substrates also appeared to be important for Northern Waterthrushes. When > 30% of the forest floor was saturated—but not flooded—the probability of Northern Waterthrush occurrence exceeded 0.8; when coverage dropped below 10%, this species was more likely to be absent than present.

Five other habitat variables also were positively related to Northern Waterthrush occurrence, but conditions were generally suitable (i.e., incidence > 0.5) across the entire range of each. Evergreen canopy cover (Fig. 3I), tree diversity (Fig. 3J), basal area of snags (Fig. 3K), *Sphagnum* moss cover (Fig. 3G), and peat thickness (Fig. 3M) were included in this category. Total foliage cover in the 2- to 4-m stratum (Fig. 3N), deciduous foliage cover within 0.5 m of the ground (Fig. 3H), and surface water cover (Fig. 3P) were unrelated to Northern Waterthrush incidence.

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Multivariate Models

Bird presence was predicted accurately by all of the multivariate models (mean correct classification rate [CCR] = 89.9%, range = 84.9% to 94.3%; Table 5). Differences among the models in overall correct classification rates (mean CCR = 79.8%, range = 73.8% to 86.3%) were primarily due to variation in the models' ability to accurately predict absence (mean CCR = 57.7%, range = 29.2% to 70.4%). Chi-square tests (Table 5) suggest that all models predicted bird presence significantly better than chance alone.

Correct classification rates were highest for both presence and absence in the Canada Warbler model containing only landscape variables (Table 5). This model predicted presence correctly 94.3% of the time and absence 70.4% of the time with only four variables. Distance to the nearest paved road was the first variable selected in both the landscape model and the combined model for this species. The combined model also predicted Canada Warbler absence at a 70.4% rate. Although the habitat model predicted Canada Warbler presence very well (CCR = 90.6%), it was only slightly better at predicting absence (CCR = 55.6%) than chance alone. *Sphagnum* moss cover was selected first in the habitat model.

The model combining landscape and habitat variables predicted Northern Waterthrush absence most accurately (CCR = 66.7%), and therefore produced the best overall classification rate for this species (82.5%). This model incorporated five habitat variables and two landscape variables. The five habitat variables—foliage evenness, basal area of snags, tree diversity, surface water cover, and saturated substrate cover— also comprised the habitat model. Both models selected these variables in the same

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order. The habitat model explained presence reasonably well (CCR = 87.5%), but predicted absence only slightly better than chance alone (CCR = 54.2%). Although the landscape model was the best predictor of Northern Waterthrush presence (CCR = 92.9%), landscape variables alone were not sufficient to predict absence (CCR = 29.2%). The residual amount of very poorly drained forested wetland within 2 km was the first variable selected in the Northern Waterthrush landscape model; it also appeared in the combined model.

Discussion

Using multivariate logistic regression analyses, Bolger et al. (1997) recently found that the relative influence of landscape and habitat characteristics on bird species of southern California shrub habitats was species-specific. I obtained similar results in this study of Canada Warblers and Northern Waterthrushes breeding in Rhode Island swamps. These two area-sensitive, forest-interior species selected similar habitats for breeding, but responded differently to many features of those habitats and the surrounding landscape. Landscape context influenced Canada Warbler presence and absence to a greater degree than swamp habitat characteristics, and had higher predictive power for Canada Warblers than for Northern Waterthrushes (Pearson Chi-square = 3.9, df = 1, p < 0.05). The Northern Waterthrush landscape model predicted presence in most cases where birds were actually absent. The Waterthrush habitat model was somewhat more successful than the landscape model in predicting absence. These findings suggest that landscape context may have been adequate for Northern Waterthrushes in most situations, but the birds were absent at certain sites because swamp habitat characteristics were not suitable.

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Overall, the occurrence of this species was best explained by a combination of landscape and habitat variables.

Influence of Landscape Context

Canada Warblers and Northern Waterthrushes have consistently been categorized as forest-interior, area-sensitive species (Robbins et al. 1989; Freemark and Collins 1992). Robbins et al. (1989) concluded that Canada Warblers required forest patches ≥ 400 ha for breeding, and Northern Waterthrushes required patches ≥ 200 ha. Using a similar approach, but redefining patches to include only suitable habitat, I determined that very poorly drained forested wetland patches as small as about 6 ha were suitable for Canada Warblers; Northern Waterthrushes required patches ≥ 1.5 ha. However, characteristics of surrounding uplands must be considered in conjunction with habitat patch area to accurately assess the landscape-level requirements of either species. Increasing regional abundance of forest cover had a positive influence on Canada Warblers; although not significant, the same trend was apparent for Northern Waterthrushes. Neither species occurs in upland forests during the breeding season in Rhode Island (F.C. Golet, pers. comm.), but upland forests may serve as buffers against edge effects. Although regional forest cover was not a predictor of abundance for either species in linear regression analyses conducted by Robbins et al. (1989), numerous studies have identified this landscape characteristic as an important influence on forest-interior, area-sensitive species in general (Whitcomb et al. 1981; Lynch and Whigham 1984; Askins et al. 1987; Robbins et al. 1989; Freemark and Collins 1992).

As the relative amount of very poorly drained forested wetland within 2 km increased, the probability of Northern Waterthrush occurrence also increased. Canada

Warblers, however, were unaffected. This difference in response may reflect differing degrees of habitat specialization over the ranges of these species. Northern Waterthrushes might consistently seek out landscapes rich in forested wetlands because they require this specific habitat type throughout their breeding range. Canada Warblers require microhabitat conditions that, in Rhode Island, are met only by forested wetlands. In other portions of the Canada Warbler's breeding range these conditions (e.g., dense tall shrubs, moss cover) are available in upland forests as well. Thus it is not surprising that total forest cover is a more important cue than forested wetland cover for Canada Warbler habitat selection.

Few studies have investigated the direct influence of urbanization on forest-interior, area-sensitive bird populations. In part, that is because urban and agricultural land uses are usually strongly negatively correlated with the regional abundance of forest. By statistically separating the variability due to forest cover from urban and agricultural land use, I determined that forested swamps were less likely to support Canada Warblers when the extent of these land use types in the surrounding area was unusually high. The specific land uses varied widely, and included residential, commercial, industrial, agricultural, and barren land. For this reason, associated impacts also may range widely. Proximity to residential land may increase rates of nest predation by domestic cats and dogs. Swamps near commercial, industrial, agricultural, and residential centers may be subjected to more chemical and noise pollution. Greater amounts of forest-nonforest edge associated with barren land and farmland may facilitate brood parasitism by Brown-headed Cowbirds (*Molothrus ater*). Cowbird parasitism frequently poses problems for Canada Warblers, but is only a moderate problem for Northern Waterthrushes (Dunn and

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Garrett 1997). In this study, the occurrence of Northern Waterthrushes was not influenced by the residual amount of urban and agricultural land within 2 km of a bird survey point; however, there was a trend toward increasing occurrence with an increase in total forest cover within 2 km.

Proximity to paved roads did not affect Northern Waterthrushes, but was the most important landscape variable for Canada Warblers. Similarly, the total length of paved roads in nearby forests was negatively related to the occurrence of Canada Warblers, but was unrelated to Northern Waterthrush occurrence. The total length of paved roads within forests serves as a more subtle indicator of human impact than the area of urban and agricultural lands alone. Many authors (e.g., Askins et al. 1987, Robbins et al. 1989) have considered the regional abundance of forest to be an indicator of low human impact. Distance from roads may be a more direct measure. In a review of research addressing ecological impacts of roads, Forman and Alexander (1998) identified a number of possible causes for road avoidance. These included songbird sensitivity to increased decibel levels and increased visual disturbance, pollution levels, and predator densities near roads. Local changes in hydrology caused by roads may also negatively impact the ground-nesting Canada Warbler. Reijnen et al. (1995) reported decreased densities of particularly sensitive woodland bird populations within 305 m of roads with traffic rates of up to 10,000 vehicles per day. This distance corresponds well with the distance from roads at which the probability of Canada Warbler occurrence fell below 0.5 in the current study.

Influence of Swamp Habitat Characteristics

Hydrology controls most characteristics and functions of wetlands, including habitat conditions and wildlife communities supported by those habitats (Mitsch and Gosselink 1993). Robbins et al. (1989) developed a very coarse moisture gradient variable by classifying forests surveyed according to the moisture associations of the dominant tree species. This variable was selected second in their linear regression model designed for predicting Canada Warbler numbers at a site; it was the first variable selected for Northern Waterthrushes in that study. Many other descriptions of habitat requirements for both species (e.g., Bent 1953; Craig 1985; Curson et al. 1994) highlight moist, even swampy conditions. I detected a strong positive relationship between Northern Waterthrushes and the extent of saturated substrates. Waterthrushes forage for insects, crustaceans, and mollusks by flipping over leaves around the perimeter of surface water pools (Craig 1984) and in saturated zones (pers. obs.). Although no relationship between Northern Waterthrush occurrence and the percent cover of surface water was evident in univariate analyses, multivariate models suggested that this variable had a positive influence; swamps with extensive surface water (e.g., > 45%) were unlikely to support Canada Warblers.

Nest site availability may be a key factor limiting habitat suitability for either species. Canada Warblers sometimes build nests in tree stumps or exposed roots of downed trees, but usually in small clumps of *Sphagnum* moss (Curson et al. 1994; Dunn and Garrett 1997; F. Golet, pers. comm.). Percent cover of *Sphagnum* had the lowest p-value (0.008) of all habitat variables in the Canada Warbler univariate logistic regression analyses, and it was the first variable selected in the multivariate habitat model. Northern

Waterthrushes use moss to line nests (Dunn and Garrett 1997), but they usually build

nests in stump cavities or in the exposed root masses of downed trees (Curson et al. 1994;

Dunn and Garrett 1997). Northern Waterthrush nests are generally constructed within 60

cm of the ground, while Canada Warbler nests typically are built directly on the ground

or within 15 cm (Ehrlich et al. 1988). This difference in height might explain the lower

frequency of occurrence of Canada Warblers at sites with extensive surface water. The

availability of potential nest sites was not assessed in this study. Incorporation of data on

nest-site availability (e.g., presence of windthrown trees) in the multivariate models

might have enhanced their ability to predict Northern Waterthrush absence.

Dense shrub and herb layers provide foraging habitat and protection from

predators for many species of woodland birds (Golet et al. 1993). Extensive shrub cover

has been identified as a requirement of Northern Waterthrushes (Bent 1953; Craig 1985)

and Canada Warblers (Curson et al. 1994). Shrub and herb layers are often denser in

forested wetlands than in surrounding forested uplands (Golet et al. 1993).

Characteristics of foliage cover within 4 m of the ground influenced both species in the

current study, particularly Northern Waterthrushes. Foliage evenness was a significant

predictor of Northern Waterthrush occurrence in all analyses conducted, and appeared in

one of the Canada Warbler multivariate models. Although such indices have the

potential to confound abundance with distribution (Krebs 1989), in this study high values

of this index generally indicated high foliage cover in all layers, while low values

indicated sparse cover in certain layers. Because of the very small range of values

observed for this variable, even slight changes were readily apparent in the field (pers.

obs.). Canada Warbler incidence was > 0.5 where foliage cover exceeded 22% in the 2-

to 4-m stratum. This insectivorous species gleans and hawks for insects at all levels within tall shrubs (Curson et al. 1994; pers. obs.). A negative relationship existed between Canada Warbler occurrence and deciduous foliage cover within 0.5 m of the ground. Robbins et al. (1989) also found that Canada Warblers prefer sites with sparser ground cover. As a ground-nesting species, Canada Warblers may prefer an open ground layer to enhance visibility of approaching predators.

Northern Waterthrushes and Canada Warblers both occurred in deciduous, mixed, and evergreen swamps throughout the study area. However, evergreen or mixed swamps appeared more likely to support breeding populations of both species than deciduous swamps. For example, a positive relationship was apparent between Northern Waterthrush occurrence and evergreen canopy cover. A similar, but nonsignificant, trend was detected for Canada Warblers. There were comparable trends for both species for three other variables that, in turn, were positively correlated with evergreen canopy cover; these included tree diversity ($r = 0.499$, $p < 0.001$), basal area of snags ($r = 0.456$, $p < 0.001$), and peat thickness ($r = 0.462$, $p < 0.001$). In combination, high values for all four of these features create a typical profile of evergreen or mixed forested swamps in Rhode Island. Preference for mixed or evergreen forests has been reported previously for Northern Waterthrushes (Craig 1985; Robbins et al. 1989), but not for Canada Warblers. Evergreen swamps, composed primarily of Atlantic white cedar (*Chamaecyparis thyoides*), white pine (*Pinus strobus*), or eastern hemlock (*Tsuga canadensis*), are relatively scarce in Rhode Island; only 15% of forested wetlands in the study area are evergreen (RIGIS data).

Research Needs

Knowledge of general habitat requirements is often sufficient to explain the presence of a species at a certain location. The challenge in constructing accurate predictive models lies in identifying the characteristics that explain absence. Canada Warblers were generally excluded from sites near paved roads and from sites with surrounding uplands subjected to encroaching urbanization. Nest site availability may be a key limiting factor for Northern Waterthrushes; however, this habitat feature was not assessed in this study.

Wetland hydrology may be very dynamic (Mitsch and Gosselink 1993). Annual fluctuations in the local water table may affect many aspects of wetlands, including wildlife populations. Future research should investigate the influence of annual variations in saturated substrate and surface water cover on breeding habitat selection by Canada Warblers and Northern Waterthrushes.

The mere presence of birds at a site does not necessarily indicate that those birds are breeding successfully (Wenny et al. 1993; Van Horn et al. 1995). Future research should evaluate nesting or pairing success to distinguish between source and sink populations of these species. It would also be useful, for management purposes, to examine the effects of specific human land uses on each species. The urban and agricultural land use variable employed in this study comprised a broad range of land use types.

Conservation Implications

Current state and Federal regulations protect most forested wetland habitat, but they do not adequately address cumulative permitted losses (Gosselink and Lee 1989). Impacts

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to wetlands from land use changes in bordering uplands are often regulated through the establishment of buffer zones (Golet et al. 1993), but the broader impacts of urbanization at the landscape scale cannot be addressed effectively by wetland regulations. In this study, the likelihood of encountering a Canada Warbler or a Northern Waterthrush increased with the size of the swamp, but the probability of occurrence for both species exceeded 0.5 even in swamps as small as 6 ha; both species were observed in sites as small as 0.8 ha. Landscape context must be considered in any attempts to conserve these swamp-dependent species. Canada Warblers appear to prefer heavily forested landscapes that are relatively undisturbed by human activity. Such conditions are becoming increasingly scarce as urbanization proceeds. The current decline in Canada Warbler populations (Sauer et al. 1997) may be a result of these land use changes. Northern Waterthrushes seem to be influenced more by the abundance of additional very poorly drained forested wetland habitat nearby. Increased protection of mixed and evergreen swamps, which are relatively rare in this region, may benefit both species.

The occurrence of Canada Warblers in forested wetlands may be predicted accurately from landscape characteristics alone. If appropriate GIS datasets are available, this approach would be much more efficient than conducting field surveys, and should produce comparable results. To accurately predict Northern Waterthrush occurrence, landscape and swamp habitat characteristics must be considered in combination.

APPENDIX

Spatial Correlation Analyses of Multivariate Logistic Regression Model Residuals, and of Landscape, Habitat, and Species Occurrence Variables

The results of spatial correlation analyses are presented for the residuals of my multivariate logistic regression models (Fig. 4), and for landscape-scale variables (Fig. 5), habitat variables (Figs. 6 and 7A – 7D), and species occurrence variables (Figs. 7E – 7F), using Moran's I analyses. Moran's I Coefficient is defined as follows (Gamma Design Software 1999):

$$I(h) = N(h) \, \Sigma \, \Sigma \, z_i \, z_j \, / \, \Sigma \, z_i^2$$

where: $I(h)$ = autocorrelation for interval distance class h;

z_i = the measured sample value at point i;

z_j = the measured sample value at point i + h.

Values of this statistic range from −1.0 to +1.0 and can be interpreted similarly to Pearson's Product Moment correlation statistic.

Table 1. Stratification of study sites, based on forested wetland size and total forest cover within 2 km.

Swamp size class (ha)	Plots[b]/site	Forest cover[a]						Total sites	Total plots
		0 - 50%		50 - 75%		75 - 100%			
		Sites	Plots	Sites	Plots	Sites	Plots		
0.5 - 5	1	4	4	4	4	4	4	12	12
5 - 10	1	4	4	4	4	4	4	12	12
10 - 20	2	2	4	2	4	2	4	6	12
20 - 50	2	2	4	2	4	2	4	6	12
50 - 100	4	1	4	1	4	1	4	3	12
100 - 200	4	0	0	2	8	0	0	2	8
200 - 400	4	0	0	2	8	1	4	3	12
Totals		13	20	17	36	14	24	44	80

[a] *Total forest cover (upland and wetland) within a 2-km radius of the center of each swamp.*

[b] *Bird survey plots were circular, with a 50-m radius.*

Table 2. Definitions of landscape and habitat variables selected for analyses.

Variable	Definition
Landscape	
D_RDS	Distance (km) to the nearest paved road.
LOGAREA	Log base 10 of area (ha) of the very poorly drained forested wetland study site.
FOR2K	Percent cover of forest (upland and wetland) within 2 km.
FORESTRD	Total length (km) of paved roads in forested areas within 2 km.
RZ_URB	Residual value of combined percent cover of urban and agricultural land uses within 2 km, after variability due to FOR2K was removed.
RZ_VFW	Residual value of total area of very poorly drained forested wetland within 2 km, after variability due to study site area was removed.
Habitat	
CCEVG	Percent cover of evergreen tree canopy.
TREEDIV	Index of tree diversity, based on average basal area of individual species within each plot, using the Shannon-Wiener formula (Krebs 1989). A value of zero indicates the presence of only one species.
BA_SNAG	Basal area (m^2/ha) of snags.
FC2-4	Percent cover of deciduous and evergreen foliage, 2 - 4 m from ground.
FCD<0.5	Percent cover of deciduous shrub and herb foliage, 0 - 0.5 m from ground.
FEI	Index of foliage evenness, created from cover estimates from four vertical strata (0 - 0.5 m, 0.5 - 1 m, 1 - 2 m, 2 - 4 m), based on the Shannon-Wiener formula. Low values indicate low evenness and low overall foliage cover; high values indicate high evenness and high overall foliage cover.
W	Percent cover of surface water.
S	Percent cover of saturated substrates.
MOSS	Percent cover of *Sphagnum* moss.
PEAT	Thickness (cm) of peat layer.

Table 3. Spearman rank correlation coefficients for independent variables used in the logistic regression analyses.

Variable[a]	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1. D_RDS	1.000															
2. LOGAREA	0.454	1.000														
3. FOR2K	0.399	0.043	1.000													
4. FORESTRD	-0.398	-0.302	0.084	1.000												
5. RZ_URB	-0.329	-0.182	-0.053	0.382	1.000											
6. RZ_VFW	-0.091	0.295	-0.224	-0.169	-0.193	1.000										
7. MOSS	0.283	-0.157	0.307	0.044	-0.152	-0.079	1.000									
8. CCEVG	0.301	0.285	0.417	-0.048	0.099	-0.007	0.201	1.000								
9. BA_SNAG	0.381	0.331	0.233	-0.262	-0.067	0.088	0.113	0.456	1.000							
10. FCD<0.5	-0.339	-0.324	-0.131	0.299	-0.014	-0.157	0.060	-0.397	-0.407	1.000						
11. FC2-4	0.058	0.064	0.288	0.042	-0.059	-0.102	0.082	-0.094	-0.070	-0.221	1.000					
12. W	-0.217	-0.321	-0.091	0.229	0.090	0.010	0.283	-0.173	-0.214	0.075	0.138	1.000				
13. TREEDIV	0.136	0.206	0.354	0.038	0.137	-0.097	0.017	0.499	0.178	0.019	-0.086	-0.278	1.000			
14. FEI	-0.050	0.102	-0.105	-0.041	-0.126	0.100	0.179	-0.032	-0.019	0.394	-0.239	-0.026	0.053	1.000		
15. S	-0.105	-0.123	-0.054	0.057	0.067	-0.031	0.471	-0.023	-0.027	0.182	0.061	0.224	-0.123	0.350	1.000	
16. PEAT	0.053	0.184	0.017	0.024	0.239	-0.191	-0.117	0.462	0.116	-0.276	0.064	-0.258	0.128	0.195	0.190	1.000

[a]Variable codes defined in Table 2.

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Table 4. Characteristics of forested wetland survey plots where Canada Warblers and Northern Waterthrushes were present and where they were absent during the breeding season in Rhode Island, 1997-1998.

	Canada Warbler								*Northern Waterthrush*							
	Absent *n = 27*			*Present* *n = 53*					*Absent* *n = 24*			*Present* *n = 56*				
Variable[a]	Median	*25th %ile*	*75th %ile*	Median	*25th %ile*	*75th %ile*	Z^b	p^c	Median	*25th %ile*	*75th %ile*	Median	*25th %ile*	*75th %ile*	Z^b	p^c
D_RDS (km)	0.25	0.18	0.42	0.63	0.42	0.78	4.74	<0.001	0.45	0.22	0.67	0.48	0.27	0.72	0.60	0.550
AREA (ha)	7.14	1.42	36.16	48.44	15.11	108.44	3.60	<0.001	16.52	2.29	50.12	26.49	11.31	106.04	1.99	0.047
FOR2K (%)	56.85	47.08	68.17	71.28	63.92	85.35	3.23	0.001	57.97	47.95	84.41	68.98	58.30	81.42	1.50	0.133
FORESTRD (km)	17.30	11.94	24.99	14.50	10.60	16.85	-2.45	0.014	14.48	11.84	20.03	15.19	10.99	18.82	-0.40	0.686
RZ_URB (%)	3.69	0.49	7.20	1.30	-2.65	2.90	-2.87	0.004	1.80	-2.41	6.09	1.91	-0.68	3.48	-0.23	0.817
RZ_VFW (ha)	-6.36	-32.17	8.32	-11.59	-34.39	22.89	0.04	0.972	-18.34	-33.09	-5.11	-5.96	-33.28	33.37	1.64	0.101
CCEVG (%)	0.00	0.00	5.11	6.82	0.00	30.68	2.70	0.007	0.00	0.00	5.97	4.83	0.00	32.67	2.59	0.010
TREEDIV	0.41	0.12	0.96	0.69	0.38	0.91	1.39	0.165	0.39	0.10	0.78	0.73	0.35	0.92	2.25	0.025
BA_SNAG (m²/ha)	1.60	0.64	4.12	3.17	1.83	5.49	2.26	0.024	1.85	0.49	3.91	3.07	1.42	6.79	2.52	0.012
FC2-4 (%)	46.62	38.34	56.42	54.73	42.06	67.06	1.76	0.079	53.97	39.27	73.65	49.75	40.12	62.75	-1.00	0.319
FCD<0.5 (%)	47.30	38.29	63.68	38.34	21.45	51.86	-2.01	0.044	37.08	20.69	60.05	42.15	23.99	56.33	0.30	0.765
FEI	0.97	0.93	0.99	0.98	0.95	0.99	0.62	0.538	0.94	0.92	0.97	0.98	0.96	0.99	3.96	<0.001
W (%)	7.10	2.84	31.44	4.26	1.42	18.18	-1.57	0.116	2.84	0.85	11.79	7.10	2.13	24.81	1.29	0.196
S (%)	17.33	9.09	29.55	23.01	17.61	26.99	1.08	0.278	13.59	8.10	24.57	24.15	17.90	30.40	3.18	<0.001
MOSS (%)	10.14	0.68	21.62	23.31	14.36	35.98	3.30	0.001	10.30	0.68	23.23	22.97	14.70	34.21	2.90	0.004
PEAT (cm)	147.50	42.50	266.25	202.50	128.75	256.25	1.01	0.314	140.00	42.50	262.50	206.88	128.13	262.50	1.73	0.083

[a]*Variable codes defined in Table 2.*

[b]*Adjusted Z-scores from Mann-Whitney U test.*

[c]*P-values from Mann-Whitney U test.*

Table 5. Stepwise logistic regression models explaining presence and absence of Canada Warblers and Northern Waterthrushes at 80 survey points in 44 Rhode Island forested wetlands. Models were developed from landscape variables only, habitat variables only, and landscape and habitat variables combined. Variable codes are defined in Table 2.

Variable selected	Models					
	Canada Warbler landscape	Canada Warbler habitat	Canada Warbler combined	Northern Waterthrush landscape	Northern Waterthrush habitat	Northern Waterthrush combined
Constant	-4.749	1.398	-29.003	-1.305	-26.502	-24.200
1	D_RDS 3.812[a]	MOSS 0.061	D_RDS 6.243	RZ_VFW 0.014	FEI 23.294	FEI 18.299
2	LOGAREA 1.218	FCD<0.5 -0.033	FEI 24.826	FOR2K 0.024	BA_SNAG 0.396	BA_SNAG 0.368
3	RZ_URB -0.104	W -0.035	FC2-4 0.042	LOGAREA 0.558	TREEDIV 2.623	TREEDIV 3.178
4	FOR2K 0.036		FOR2K 0.055		W 0.044	W 0.069
5			FORESTRD -0.142		S 0.077	S 0.109
6						LOGAREA 1.013
7						RZ_VFW 0.018
CCR[b] present (%)	94.3	90.6	84.9	92.9	87.5	89.3
CCR absent (%)	70.4	55.6	70.4	29.2	54.2	66.7
CCR overall (%)	86.3	78.8	80.0	73.8	77.5	82.5
Model Chi-square[c]	39.4***	20.2***	45.8***	11.5**	35.2***	43.4***

[a]*Coefficient*

[b]*Correct classification rate.*

[c]*$**p < 0.01$, $***p < 0.001$.*
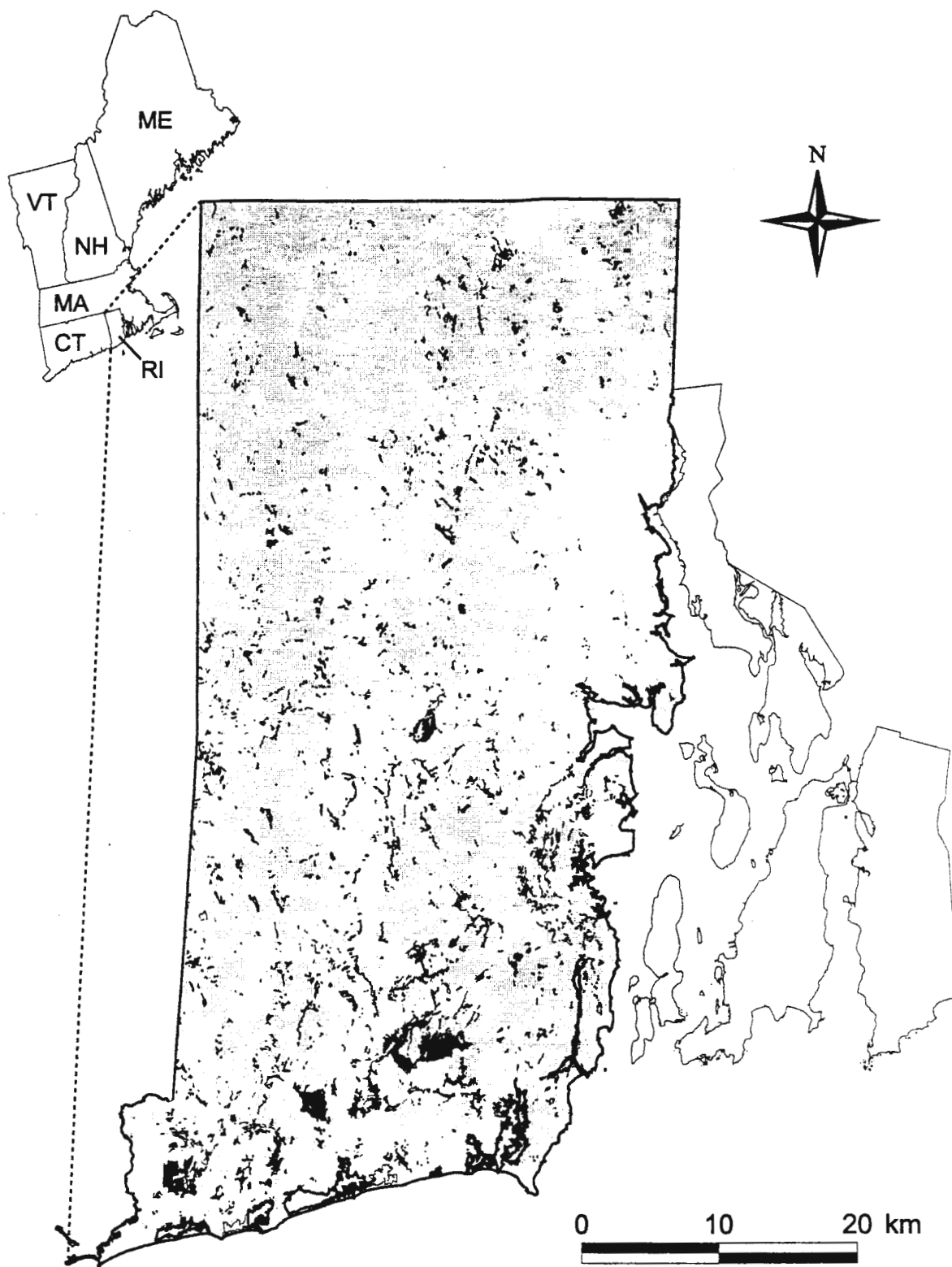
Figure 1. Distribution of very poorly drained forested wetland (black) and other forest cover (gray) in the study area, which comprises most of mainland Rhode Island and is bounded by bold lines.
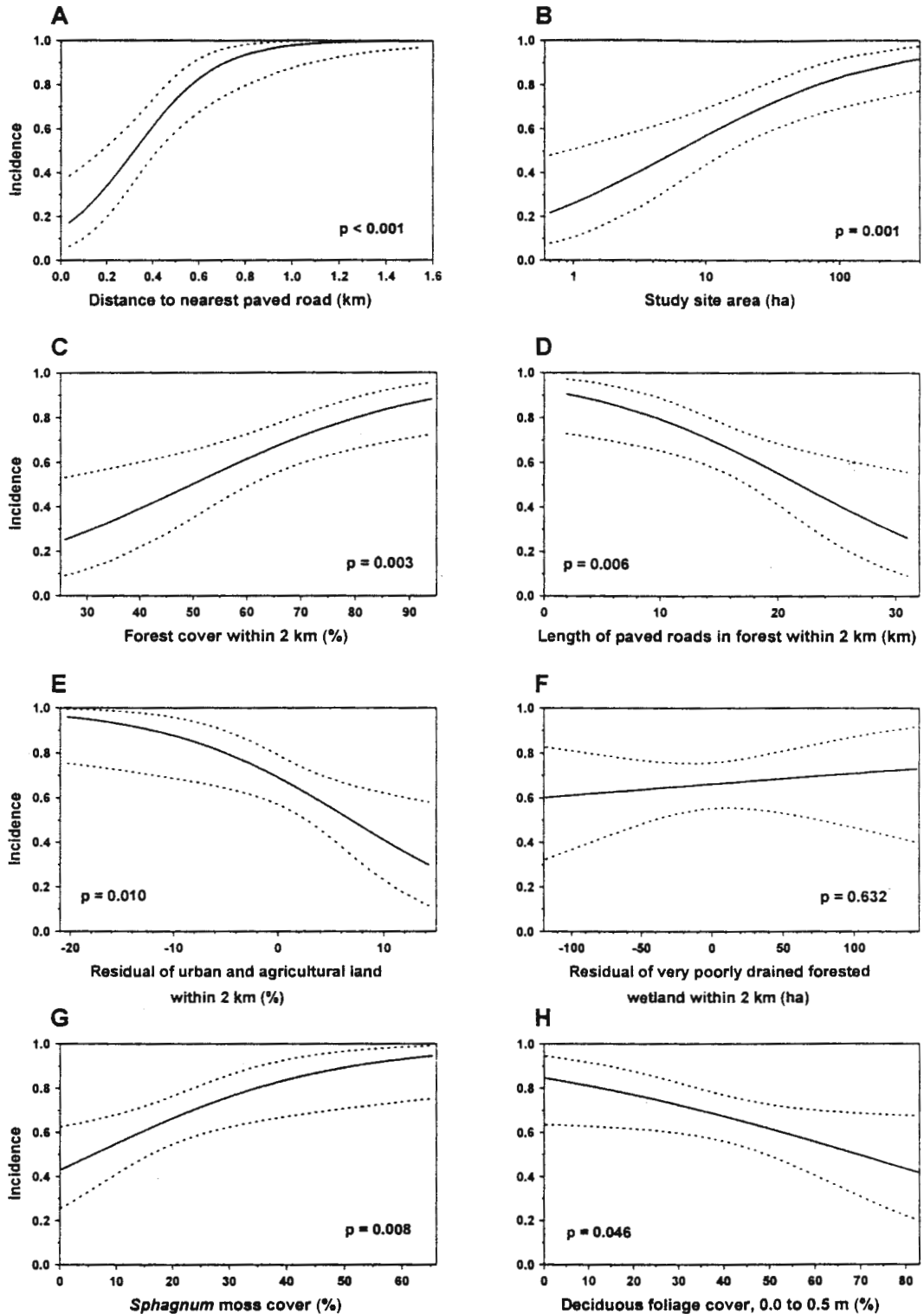
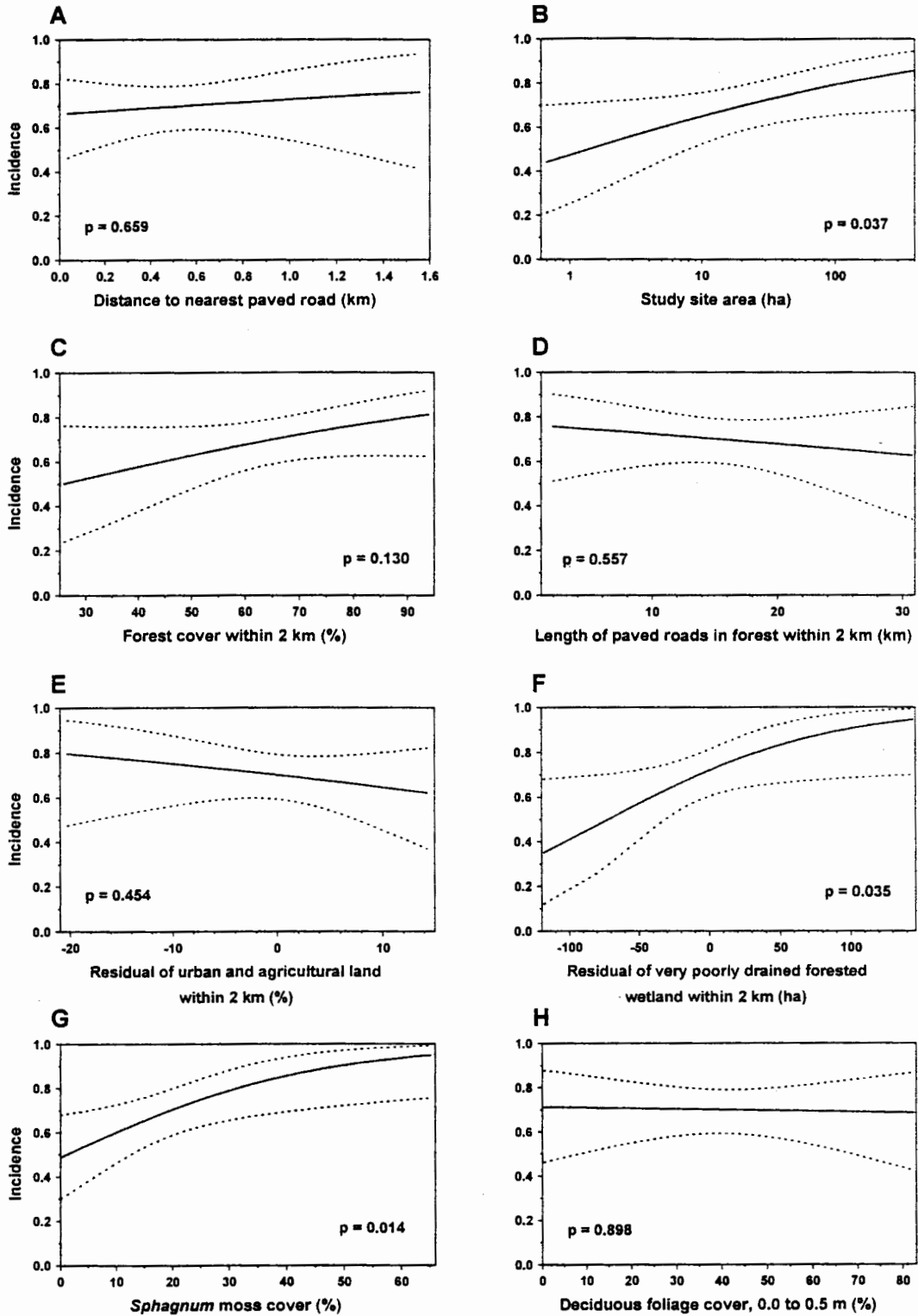*Figure 2. Incidence of Canada Warblers in Rhode Island forested wetlands as a function of landscape and habitat variables. Incidence is the probability of occurrence of Canada Warblers at a survey point for each value of the independent variable. Graphs were created using univariate logistic regression. Dashed lines indicate 95% confidence intervals.*
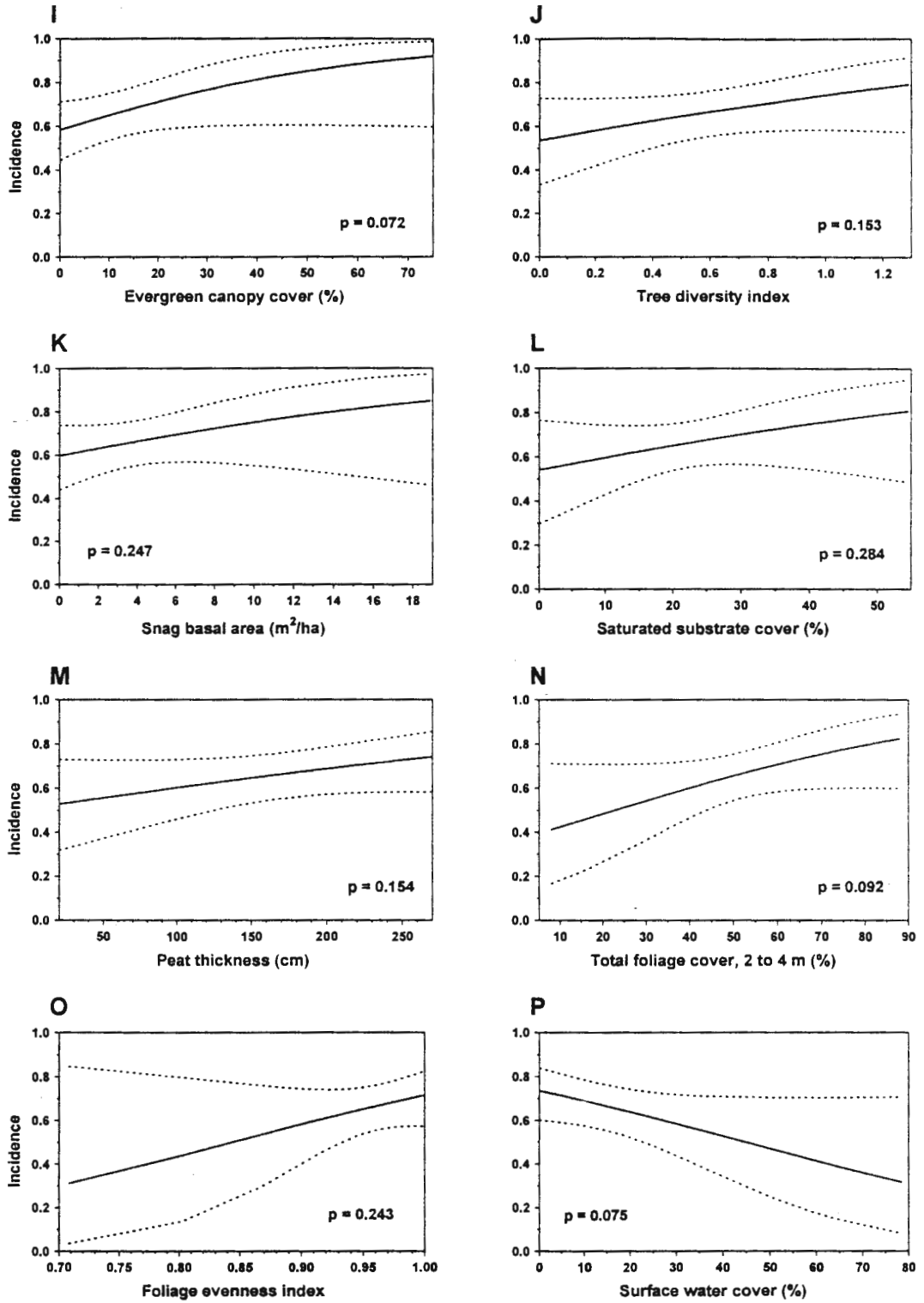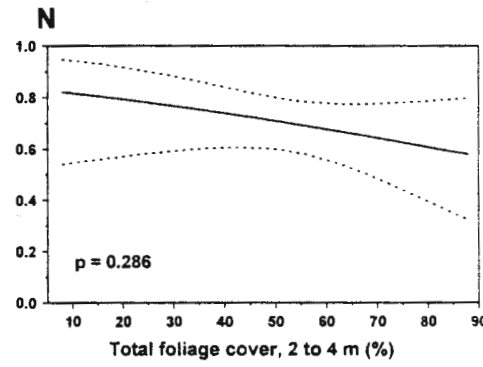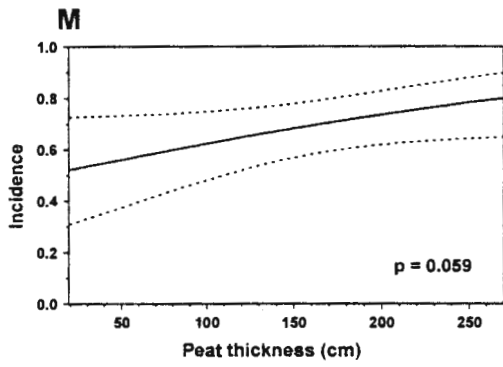
Figure 2. (continued)

Figure 3. Incidence of Northern Waterthrushes in Rhode Island forested wetlands as a function of landscape and habitat variables. Incidence is the probability of occurrence of Northern Waterthrushes at a survey point for each value of the independent variable. Graphs were created using univariate logistic regression. Dashed lines indicate 95% confidence intervals.
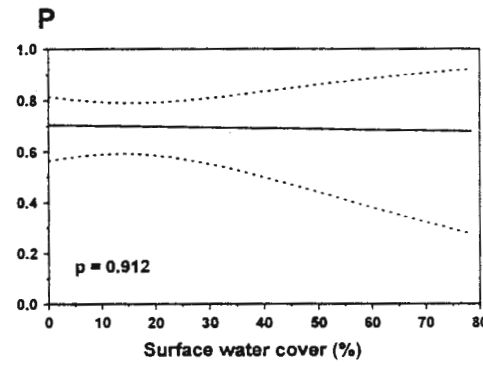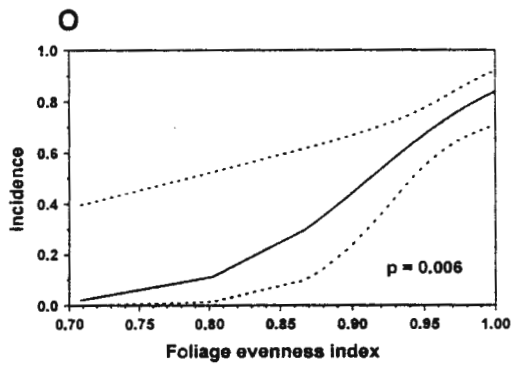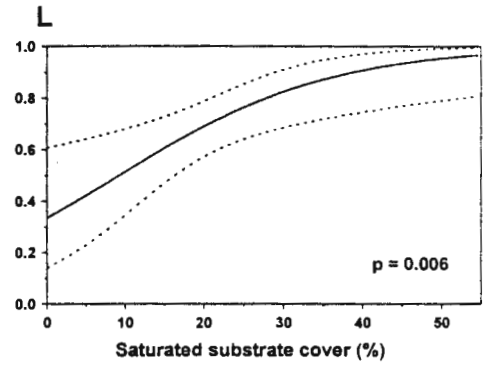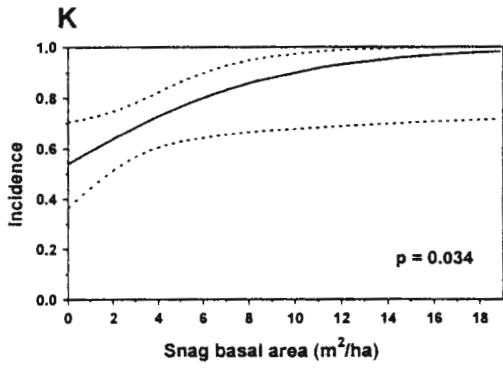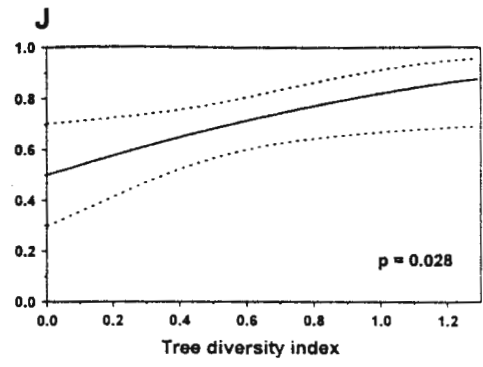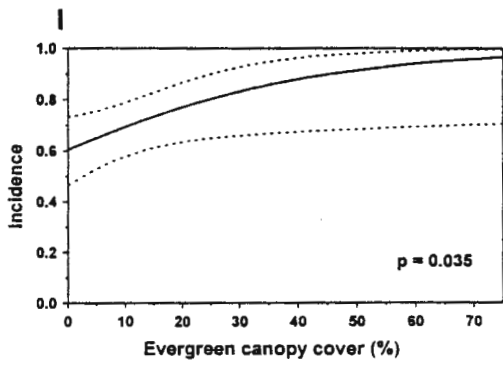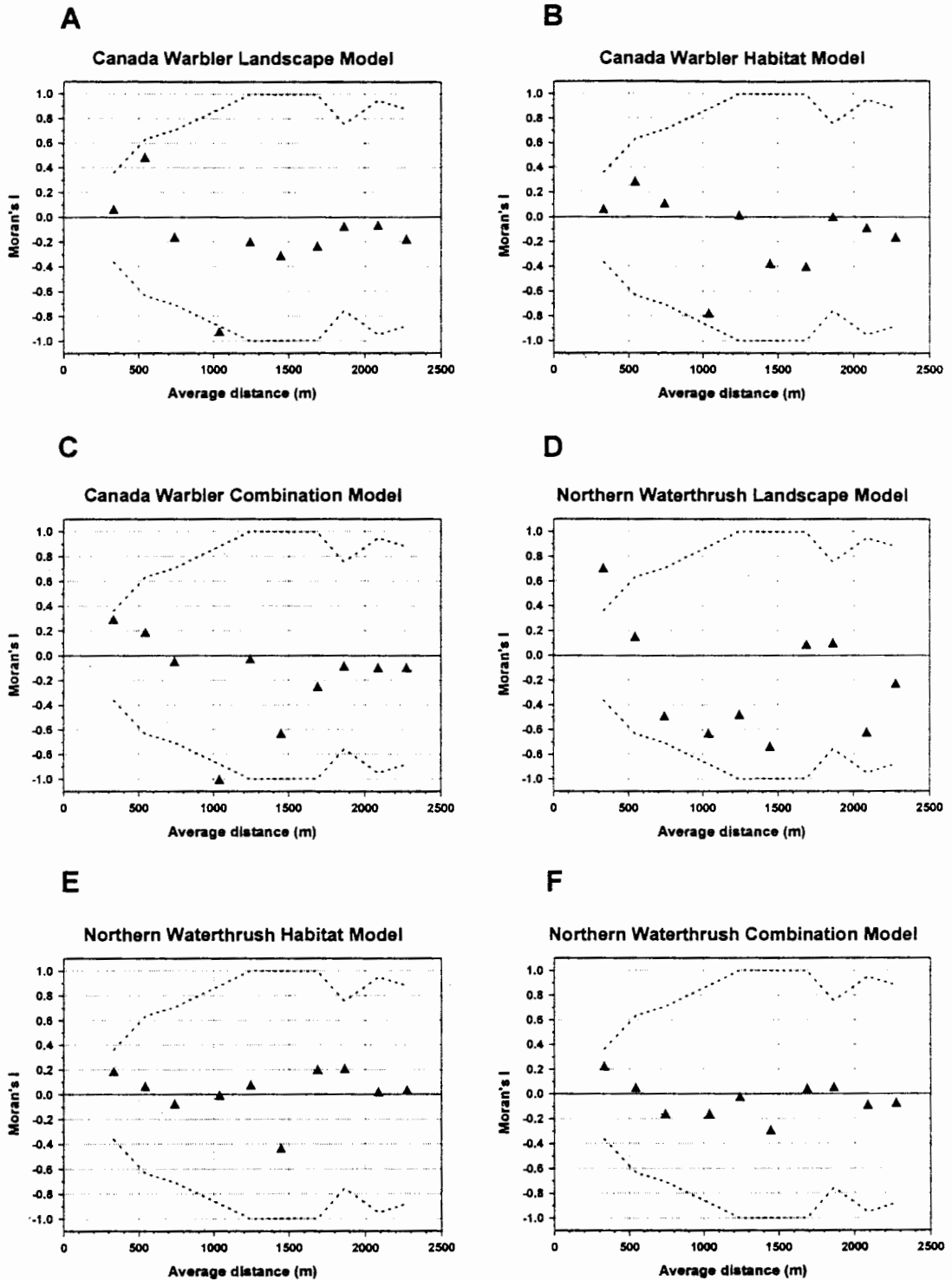
Figure 3. (continued)

Figure 4. Spatial correlation analyses of the residuals of multivariate logistic regression models, based on Moran's I Coefficient. Dashed lines indicate critical values of I (p < 0.05).
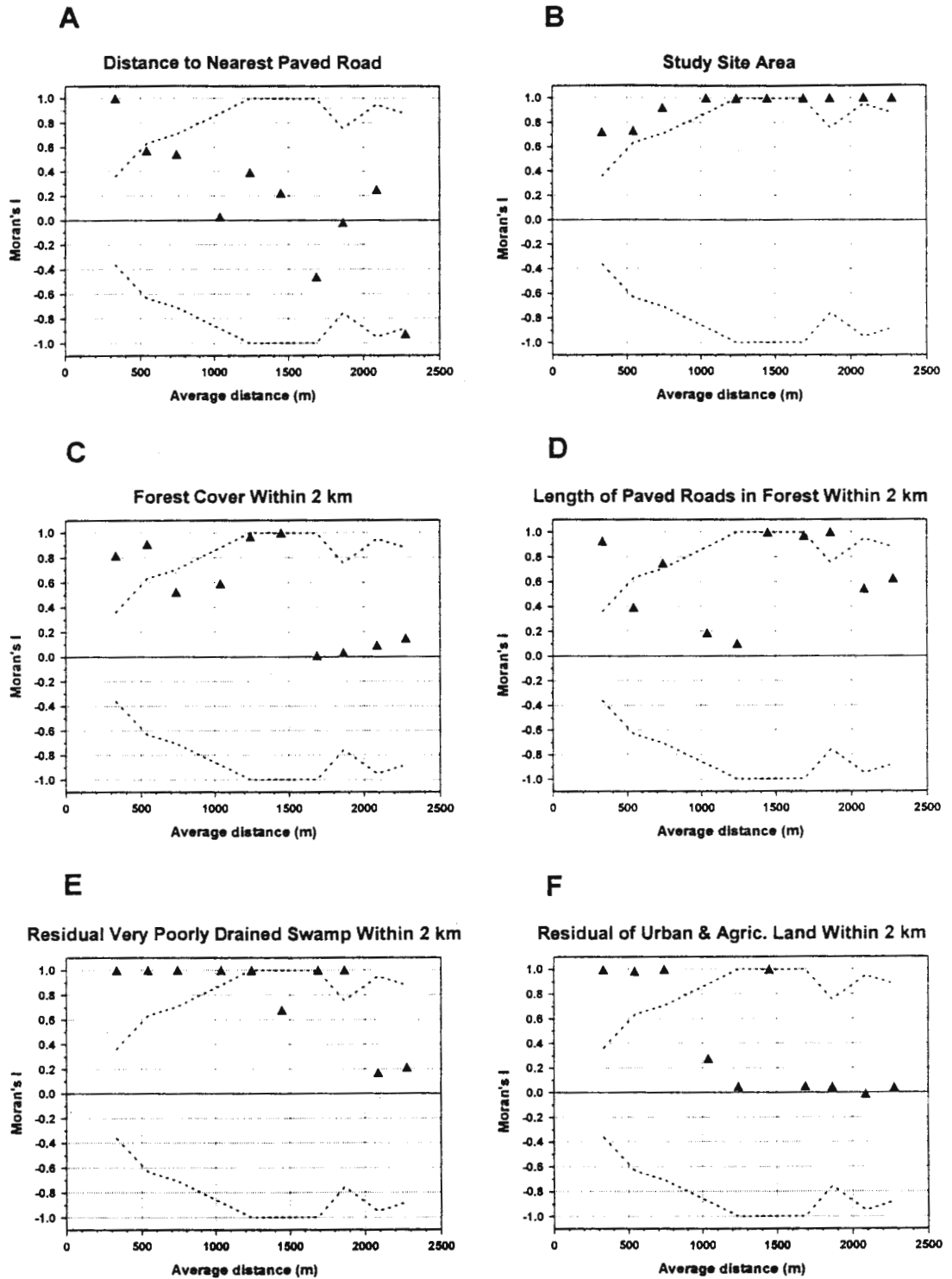
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Figure 5. Spatial correlation analyses of landscape variables, based on Moran's I Coefficient. Dashed lines indicate critical values of I (p < 0.05).
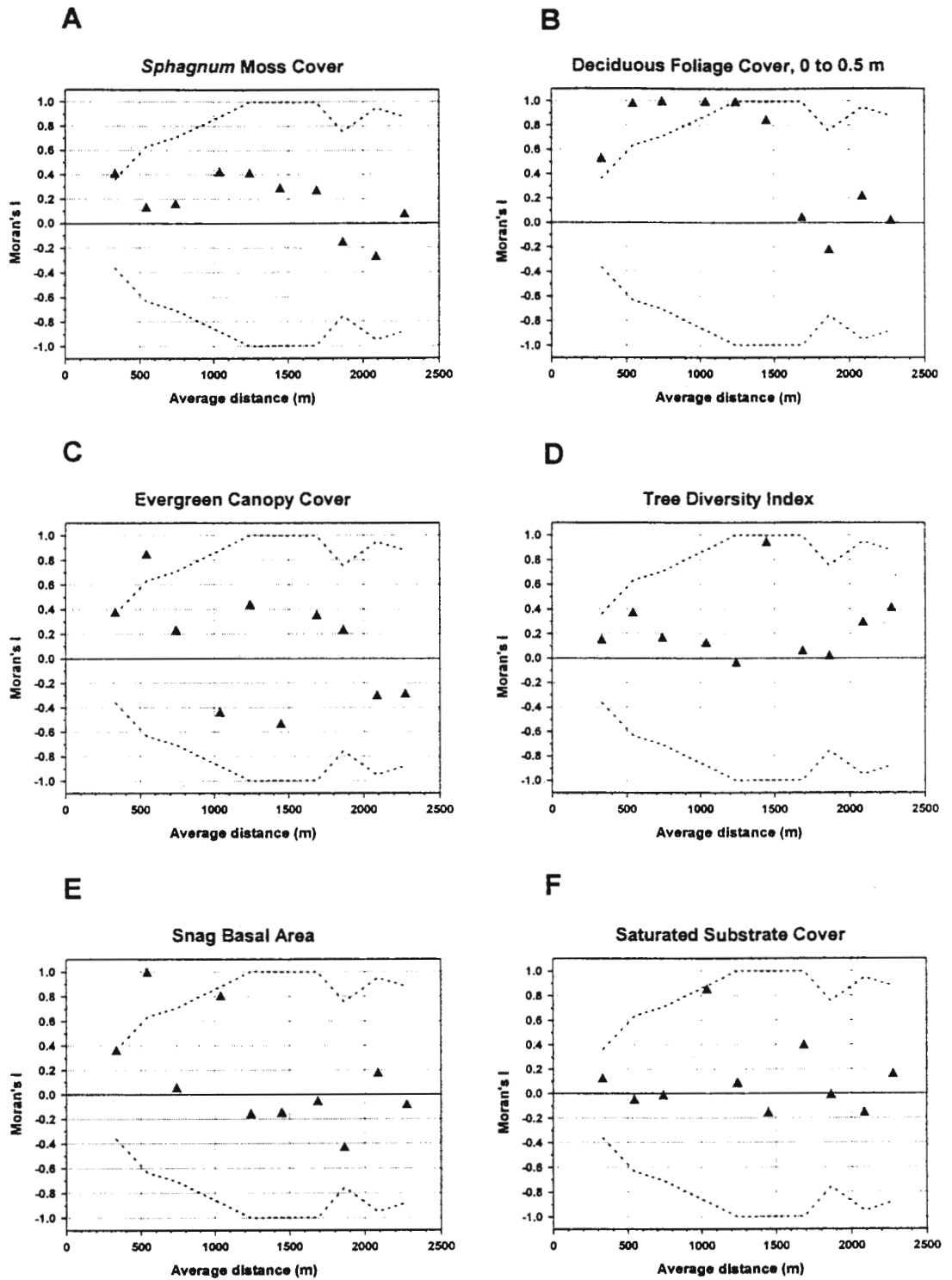
Figure 6. Spatial correlation analyses of habitat variables, based on Moran's I Coefficient. Dashed lines indicate critical values of I (p < 0.05).
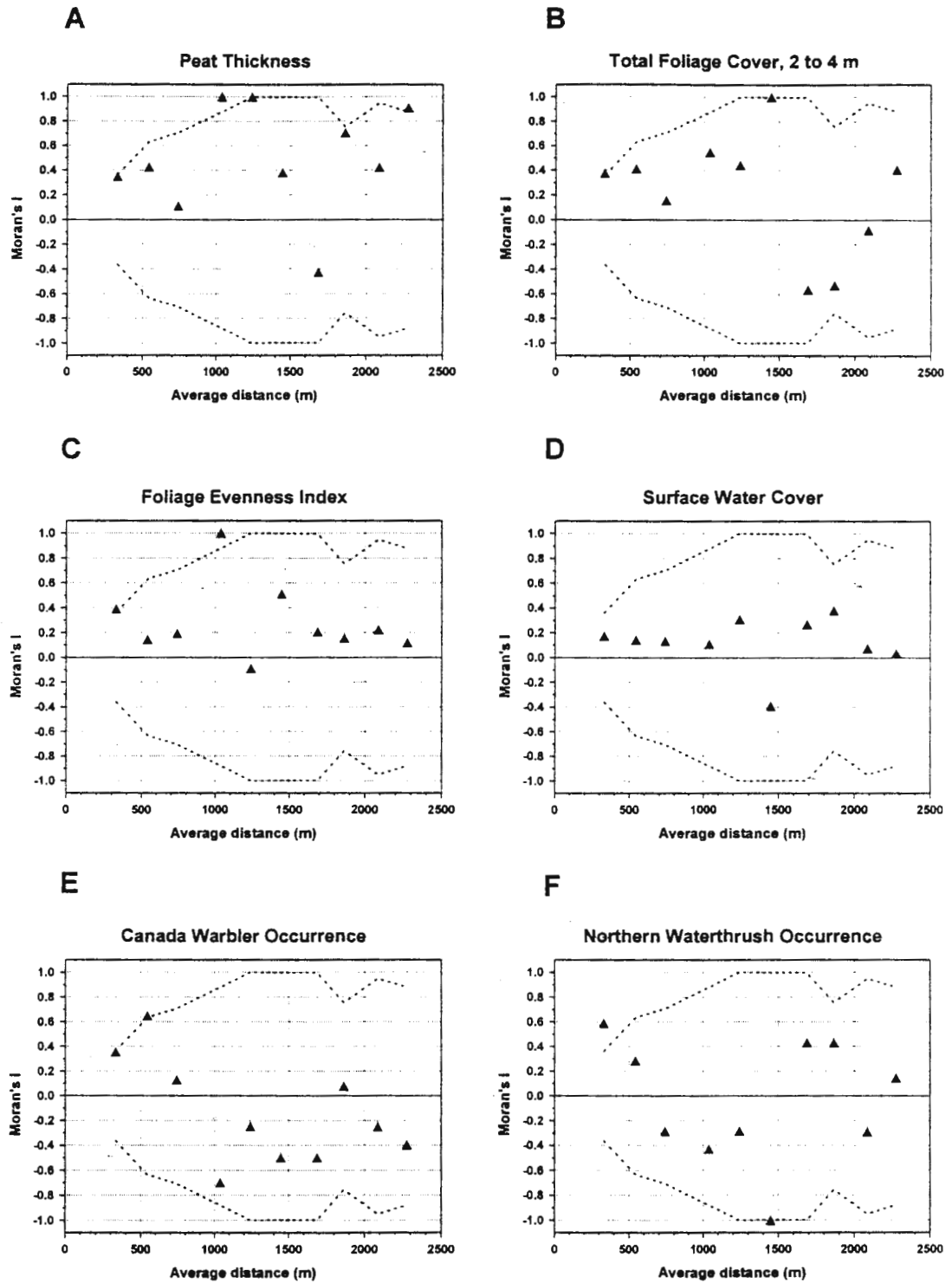
Figure 7. Spatial correlation analyses of habitat and species occurrence variables, based on Moran's I Coefficient. Dashed lines indicate critical values of I (p < 0.05).

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