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TESTING THE GENERALITY OF PATCH AND LANDSCAPE-LEVEL PREDICTORS OF TREE SQUIRREL OCCURRENCE AT A REGIONAL SCALE

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Few investigators have considered whether predictors of species occurrence from 1 locality are useful predictors in others, or how regional factors may constrain occurrence. We used landowner questionnaires over 6 regions in Indiana to test the performance of predictors from prior studies of more limited spatial extent. Logistic regression and classification tree models were constructed using data on 577 forest patches supplied by 362 landowners. Consistent with predictions, probability of occurrence of eastern gray squirrels (*Sciurus carolinensis*) was related positively to forest patch size and percent of forest in the surrounding landscape. Also, probability of occurrence of North American red squirrels (*Tamiasciurus hudsonicus*) was related positively to the presence of black walnut trees (*Juglans nigra*) and conifers in forest patches, and negatively to the presence of gray squirrels. Occurrence rates of *S. carolinensis* increased from north to south, whereas occurrence rates of *T. hudsonicus* increased from south to north and from west to east. Based on landowner perceptions, abundance of *T. hudsonicus* was more likely to increase in north and central regions, and to decline in patches with walnuts and at sites with longer periods of observation by landowners. Although less detailed than studies restricted to a particular locality, questionnaire data permit ecologists to test the generality of local findings and to further formulate and refine hypotheses about processes underlying large-scale patterns.

Key words: agriculture, eastern gray squirrel, forest, fragmentation, North American red squirrel, occurrence, scale, *Sciurus carolinensis*, *Tamiasciurus hudsonicus*

A species' distribution results from a complex interplay of ecological factors operating at relatively restricted spatiotemporal scales, and evolutionary factors operating across broader scales (Brown 1984; Brown et al. 1996). However, anthropogenic change can rapidly create novel environments and destroy native habitat. Many regions around the world have experienced radical human-induced shifts in ecosystems due to agriculture and, to a lesser extent, urban development. Such wholesale changes occurring over large spatial scales preclude evolutionary responses from many species, and could disrupt ecological processes that historically governed local dynamics. Clearly, consideration of multiple scales in studies of resource selection and biodiversity is especially important when considering anthropogenic disturbances (Beever et al. 2006; Bowyer and Kie 2006; Swihart et al. 2006). In particular, habitat loss and fragmentation can diminish the importance of interspecific interactions and emphasize the role of colonization ability in shaping patterns of local occurrence or abundance (Diffendorfer 1998; Hanski 1999).

Despite the importance of multiscale studies, progress has been slow because few projects have sufficient replication beyond modest spatial scales. When sampling across broader spatial scales has occurred, occurrence often is affected by variation among landscapes. Johnson et al. (2002) observed significant effects of landcover on occupancy of amphibians across 13 watersheds in the upper midwestern United States. Radford and Bennett (2004) demonstrated a relationship between patch occurrence of white-browed treecreepers (*Climacteris affinis*) and the proportion of woodland cover in replicated 100-km^2 landscapes in Australia. Similarly, Rizkalla and Swihart (2006) noted that wetland occupancy by aquatic turtles was strongly associated with variation in attributes of thirty-five 23-km^2 landscapes within the upper Wabash River basin, Indiana.

In addition, lack of generality plagues studies where predictive models of species richness, occurrence, or abundance are

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generated from data collected in a limited spatiotemporal context. For instance, habitat models make predictions that, strictly speaking, are relevant only for the target population for conditions under which the particular data were collected (Van Horne 2002). Only by broadening the spatiotemporal extent of sampling will we understand the range of conditions over which environmental variables can predict occurrence or abundance (Van Horne 2002). From the perspective of wildlife management and conservation, it is critical to understand the domain over which predictive models are applicable (Elith and Burgman 2002). Clearly, a broadening of the domain of applicability can enhance model utility.

Because of the challenges posed by field studies over broad spatiotemporal extents, complementary methods are needed to assess how factors at landscape, regional, or continental scales drive patterns of species occurrence and abundance. Synthesizing information derived from numerous smaller-scale studies is one approach that has been applied recently to mammals. For instance, a meta-analysis of 12 populations of white-tailed deer (*Odocoileus virginianus*) in North America revealed a strong negative effect of forest cover on dispersal distances for juvenile males (Long et al. 2005). Here, we use landowner questionnaires to complement previous field sampling and to test whether environmental predictors of local occurrence were associated with patterns of occurrence in areas outside of the original study site, and how regional factors themselves were related to variation in occurrence. We conducted our study in Indiana, a state that exhibits a spatial gradient in forest loss, fragmentation, and agricultural intensity (Fig. 1). We focused on 2 species that differ dramatically in patch- and landscape-level responses to agriculturally induced forest fragmentation: eastern gray squirrels (*Sciurus carolinensis*) and North American red squirrels (*Tamiasciurus hudsonicus*).

Eastern gray squirrels (hereafter, gray squirrels) occur throughout the state (Mumford and Whitaker 1982), but are negatively affected by forest loss and fragmentation and have declined in abundance since the advent of extensive land clearing. Specifically, in an agricultural landscape of west-central Indiana, density of gray squirrels within a patch was associated positively with patch area, and probability of occurrence in forest patches was associated positively both with forest patch area and proximity of a patch to other forest patches (Nupp and Swihart 2000). Experimental translocations verified that agricultural fields are a barrier to dispersal by gray squirrels (Goheen et al. 2003a), and a subsequent analysis of occupancy data from 35 landscapes across central Indiana revealed that gray squirrels were restricted principally to landscapes with relatively large forest patches in close proximity to other patches (Moore and Swihart 2005). Gray squirrels rely on hard mast, and are more likely to occur at greater densities in forest patches with a well-developed overstory of mast-producing trees (Moore and Swihart 2005; Nupp 1997). Feeding trials demonstrated a strong preference for black walnuts (*Juglans nigra*—Ivan and Swihart 2000).

North American red squirrels (hereafter, red squirrels) are found in 65 of 92 counties in Indiana, and evidence suggests that they have expanded their range southward throughout the state over the past century (Mumford and Whitaker 1982). In west-central Indiana, density of red squirrels was greatest in patches of intermediate size, and probability of occurrence was highest in medium-sized patches (Nupp and Swihart 2000). Local density also was related positively to the presence of conifers in forest patches (Nupp 1997). Experimental translocations verified that red squirrels are more capable of moving through agricultural landscapes than are gray squirrels (Goheen et al. 2003a). Analysis of occupancy data from 35 landscapes across central Indiana indicated that isolated patches with low basal area of mast-producing trees were more likely to harbor red squirrels, in contrast to the relationships observed for gray squirrels (Moore and Swihart 2005). Feeding trials demonstrated a strong preference for black walnuts (*J. nigra*—Ivan and Swihart 2000), although red squirrels are significantly less efficient than gray squirrels at extracting energy from walnuts and other hard mast (Goheen et al. 2003b). Anecdotal evidence suggests that interspecific competition may limit local occurrence of red squirrels; red squirrels were 3 times more abundant at sites without gray squirrels (Moore and Swihart 2005), and a negative effect of the density of gray squirrels on that of red squirrels was noted after accounting for variation in density due to local habitat and patch variables (Nupp and Swihart 2001).

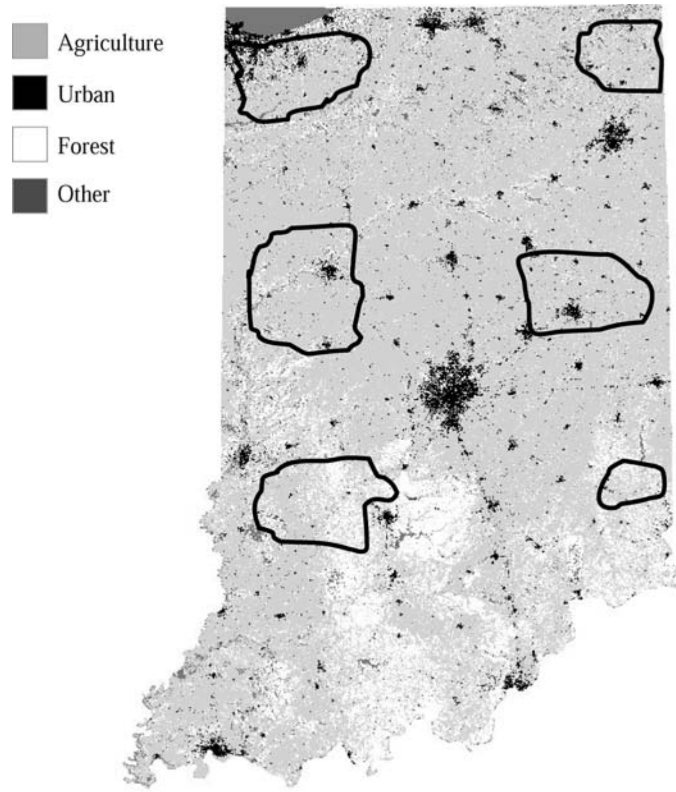

FIG. 1.—Land-use in Indiana, showing the 6 regions in which landowners received surveys.

We use the findings detailed above to address the generality on a statewide basis of specific patch and landscape attributes, as well as regional factors, in predicting local occurrence of tree squirrels (Table 1). Our previous research portrays gray

TABLE 1.—Predictions regarding effects of environmental features on occurrence or density of eastern gray squirrels and North American red squirrels. See text for descriptions of prior work on which predictions were based.

Variable	Gray	Red
Local habitat features		
Availability of black walnut	+	+
Availability of conifers	None	+
Area of forest patch	+	+[a]
Density of other species of squirrel	None	−
Landscape features		
Availability of forest in surrounding landscape	+	−
Prevalence of agriculture in surrounding landscape	−	None
Regional features		
Degree of forest loss and fragmentation	−	+

[a] Positive effect at intermediate patch sizes only.

squirrels as a species sensitive to forest fragmentation and reliant on mature hardwood forest. In contrast, red squirrels appear to occur in forest patches and landscapes considered suboptimal for gray squirrels, especially when conifers are present. How well do these characterizations generalize to other areas or times? We expected that local constraints on resource selection and population viability, that is, presence of seed sources and size of a forest patch, would influence occurrence of 1 or both species. Occurrence within a patch also was predicted to change with landscape context, that is, the availability of other forest patches and the prevalence of agriculture. Finally, we predicted that forest loss and fragmentation measured regionally impose additional constraints by altering environmental suitability over sizable portions of each species' range.

Materials and Methods

Survey.—During autumn 2000, a letter, questionnaire, and postage-paid return envelope were mailed to 1,488 landowners, evenly distributed among 6 regions in Indiana (Fig. 1). Recipients were selected randomly from within each region using a statewide database of landowners with at least 4 ha of woodland on their property. In the letter we introduced the study objectives (Appendix I). We emphasized the need for data to be reported for each forest patch > 0.4 ha on their property. To minimize confusion associated with varying vernacular names for species, we also provided recipients with a separate sheet containing copies of photographs and diagnostic characteristics for each species of tree squirrel in the state, as well as eastern chipmunks (*Tamias striatus*).

The survey consisted of one 2-sided sheet and had 3 parts (Appendix I). In part 1, respondents completed a table in which they provided the following information for each woodlot: size; presence of conifers; presence of black walnuts; percent of forest in a 0.8-km-radius circle surrounding the woodlot; presence of eastern fox squirrel (*Sciurus niger*), gray squirrel, red squirrel, or eastern chipmunk; county in which the woodlot occurred; and dominant land use in a 0.8-km (i.e., 0.5-mile) radius around the forest patch. Categories for land use included agriculture (further divided into row crops, small grains, and pasture/hay), forest (divided into timber production and recreation), residential, industrial, urban, and other. To facilitate accurate entry and reduce confusion, we provided a hypothetical example, with values entered in the 1st column of the data table (Appendix I).

In part 2 of the survey, we asked landowners to indicate for each species whether it had declined, increased, or stayed the same on their property. Because we were concerned about variation due to tenure length of landowners, we also asked them to provide us with a time span over which their observations had been based. Finally, in part 3 of the survey, we asked landowners to circle any pairwise interspecific aggressive encounters they had observed, and to identify the "winner" of these interactions.

In addition to the landowner survey, in November 2000 we mailed letters to 92 high school biology departments and all of the state's conservation officers to request distributional information on red squirrels. For high schools, we targeted counties for which no verified records of occurrence had been made (Mumford and Whitaker 1982). In each letter to high schools, we provided a high-resolution color photocopy of a red squirrel, along with a verbal description and a request to post the photocopy and record any information on locations about which they or their students were aware.

Statistical analysis.—We received responses from 362 landowners reporting data on 577 forest patches. The distribution of responses was homogeneous among the 6 regions ($\chi^2 = 2.04$, $d.f. = 2$, $P = 0.36$). We developed species-specific models for 2 response variables based on environmental predictors identified in prior studies over a small spatial extent (Table 1). The responses were occurrence in a forest patch, and whether an increasing (as opposed to decreasing) trend in abundance had been observed. We constructed models of occurrence for eastern gray squirrels in a forest patch based on local features of the patch (occurrence of black walnut and size of the forest patch) and features of the landscape in the surrounding 0.8-km-radius circle (percent in forest, whether agriculture was the dominant land use, and whether forest was the dominant land use). We used indicator variables for longitude (0 = west, 1 = east) and latitude (00 = south, 01 = central, 10 = north) as surrogates for regional predictors of occurrence. Based on the gradient in forest loss and fragmentation (Fig. 1), we expected the probability of gray squirrel patch occupancy to increase from north to south. Models predicting probability of increasing abundance relied on the same set of predictor variables, and time was included as a nuisance covariate.

For red squirrels, the probability of occurrence in a forest patch was modeled based on local features (occurrence of black walnut, conifers, and gray squirrels; and size of the forest patch) and features of the surrounding landscape (percent of forest and whether forest was the dominant land use). Latitude and longitude indicator variables were used to test predictions regarding regional effects; namely, we expected red squirrels to respond positively to the more heavily agricultural regions to the north and east. As with gray squirrels, models predicting probability of increasing abundance relied on the same set of predictor variables, with time included as a nuisance covariate.

Models were constructed using both logistic regression and classification trees. Logistic regression is a traditional method for modeling binary responses (Hosmer and Lemeshow 2000) and was adopted for consistency with prior modeling efforts in this system (Goheen et al. 2003a; Nupp and Swihart 2000). Because we were interested in testing the generality of variables previously identified as correlates of occurrence or density from a subset of the area contained in this study, no attempt at model selection was made. A single logistic model was fitted for each species and response variable. Goodness of fit was assessed using the test of Hosmer and Lemeshow (2000:148). Classification accuracy was assessed using the area under the receiver operating characteristic (ROC) curve. The area under the ROC curve provides a measure of a model's ability to discriminate between subjects who experience an outcome of interest (i.e., success) and those who do not (Hosmer and Lemeshow 2000:160–163). The ROC curve is determined by plotting sensitivity against 1 − specificity for the range of possible cutpoints, that is, probability values for determining a "success." A value of 0.5 for area under a ROC curve is what one would expect if the model did no better at discrimination than expected by chance. Values of 0.5–0.7 represent poor classification accuracy, whereas values of 0.7–0.9 are acceptable, and values > 0.9 represent excellent accuracy (Fielding and Bell 1997).

Classification trees are a nonparametric alternative to regression models, which recursively partition the data set into increasingly homogenous groups with respect to the response variable (Breiman et al. 1984; Vayssières et al. 2000). They are especially useful for demonstrating nonlinear relationships, and can handle missing data (De'ath and Fabricius 2000). The tree is structured hierarchically, with the undivided data set at the top (root node), followed by binary splits of the predictor variables (branches), ending at the terminal nodes (leaves) with the response. The proportion of variance explained by each predictor variable is represented by the branch length. The size of the tree is measured by the number of terminal nodes. Cross-validation and a cost-complexity index were used to determine the optimally sized tree (Vayssières et al. 2000). The cost-complexity index measures the additional accuracy of a tree given an increase in the number of nodes, and is thus similar to Akaike's information criterion (Burnham and Anderson 2002). A single tree was fit for each species and response variable using the RPART library (Therneau and Atkinson 1997) in R 2.1.1. Each model was evaluated with a misclassification rate and a ROC curve.

Throughout the remainder of the paper, we will use the following terms to refer to the 3 spatial scales examined in our analysis: local (i.e., attributes of a forest patch); landscape (i.e., attributes of the area within a 0.8-km radius of a focal patch); and regional (i.e., 1 of the 6 sampling areas targeted in the mailing and depicted in Fig. 1).

Table 2.—The proportion of patches for which tree squirrels were reported to occur in each of 6 regions of Indiana, based on questionnaires returned by landowners. For each entry, the numerator represents the number of forest patches in which presence was indicated, whereas the denominator represents the total number of forest patches for which data were reported in the region.

	Region		
Species	North	Central	South
Gray squirrel			
East	24/89	41/110	65/109
West	22/84	38/81	73/103
Red squirrel			
East	54/89	49/110	15/109
West	42/84	21/81	7/103

Results

Based on questionnaires returned, the percentage of patches containing gray squirrels was 65.1% in the southern regions, 41.4% in the central regions, and 26.6% in the northern regions (Table 2). For red squirrels, the occurrence rate in patches increased from 10.4% in southern regions, to 36.6% in central regions, and 55.5% in northern regions (Table 2). Occurrence rates in patches were 48.0% and 26.1% for red squirrels from eastern and western regions, respectively (Table 2).

Models of occurrence.—The logistic regression of gray squirrel occurrence demonstrated reasonable fit (Hosmer and Lemeshow $\chi^2 = 9.70$, $d.f. = 8$, $P = 0.29$) and acceptable accuracy (area under ROC curve = 0.77). Probability of occurrence in a patch was significantly related to patch size, percent of the surrounding landscape in forest, and latitude; occurrence rates were greater in larger patches in more forested, southerly landscapes (Table 3). The classification tree demonstrated acceptable accuracy (area under ROC curve = 0.73% and 27.1% misclassification). Latitude was the most important predictor, with occurrence most likely in southern regions. Occurrence was more likely in north and central regions when there was less than 43.75% forest in the surrounding landscape and patch size was greater than 22.7 ha (Fig. 2a). When surrounding forest (i.e., forest cover within a 0.8-km radius) was greater, occurrence was more likely in central than northern regions. In southern regions, gray squirrels were more likely to occur when there was greater than 11.25% forest in the surrounding landscape.

Six landowners reported aggressive interactions between gray and red squirrels. In all 6 cases, red squirrels were listed as the winner in these encounters. We tested for a negative effect of red squirrel occurrence on gray squirrel occurrence by regressing the Pearson residuals from our gray squirrel occurrence model against presence or absence of red squirrels. The effect of presence of red squirrels on occurrence of gray squirrels was negative but only marginally significant after controlling for variation explained by abiotic environmental features (standardized regression coefficient = −0.08, $F = 2.81$, $d.f. = 1, 472$, $P = 0.09$).

Table 3.—Results of logistic regression models predicting the probability of species occurrence or the probability of an increasing trend in abundance. Model coefficients are depicted for gray squirrels and red squirrels based on mail surveys from 6 regions in Indiana, during autumn 2000. *** $P \leq 0.01$; ** $0.01 < P \leq 0.05$; * $0.05 < P \leq 0.10$; ^{NS} $P > 0.10$.

Predictor variable	Occurrence models: Gray	Occurrence models: Red	Trend models: Gray	Trend models: Red
Local features				
Presence of black walnut	-0.15^{NS}	0.96***	-0.09^{NS}	−2.79**
Presence of conifers	—	0.82***	—	1.16^{NS}
Area of forest patch	0.01***	0.00^{NS}	0.01^{NS}	0.00^{NS}
Presence of other species of squirrel	—	−0.48*	—	0.43^{NS}
Landscape features				
Percent of forest in 0.8-km radius surrounding patch	0.02***	0.00^{NS}	0.00^{NS}	0.01^{NS}
Agriculture dominant land use in 0.8-km radius	-0.02^{NS}	0.52^{NS}	-0.40^{NS}	-1.11^{NS}
Forest dominant land use in 0.8-km radius	-0.02^{NS}	0.90**	-0.30^{NS}	-2.22^{NS}
Regional features				
Latitude indicator variable 1 (north = 1)	−1.64***	2.59***	-0.01^{NS}	3.69***
Latitude indicator variable 2 (central = 1)	−0.79***	1.78***	-0.14^{NS}	2.50**
Longitude (east = 1)	0.58^{NS}	0.96***	0.83*	-0.85^{NS}
n	474	474	117	71

The logistic regression of red squirrel occurrence resulted in a good fit (Hosmer and Lemeshow $\chi^2 = 5.24$, $d.f. = 8$, $P = 0.73$) and acceptable accuracy (area under ROC curve = 0.80). Probability of occurrence in a patch was significantly related to the presence of walnuts and conifers, forest as a dominant land cover, longitude, and latitude; occurrence rates were greater in patches containing walnuts or conifers and in forest-dominated landscapes of northern or eastern regions (Table 3). The occurrence of gray squirrels also had a negative effect on the probability of red squirrels in a patch (Table 3). The classification tree demonstrated acceptable accuracy (area under ROC curve = 0.78 and 23.6% misclassification). Latitude was the most important predictor, with occurrence most likely in northern and central regions. Red squirrels were likely to be absent in southerly regions (Fig. 2b). In the central region, occurrence was more likely in patches surrounded by more than 17.5% forest within 0.8 km, with patch size less than 19.2 ha, and in the east-central region. In northern regions, red squirrels were more likely to occur in patches containing walnuts.

Models of population trends.—The logistic regression model for temporal trends in the abundance of gray squirrels yielded a reasonably good fit (Hosmer and Lemeshow $\chi^2 = 4.79$, $d.f. = 8$, $P = 0.78$) but poor accuracy (area under ROC curve = 0.62). No predictors were significant, although there was a marginal tendency for gray squirrels to increase in eastern regions of the state (Table 3). On the other hand, the classification tree demonstrated acceptable accuracy (area under ROC curve =

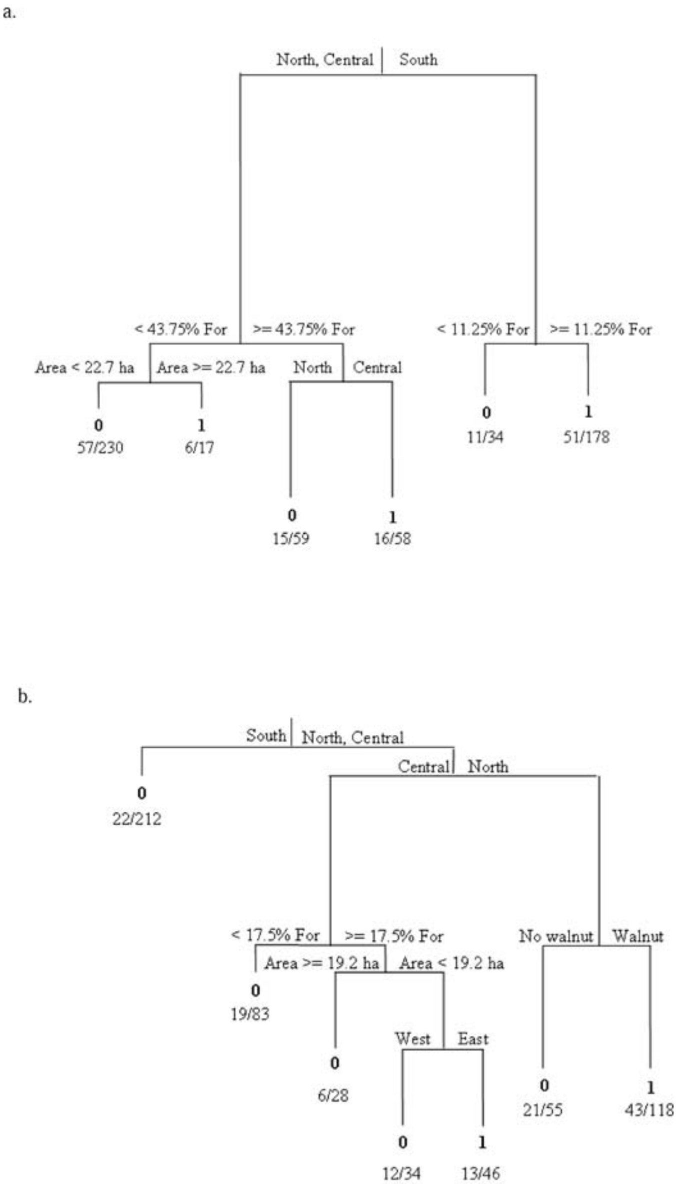

Fig. 2.—Classification trees for squirrel occupancy. Predictor variables and the level defining a split are labeled at each branch split. Branch lengths are proportional to the amount of variance explained by the variable at the split. Terminal nodes represent the presence (1) or absence (0) of squirrels. The proportion of misclassifications is provided below each node. a) Gray squirrel occupancy; misclassification was 27.1%. b) Red squirrel occupancy; misclassification was 23.6%. Abbreviations: % For = percentage of forest in the surrounding 0.8-km-radius circle; Area = area of forest patch.

0.79 and 24.3% misclassification). Gray squirrels tended to decrease in patches with less than 12.5% forest in the surrounding landscape (Fig. 3a). With greater than 37.5% of the surrounding landscape forested, decreasing abundance was noted when landowners had made the observations between 10.5 and 15.5 years. When observations were made over 15.5 years, abundance also decreased in patches where agriculture was not the dominant surrounding land use. Increasing

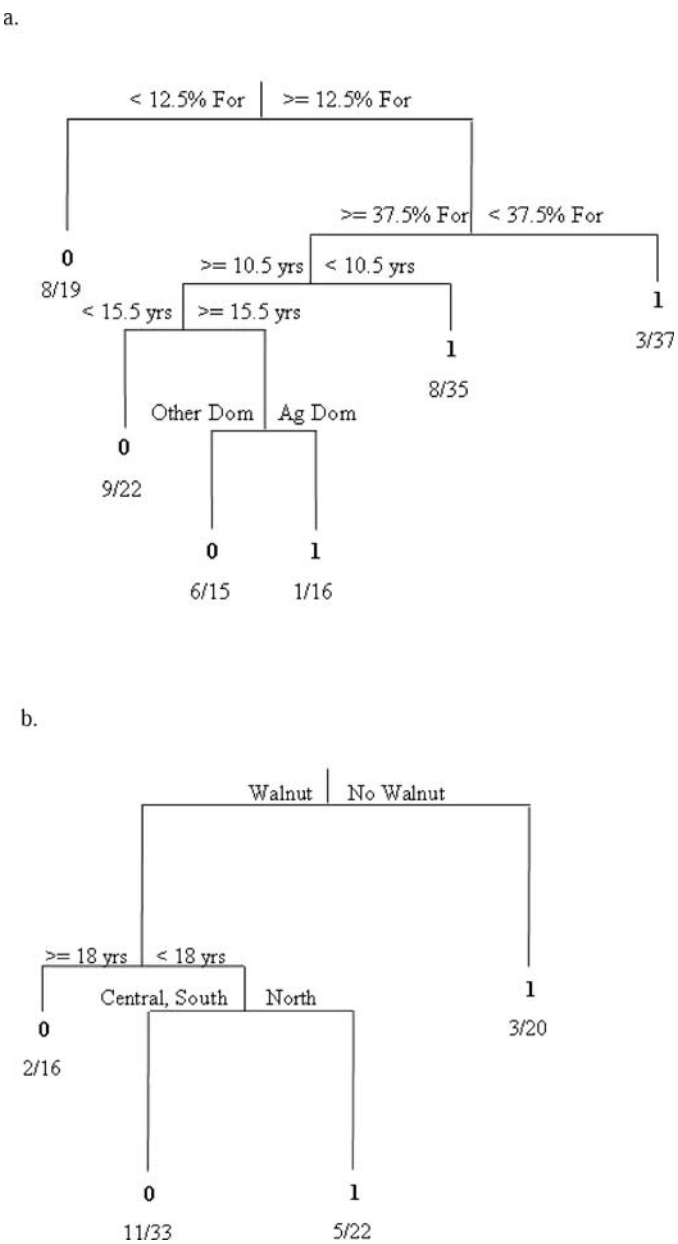

FIG. 3.—Classification trees for reported trends in squirrel abundance. Predictor variables and the level defining a split are labeled at each branch split. Branch lengths are proportional to the amount of variance explained by the variable at the split. Terminal nodes represent decreasing (0) or increasing (1) trends for squirrels. The proportion of misclassifications is provided below each node. a) Classification tree for gray squirrel trends; overall misclassification was 24.3%. b) Classification tree for red squirrel trends; overall misclassification was 23.1%. Abbreviations: Ag Dom = dominant land use is agriculture in surrounding 0.8-km-radius circle; Other Dom = dominant land use is something other than agriculture.

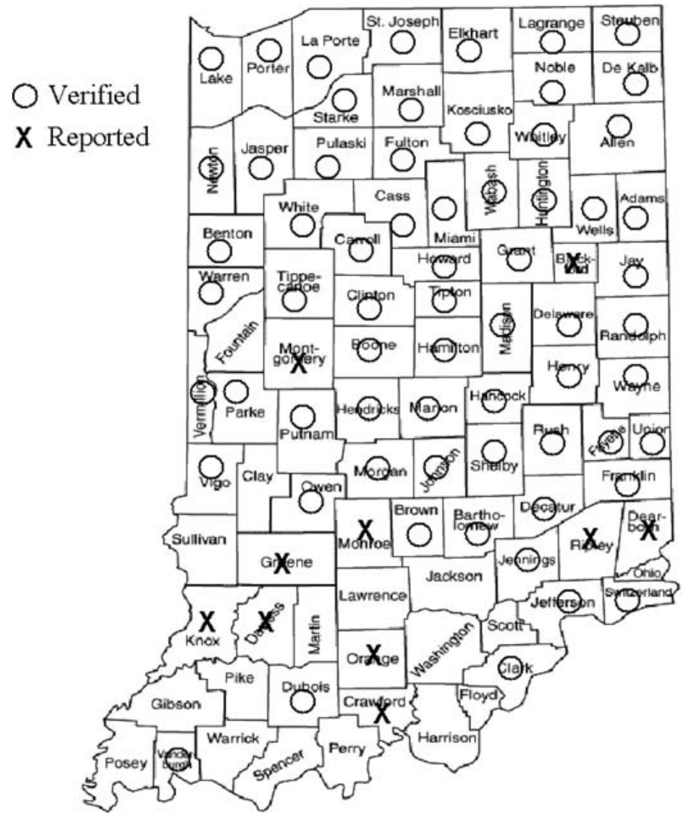

FIG. 4.—Map of Indiana showing verified occurrences of red squirrels (Mumford and Whitaker 1982) and occurrences reported by respondents to mailings sent to landowners, conservation officers, and high school biology teachers during October–November 2000.

abundance was observed with 12.5–37.5% forest in the surrounding landscape. When there was greater than 37.5% forest, increases also were observed in less than 10.5 years.

In contrast to gray squirrels, the logistic regression model for population trends in red squirrels exhibited both a reasonable fit (Hosmer and Lemeshow $\chi^2 = 11.41$, $d.f. = 8$, $P = 0.18$) and acceptable accuracy (area under ROC curve = 0.84). The probability of red squirrels increasing at a site was greater in northern and central regions (Table 3), whereas the probability of declining red squirrel populations increased at sites with walnuts, in landscapes dominated by forest, and over longer observation periods (Table 3). The classification tree also demonstrated reasonable accuracy (area under ROC curve = 0.81 and 23.1% misclassification). Decreasing abundance was reported in patches containing walnuts, when observations had been made over 18 years, and in fewer years in central and southern landscapes (Fig. 3b). Increasing abundance was observed in patches without walnuts.

Returns from conservation officers, landowners, and a single high school biology teacher provided putative records of red squirrels in 10 of the 27 Indiana counties for which verified occurrences had not been recorded (Fig. 4). All but 2 of these reports occurred in counties adjacent to a county with a verified record (Fig. 4).

DISCUSSION

Of 11 predictions regarding determinants of patch occupancy stemming from prior studies of limited extent (Table 1), 7 were supported by our regional analyses. Attributes of forest patches were important for both squirrel species, with support evident for 4 of 6 predictions. Specifically, questionnaire results reinforced the close affiliation of gray squirrels to large forest tracts (Moore and Swihart 2005; Nupp and Swihart 2000; Rosenblatt et al. 1999). They also supported the importance of black walnut and coniferous trees to red squirrels. Within forest patches, red squirrels select habitat containing black walnut (Goheen and Swihart 2005), presumably because it is a highly preferred food (Goheen et al. 2003b; Ivan and Swihart 2000). Conifers appear important for safety from predators; red squirrels with home ranges whose core areas contain conifers experience greater survival (Goheen and Swihart 2005). Finally, the presence of gray squirrels in a forest patch negatively affected occurrence of red squirrels, consistent with data published previously from a single landscape (Nupp and Swihart 2001) and 35 landscapes (Moore and Swihart 2005) of central Indiana. A weakness of statistical tests for competition, though, is their inability to account for the role of other important environmental predictors that were not recorded but that may explain substantial variation in abundance. Thus, we consider the evidence for competition circumstantial, with future verification requiring experimental manipulation.

Only 1 of the 3 landscape-scale predictions was supported by our questionnaire results; percent of forest in the surrounding landscape was an important predictor of the occurrence of gray squirrels. A larger percent of forest tends to be highly correlated with closer proximity of neighboring forest patches, and greater proximity favors occurrence of gray squirrels (Nupp and Swihart 2000). Proximity is important for gray squirrels because of their poorly developed ability to move between forest patches, at least when a matrix of row-crop agriculture is involved (Goheen et al. 2003a). It was somewhat surprising that agriculture as a dominant land use did not emerge as a significant determinant of occurrence of gray squirrels. It is possible that our decision to lump the different types of agricultural land uses into a single category masked the effects of row crops. A separate classification tree for occurrence of gray squirrels, using all land-use categories and the patch and regional predictors, produced a tree (not shown here) with acceptable accuracy but no contribution by row crops. Regional effects on occurrence were substantial (see below) and correspond to differences in land use (Fig. 1) that may have dwarfed any effects described at the 0.8-km scale we used for landscapes.

Regional variation in occurrence was pronounced, and varied in the manner expected based on the statewide gradient in forest loss and fragmentation. The 2 southern regions contained 35–40% forest cover, whereas the 4 more northern regions each contained 15–20% forest. Occurrence of gray squirrels was more likely in southern, more heavily forested regions, and least likely in the highly agricultural central and northern regions with few forests. Interestingly, our alternative classification tree using all land-use categories revealed a significant positive effect of residential land use on occurrence of gray squirrels in northern and central areas characterized by high levels of isolation and small patch size. This finding fits well with anecdotal observations that gray squirrels in the northern half of the state commonly are found in residential areas and parks. It also suggests that residential populations of gray squirrels may be demographically or genetically distinct from populations in forest stands because of their inability to cope with forest fragmentation.

In contrast to gray squirrels, occurrence of red squirrels was more likely in the highly fragmented northern regions, and least likely in the more forested southern regions. Also, increasing trends in abundance of red squirrels were reported in north and central regions. These increases could be a consequence of saturation of high-quality habitat by red squirrels, which is suggested by the trend for increasing populations in areas lacking black walnut, a preferred food resource associated with high-quality sites. The reason for a declining trend in patches with black walnut is less clear, although preferences for walnuts coupled with greater predation on red squirrels in walnut stands (Goheen and Swihart 2005) may result in walnut stands functioning as population sinks in some instances. Red squirrels routinely occupy woodlands considered to be poor-quality habitat for gray squirrels (Moore and Swihart 2005). It is possible that the restriction of gray squirrels to large, contiguous forests has increased the carrying capacity per unit forested area of north-central Indiana for red squirrels by effectively releasing them from interspecific competition with a granivore more efficient at exploiting food resources (Goheen et al. 2003b).

Although typically regarded as having strong affinities with coniferous forests, red squirrels have successfully expanded throughout Indiana in conjunction with agriculturally induced fragmentation. Human facilitation of red squirrel range expansion may have far-reaching effects on the composition of deciduous forests, because red squirrels larder-hoard seeds and thus are functionally distinct from scatter-hoarding gray squirrels (Goheen and Swihart 2003).

We believe that the use of questionnaires provides a potentially valuable tool for testing the scope and generality of prior findings, and for identifying new patterns worthy of investigation. Almost certainly, data from questionnaires are less reliable than data collected by trained professionals, but sacrificing precision may be acceptable to broaden inference and increase the generality of field studies, particularly when relatively easily identified organisms are targeted. Using questionnaire data, we demonstrated strong concordance between the distribution of 2 species of tree squirrel and predictions based on previous patch and landscape-level studies. Moreover, our study highlighted the importance of regional context in predicting local distributions of squirrels. Schweiger et al. (1999) similarly noted the importance of landscape context in predicting local distributions of grassland small mammals. Finally, analysis of questionnaire data revealed additional patterns (e.g., residential affinities of gray squirrels, expanded range of red squirrels, and population trends) that are plausible and merit verification via intensive field observation and experimentation.

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Appendix I

Letter and questionnaire sent to landowners in 6 regions of Indiana.

Dear Landowner:

Indiana is home to 3 species of squirrels that are active during daylight hours—fox, gray, and red (often called piney) squirrels—in addition to another member of the squirrel family, the chipmunk. Photographs and distinguishing characteristics of each species are provided on the enclosed sheet. Squirrels in Indiana are important game species. They also disperse acorns, walnuts, and hickory nuts, aiding in regeneration of these valuable hardwoods. We at Purdue are interested in updating the distribution and status of tree squirrels, something which has not been done since 1982. In addition, we are interested in learning more about the habitats they use and the extent to which they share forest habitat. But Indiana is a big state, so we need your help!

Please take a few minutes to answer the following questions as they relate to squirrels living on your property. It is equally important for us to know if no squirrels occur on your property. The information you provide is important in helping to increase our understanding of these squirrels. We would like to receive information for each woodlot or forest stand on your property. For our purpose, forest stands and woodlots are blocks of woodland at least 1 acre in size. We use the terms forest stand and woodlot interchangeably, even though woodlots typically refer to woodlands surrounded by agriculture and forest stands often imply active management of forests. We define forest stands as being distinct from each other if they are physically separated by at least 25 yards, with open ground in between.

We realize that your schedule is busy, and we truly appreciate your cooperation. Please return the completed form in the postage-paid envelope provided. Your responses will be kept confidential and will be used only to study squirrel–habitat relations statistically.

Sincerely,

Robert K. Swihart	Jacob R. Goheen
Professor of Wildlife Ecology	Graduate Student

1. Using a separate column for each forest stand on your property, please provide the following information in the table below:

√ Give an approximate size in acres for each stand or woodlot on your property.
√ Mark with an "X" all stands or woodlots in which pine trees or spruce trees (conifers) occur.
√ Mark with an "X" all stands or woodlots in which black walnut trees occur.
√ Approximate the percentage of forest land in a ½ mile radius surrounding the stand or woodlot.

Describe the dominant land use in a ½-mile radius. Please select from the following choices:

a) Agriculture–row crops
b) Agriculture–small grains
c) Agriculture–pasture/hay
d) Forest−timber production
e) Forest−recreation
f) Residential
g) Industrial
h) Urban
i) Other (please specifiy)

√ Place an "X" in the appropriate boxes according to the squirrel species found in a particular stand or woodlot. Mark the "None of the above" box if no squirrels or chipmunks occur in a stand.
√ Finally, please write the county in which your stand is located.

As an example, suppose that I have a forest stand of 6 acres that contains pines. About 10–20% of the land is forested in a ½-mile radius surrounding the stand. Corn production is the dominant land use in a ½-mile radius around the stand. Fox squirrels, red (piney) squirrels, and chipmunks are found in the stand. My stand is located in Warren County. I would fill out the table like this:

Please fill in the remainder of the above table for your property. If your property contains more forest stands than can be accommodated by the table, feel free to add columns to the bottom of this sheet or on a separate page.

Stand/Woodlot

Size (acres)	6 acres				
Contain pine or spruce?	X				
Contain black walnut?					
% surrounding forest	10−20%				
Dominant land use	a				
Fox squirrel	X				
Gray squirrel					
Red (piney) squirrel	X				
Chipmunk	X				
None of the above					
County containing stand	Warren				

2. Since you've lived at your current residence, please mark with an "X" in the following table whether you think that squirrel numbers have increased, decreased, or stayed about the same.

Squirrel species	Increased	Decreased	About the same
Fox squirrel			
Gray squirrel			
Red (piney) squirrel			
Chipmunk			

Over what period of time (for example, 1984–2000, or 1996–2000) did you make the observations upon which the conclusions about changes in squirrel numbers are based? _______ – _______.

3. Have you noticed aggressive interactions between squirrels of different species on your property? (Circle all responses that apply)

Fox squirrel–Gray squirrel
Gray squirrel–Red squirrel
Fox squirrel–Red squirrel
No aggressive interactions

For each interaction you circled, please write which species appeared to win.

Thank you for your assistance. Please return the completed questionnaire in the postage-paid envelope provided.