

Habitat associations and assemblages of small mammals in natural plant communities of Wisconsin

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Determining habitat associations of small mammal species and environmental characteristics important for site occupancy are central to understanding species biology and community organization. Most studies of small mammal communities are done at a local scale and in 1 habitat, overlooking patterns manifest over a heterogeneous landscape. During the summers of 2009 and 2010 we trapped small mammals throughout Wisconsin at 180 sites among 13 natural habitats, capturing 3,261 individuals of 23 taxa. We modeled site occupancy using habitat characteristics for 16 taxa while incorporating imperfect detection and compared small mammal community similarity among habitats. Site variation in tree density, soil moisture regimes, and winter temperatures were the most important variables in describing occupancy of species. With the exception of *Zapus hudsonius* and *Sorex hoyi*, occupancy rates of species were not the same across habitats. Species-specific responses to habitat characteristics created distinct natural habitat associations leading to unique and predictable small mammal assemblages. This study demonstrates the importance of sampling across a wide range of environmental gradients and habitats when determining the distribution of species and how communities are organized at a landscape level.

Key words: habitat associations, landscape ecology, natural plant communities, occupancy modeling, small mammals, spatial scale, Wisconsin

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Determining habitat associations of small mammal species and environmental characteristics important for site occupancy are central to understanding the basic ecology and community organization of small mammals. Small, nonvolant mammals (rodents and insectivores < 250 g) often constitute the majority of mammalian taxa in a region and although small, they are ubiquitous and can have profound impacts on local floral and faunal communities. Specifically, small mammals play a crucial role in structuring plant composition and diversity by consuming vegetation, seeds, and fruits, and acting as agents of dispersal for seeds and spores (Maser et al. 1978; Gibson et al. 1990; Howe and Brown 2000; Vander Wall et al. 2001). In addition to providing a vital prey base for avian and mammalian predators (Buskirk and MacDonald 1984; Knick 1990; Swengel and Swengel 1992), they prey on other small mammals and insects (Getz et al. 1992; Andersen and Folk 1993). Because small mammals play such an important ecological role and with the anticipated changes in global temperatures and concomitant changes to habitats, a clearer

understanding of the relationship of small mammals with environmental and abiotic elements has become imperative.

Most studies of small mammals are conducted at local spatial scales, and often make inferences about community composition at broader regional scales. This approach is useful for identifying local environmental variables important for the presence of a species or for shaping community structure; nevertheless, local sampling may overlook patterns at larger geographical scales. Moreover, studies of small mammals often investigate discrete ecosystems or a subset of species in a region. Interpretations of these results are limited to a single system or ecotype and can neglect spatial heterogeneity that takes place over successional, moisture, or temperature gradients within a region. Thus, in order to more thoroughly understand species distributions and small mammal community



composition within a region, it is useful to take a broadscale approach and sample small mammals over a large geographical area and a wide range of habitats. Additionally, investigating small mammals in natural habitats avoids complicated synergistic and antagonistic interactions that may occur in anthropogenically altered systems (Martell 1983; Rowe et al. 2010).

Environmental characteristics important for occurrence and community composition of small mammal species have been examined separately in North American forests (McShea et al. 2003; Coppeto et al. 2006; Zwolak 2009), prairies (Grant and Birney 1979; Grant et al. 1982; Foster and Gaines 1991), and wetlands (Francl et al. 2004). However, small mammal communities in the Great Lakes region have received remarkably little attention and those studies that have investigated small mammals did so for a subset of species (Getz 1961a, 1961b, 1961c), at a local scale (Evrard 1998), in a single ecosystem (Finnell 2000; Anthony 2003), or in systems with considerable anthropogenic perturbation (Chapman and Ribic 2002). The Great Lakes region is characterized by rich small mammal assemblages, diverse and spatially heterogeneous natural plant communities, and marked toposequence and temperature gradients, offering an exceptional landscape to investigate small mammal community composition.

Much of the Great Lakes region has been scoured by glaciations, leaving a landscape with diverse local toposequences (Dott and Attig 2004; Serbin and Kucharik 2009). This is of particular consequence in Wisconsin, where an edaphic moisture gradient coupled with a salient north to south increasing temperature gradient creates a heterogeneous abiotic landscape. During the last 10,000 years, plants colonized this landscape based on site-specific geology, hydrology, soil type, and climate (Curtis 1959). Natural disturbances such as fire, flooding, drought, and wind act in concert with these abiotic conditions to create identifiable floristic assemblages, called natural plant communities (Curtis 1959). Generally in Wisconsin, boreal plant communities in the north grade into prairie communities in the south. Mammalian taxa follow a similar trend where unique boreal and prairie species combine with ubiquitous species to provide a rich mammalian diversity. Small mammals (< 250 g and nonvolant) represent 27 of the 69 mammals of Wisconsin, in part due to the diversity of habitats that occur within the state.

In order to identify environmental variables that may influence species occurrence and determine how small mammal communities structure at the habitat level in the Great Lakes region, we live trapped small mammals across a range of natural plant communities in Wisconsin. We accounted for imperfect detection (MacKenzie et al. 2002) and used a multimodel framework to assess variables that were most important to species occupancy (Burnham and Anderson 2002). Specifically, the objectives of our study were to determine environmental characteristics that best predict the presence of a given small mammal species, individual small mammal species' associations to Wisconsin natural plant

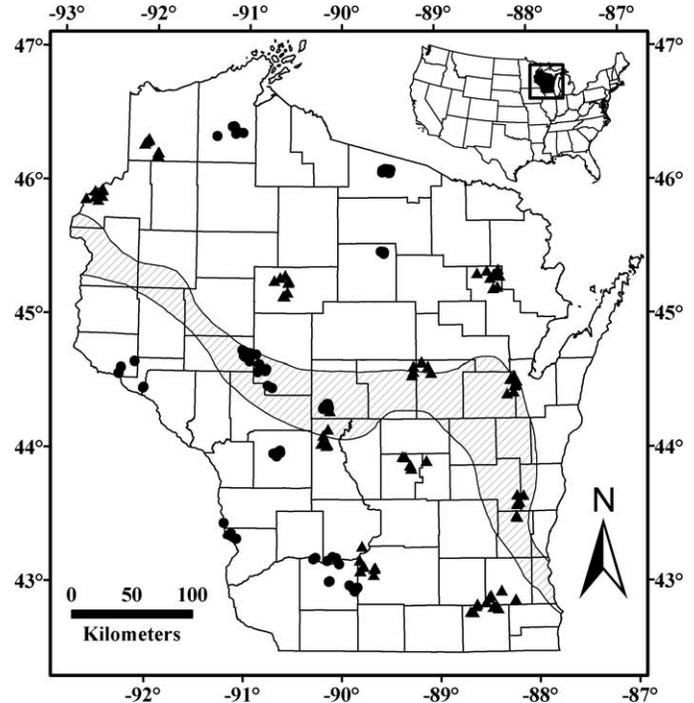


FIG. 1.—Map of Wisconsin depicting locations of small mammal trapping transects for 2009 ($n = 83$; •) and 2010 ($n = 97$; ▲) and distribution of the tension zone in crosshatch based on Curtis (1959).

communities, and how community composition varies across natural plant communities.

MATERIALS AND METHODS

Study area.—Wisconsin comprises nearly 170,000 km², extending from approximately 47°6' to 42°30' latitude and -92°54' to -86°48' longitude. It is marked by cold winters (mean January temperature from 1950 to 2006 was -9.5°C) and warm summers (mean July temperature from 1950 to 2006 was 21.1°C), with a general gradation of temperatures that are coolest in the northwest and warmest in the southeast (Serbin and Kucharik 2009). Temperatures in eastern Wisconsin are moderated by Lake Michigan (Serbin and Kucharik 2009). Across Wisconsin, total annual precipitation averages 808 mm \pm 165 SD (Serbin and Kucharik 2009). Wisconsin is relatively flat, with elevations ranging from 177 to 595 m and, with the exception of the Driftless Area in the southwestern portion of the state, has been shaped by Pleistocene glaciations (Dott and Attig 2004). Soils of the Driftless Area are largely formed by fluvial weathering of the parent material and accumulation of windblown loess, whereas glacial deposits of till, loess soils, and lacustrine soils compose the majority of the state (Dott and Attig 2004).

Abiotic factors, primarily temperature, create 2 major distinct floristic divisions in Wisconsin, a northerly zone consisting of boreal flora and a southerly region consisting of prairie flora (Curtis 1959). A band between these zones, called the tension zone, contains a mix of both boreal and prairie flora

(Fig. 1). At a coarse scale, boreal and prairie divisions contain relatively homogeneous vegetation. However, because of variability in local soil nutrient levels, pH, moisture, and microclimates, the local assemblages of plants vary by species and abundance, creating unique combinations called natural plant communities (Curtis 1959). Primary northern natural communities include boreal forest, dry to wet northern forest, pine barrens, open bog, alder thicket, and northern sedge meadow (Curtis 1959). Southern natural communities include oak barrens, oak opening, mesic to wet-mesic southern forest, shrub carr, southern sedge meadow, and dry to wet prairie (Curtis 1959).

Extensive logging in the late 1800s, fire suppression, conversion of prairie to agriculture, and the ditching and draining of wetlands for agriculture and development have drastically reduced or disturbed the acreage of natural plant communities in Wisconsin (Samson and Knopf 1994; Addis et al. 1995; Frelich 1995; Detenbeck et al. 1999; Leach and Givnish 1999). This is most evident in southern Wisconsin where < 1% of native prairies and < 25% of wetlands remain (Samson and Knopf 1994; Addis et al. 1995). Nonetheless, remnant communities have persisted in a highly modified landscape and sampling these areas offers a glimpse of what presettlement small mammal communities may have resembled. We sampled at a total of 180 sites throughout the state of Wisconsin in mature to old-growth forests, wetlands, and prairie and savanna remnants (Fig. 1). State natural areas were used extensively during the study (Wisconsin Department of Natural Resources 2009), with property ownership including state, county, federal, reservation, and private.

Site selection.—Using a stratified sampling approach, we selected 23 study areas distributed relatively evenly across the state with 7, 7, and 9 sampling areas within the northern, tension, and southern floristic zones, respectively. Within each study area we selected 6–9 sites that had representative natural communities as defined by Curtis (1959) and Epstein et al. (2008). Each study area averaged 5.4 distinct natural community types and on average sites were 8.7 km (range 0.09–30.51 km) apart to maintain independence. Natural plant communities were aggregated into 13 groups based on similar vegetation and moisture content (see Appendix I), henceforth referred to as natural habitats. Each natural habitat averaged 13.2 sites (range 4–25 sites; Fig. 2); however, 8 sites (approximately 4%) were not assigned to a natural habitat category because their vegetation composition and structure were too dissimilar to be classified within the 13 groups and they lacked sufficient replication to be classified as an additional group (see Appendix I).

Small mammal trapping.—Transects of 190 m were established in each natural habitat and marked at 10-m intervals. Transects were placed ≥ 10 m from the edge of a habitat to avoid edge effects. When possible we aligned transects in a cardinal direction; however, because of the irregular shape and small size of many natural habitats, transects were often placed to fit. Small mammals can have substantial variation in population abundance from spring to

late summer as individuals are recruited into the trappable population (Merritt et al. 2001). To balance the bias of seasonal variation we started the field season in the north and moved southward in 2009 and vice versa in 2010.

Each transect consisted of 20 Sherman live traps ($7.6 \times 8.9 \times 23.9$ cm; H. B. Sherman Inc., Tallahassee, Florida) placed every 10 m and 10 pitfall traps (38-cm-deep, 20-cm-diameter, 10-liter floral cooler buckets; Syndicate Sales, Inc., Kokomo, Indiana) placed at every other trap interval. Rocky soil precluded pitfall installation in 6 dry prairies. The combination of trap types resulted in higher species richness and diversity than using either trap type independently (Stephens and Anderson, in press). All traps were baited with peanut butter spread 4 mm thick between sheets of paper towel and cut into 2.5×2.5 -cm squares. Traps were checked twice daily for 4 consecutive days, resulting in 3 diurnal and 4 nocturnal survey periods. Captured animals were identified to species, sexed, weighed, and marked with an ear notch to identify recaptures. Shrews were marked by trimming the terminal caudal hairs. *Peromyscus leucopus* and *P. maniculatus gracilis* are cryptic and were distinguished using a genetically verified discriminant function equation based on body measurements (Stephens et al. 2014). *P. maniculatus gracilis* and *P. maniculatus bairdii* were treated as separate taxonomic entities because of notable morphological and habitat differences (Jackson 1961). Our trapping protocol was approved by the University of Wisconsin Stevens Point Animal Care and Use Committee and followed guidelines outlined by the American Society of Mammalogists (Sikes et al. 2011).

Habitat and detection covariates.—At each transect we measured 17 site-specific biotic and abiotic variables (habitat covariates) that we hypothesized could affect occurrence of small mammals. Categories of habitat covariates included forest structure ($n = 8$), ground cover ($n = 4$), edaphic moisture ($n = 1$), and climate ($n = 4$). We estimated canopy closure of deciduous trees, conifers, and total canopy using a sighting tube with an internal crosshair (Ganey and Block 1994). We visually estimated percent of vegetative cover of nonwoody stems at 5% increments using a 1×1 -m frame at every other trap site and averaged the entire transect. We also estimated leaf litter depth at every other trap site by pushing a ruler into the litter until the A-horizon of the soil was reached and averaged the values for each transect. We used the line intercept method to estimate percent cover of coarse woody debris (≥ 3 cm diameter), low shrub (≤ 2 m), and high shrub or low branches (2–10 m) by pulling a tape the full length of each transect and measuring the attributes that directly crossed its vertical plane; summations were divided by transect length (Ringvall and Ståhl 1999). We used a 10-factor prism to tally deciduous trees, coniferous trees, and snags ≥ 2.54 cm in diameter at breast height (1.4 m) at trap sites 1, 5, 10, 15, and 20. We calculated average transect basal area (m^2/ha) by pooling counts, multiplying by 10, and dividing by 5.

Because soil moisture may be strongly dependent on season and weather, the use of percent soil moisture at a given time may be misleading. Thus, to classify edaphic moisture we used

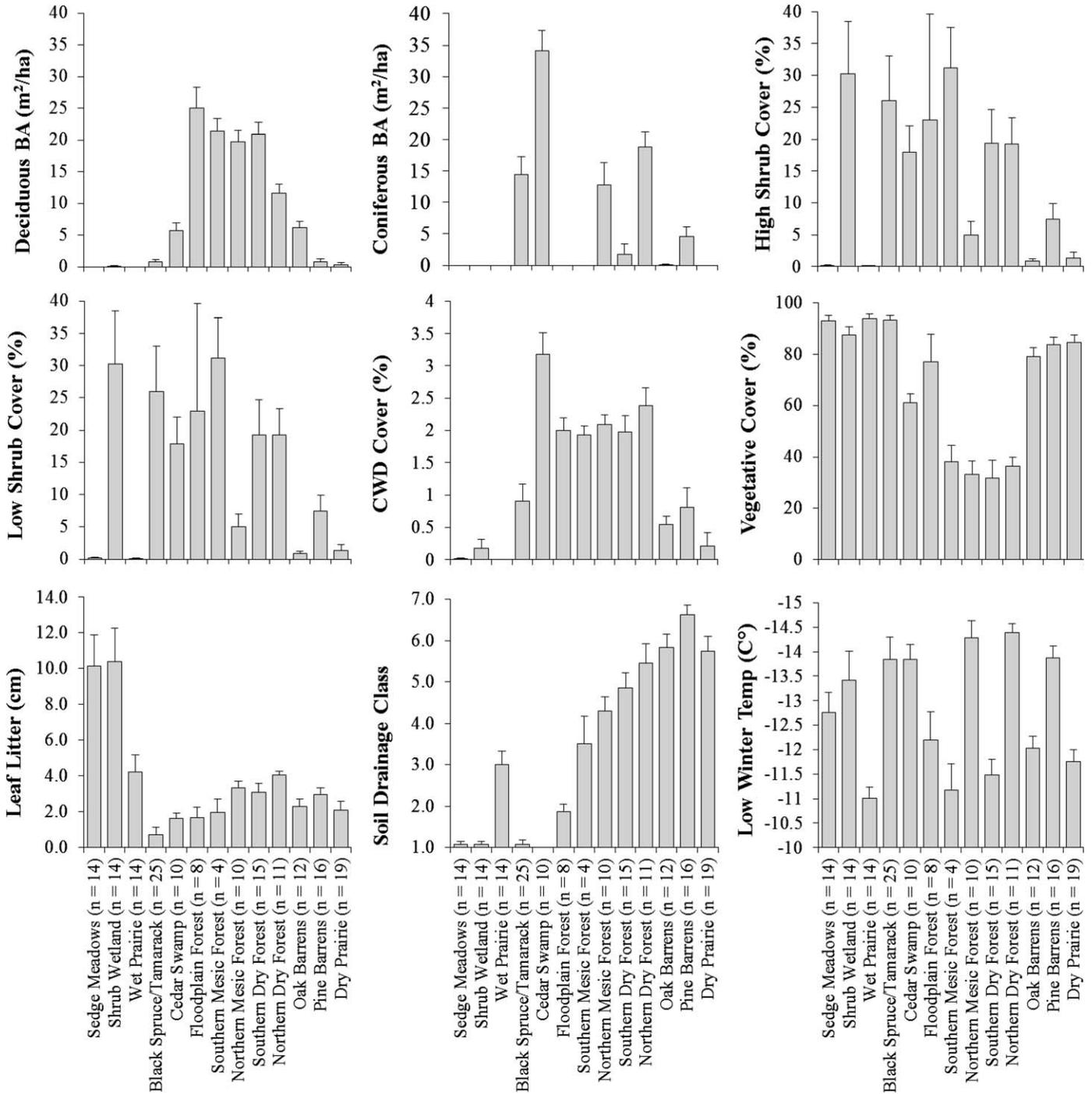


FIG. 2.—Mean values of habitat covariates for Wisconsin natural habitats surveyed during the summers of 2009 and 2010. Error bars represent 1 standard deviation. Habitats are arranged from wet to dry (left to right) and from open communities on the ends to habitats with many trees toward the middle. See “Materials and Methods” for description of how measurements were collected (BA = basal area, CWD = coarse woody debris).

the natural soil drainage class from the Soil Survey Geographic Database (Reybold and TeSelle 1989), which is a metric that incorporates the frequency and duration of wet periods. This ordinal variable ranged from very poorly drained (1) to excessively drained (7) and was measured at the center of each transect using a geographic information system. Parameter-

elevation regressions on independent slopes method (PRISM) data were used to calculate average maximum and minimum temperature for summer (June, July, and August) and winter (December, January, and February—Daly et al. 2002). Gridded values were produced with approximately 4-km resolution and extracted for each site using a geographic information system.

The probability of detecting a species (p) is known to vary by weather conditions, time, or trap effort (Getz 1961d; MacKenzie et al. 2002); therefore, in addition to the 17 site-specific variables, we identified 6 survey-specific covariates (detection covariates) that we hypothesized could cause heterogeneity in p . We acquired maximum temperature, minimum temperature, and precipitation before the morning or afternoon check from local weather stations (National Weather Service 2012) approximately 15–50 km from a transect and verified using field notes. Because time of year also may affect detectability of a species (Moore and Swihart 2005), we used Julian day starting with the 1st day of trapping. We used pitfall trap nights as a proxy of trap effort for species commonly captured in pitfall traps as most lost pitfall trap nights were due to flooding, disengaging in wetlands, or in areas that were too rocky to support installation (Stephens and Anderson, in press). However, we did not use Sherman trap nights because most trap nights were lost to animals entering a trap. Finally, because previous exposure can impact an animal's probability of recapture we included trap occasion as a variable in modeling probability of detection.

We assessed univariate correlation separately among habitat covariates and among detection covariates using a Pearson's correlation analysis. When univariate correlations were ≥ 0.70 , we removed the least biologically significant covariate or the one that was least well represented by standard sampling techniques (Burnham and Anderson 2002). This left a total of 9 habitat covariates (Fig. 2) and 5 detection covariates (minimum temperature removed) for building occupancy models for a given species.

Occupancy analysis.—Because trapping does not capture all species in a given area, nondetection does not guarantee that a species does not occur at a site. Thus, the use of naïve estimates of species occupancy, that is, total number of transects with detections divided by the total number of sites, may lead to estimates that are biased low (MacKenzie et al. 2002). We estimated site occupancy as a function of habitat covariates while incorporating imperfect detection for the 16 most common small mammal species. For species that were principally nocturnal (daytime captures $\leq 11\%$ of total), we constructed 4-digit encounter histories based solely on morning checks ($n = 11$). For crepuscular and cathemeral species with $\geq 20\%$ of total captures during afternoon checks, we built 7-digit encounter histories using both morning and afternoon checks ($n = 5$). We used a hierarchical single-season occupancy model in program PRESENCE (version 5.2—Hines 2006) to estimate site occupancy (ψ) as a function of detection probability (p), where ψ is the expected probability that a transect is occupied by a given species and p is the probability of a species being detected when present at a transect (MacKenzie et al. 2006). Because transects were not resampled and survey sites within and between years were independent, the single-season analysis did not violate model assumptions.

Because we wanted to focus on species occupancy as a function of habitat covariates, yet account for imperfect detection, we first determined the combination of detection

covariates that best accounted for heterogeneity in species detection. Holding occupancy constant we examined the effects of detection covariates on detection probability using all possible combinations of up to 3 detection covariates and the null model of no detection covariates. We then chose the detection covariates to use in the occupancy models using Akaike's information criterion with correction for small sample size (AIC_c) and ΔAIC_c values (Burnham and Anderson 2002). With competing models (i.e., $\Delta AIC_c < 2$ units), we selected the more-parsimonious model.

We developed 10–12 a priori hypotheses as to the habitat covariates we thought might cause heterogeneity in ψ based on preliminary analysis, their biology deduced from published literature, and field observations (Appendix II). Models were balanced so that each variable was present in roughly the same number of models and the best detection variables were used for all models. Models were compared using AIC_c and ranked using ΔAIC_c values (Burnham and Anderson 2002). We estimated the relative importance of each habitat covariate j in a set of models by summing the Akaike weights (w_{ij} s) across all models in which variable j occurred ($\sum w_{ij}$). This technique allowed us to investigate the importance of a given variable on species occupancy relative to all other variables in a given model set (Burnham and Anderson 2002; Arnold 2010). Habitat covariates with $w_{ij} \geq 0.8$ were considered strong predictors of species occupancy, $0.6 \leq w_{ij} < 0.8$ moderate, and $w_{ij} < 0.6$ weak. Model averaging using all models was performed to determine the directional effect of a variable on a given species (Burnham and Anderson 2002).

We also were interested in determining if each of the 16 most common species were occurring with equal probability across habitats. Using a likelihood ratio test with $\alpha < 0.05$, we compared a null occupancy model (intercept for ψ) against a model with each habitat type as a categorical variable. When this test was significant, it was considered an indication that a species was not a habitat generalist. The best detection covariates for a species were used in each test.

Community composition analysis.—We used nonmetric multidimensional scaling, a robust unconstrained ordination method, to examine compositional trends of small mammal communities. We used a Euclidian distance matrix of presence-absence data for the 16 most common species. Using common species ensured that rare species were not driving trends. We adjusted for imperfect detection and considered a species present at a given transect if ψ was ≥ 0.75 , based on the most-parsimonious occupancy model. Analysis was performed in PC-ORD (version 6.08—McCune and Mefford 2011) using a random starting configuration and 250 runs of real data and 100 runs of randomized data for a Monte Carlo test of significance (Mather and Mather 1976; McCune et al. 2002). Using overlays of individual small mammal species, the 9 habitat variables, and habitat type we examined the correlation of these variables to the ordination axes. The multiresponse permutation procedure with Euclidian distance was used to test for significant differences in community composition among habitats (McCune et al.

TABLE 1.—Captures of individuals from 2 years of small mammal trapping in natural plant communities in Wisconsin. A total of 19 species from 83 sites was captured in 2009 and 22 species from 97 sites were recorded in 2010. Occupancy analysis was conducted only for the 16 most common species (boldface type).

Species	2009	2010	Total
<i>Peromyscus leucopus</i>	436	757	1,193
<i>Myodes gapperi</i>	91	359	450
<i>Sorex cinereus</i>	179	267	446
<i>Microtus pennsylvanicus</i>	167	173	340
<i>Blarina brevicauda</i>	167	59	226
<i>Peromyscus maniculatus gracilis</i> ^a	26	96	122
<i>Zapus hudsonius</i>	32	53	85
<i>Sorex arcticus</i>	31	50	81
<i>Ictidomys tridecemlineatus</i>	47	25	72
<i>Tamias striatus</i>	12	49	61
<i>Sorex hoyi</i>	13	30	43
<i>Synaptomys cooperi</i>	11	28	39
<i>Glaucomys volans</i>	8	18	26
<i>Peromyscus maniculatus bairdii</i> ^a	20	5	25
<i>Microtus ochrogaster</i>	15	1	16
<i>Mustela erminea</i>	2	14	16
<i>Condylura cristata</i>	3	4	7
<i>Tamiasciurus hudsonicus</i>	2	4	6
<i>Glaucomys sabrinus</i>	2	0	2
<i>Sorex palustris</i>	0	2	2
<i>Mustela frenata</i>	0	1	1
<i>Reithrodontomys megalotis</i>	0	1	1
<i>Sylvilagus floridanus</i>	0	1	1

^a Woodland deer mouse (*Peromyscus maniculatus gracilis*) and prairie deer mouse (*P. m. bairdii*) are recorded as separate taxa.

2002). The multiresponse permutation procedure A-statistic describes the within- and between-group relatedness relative to that expected by chance; an A value equal to 1 indicates that species within a group are identical (McCune et al. 2002).

RESULTS

With a total effort of 22,599 Sherman trap-nights and 11,636 pitfall trap-nights, we captured 3,261 individuals comprising 23 taxa (Table 1).

Occupancy analysis.—The 16 most common species were used for occupancy modeling. With the exception of the northern short-tailed shrew (*Blarina brevicauda*), all species had ≥ 1 detection covariates in the most-parsimonious detection model (Table 2). Daily climatic conditions (temperature and precipitation) were the most influential covariates in explaining heterogeneity in detection, the direction of which was variable across species (Table 2). Time of year, expressed as Julian day, increased detection for 5 species and pitfall trap effort increased detection of 4 species (Table 2). Trap occasion was important for 3 arvicoline rodents (Table 2), namely those with high mortality rates (*Microtus pennsylvanicus*) or species for which all were removed for voucher preparation (*Microtus ochrogaster* and *Synaptomys cooperi*). For one-half of the species, incorporating imperfect detection increased mean occupancy estimates from naïve estimates (Fig. 3). However, our ability to detect *Ictidomys*

tridecemlineatus, *M. pennsylvanicus*, *Myodes gapperi*, *M. ochrogaster*, *Peromyscus* spp., and *Tamias striatus* in 4 days of trapping was exceptional and derived occupancy estimates were nearly identical to naïve estimates (Fig. 2).

With the exception of *Zapus hudsonius*, all species had moderate (> 0.6) to strong (> 0.8) occupancy responses to at least 1 habitat covariate as presented in Table 2. Covariates describing forest structure (basal area and high shrub) were the best overall descriptors of species occupancy and were moderately to strongly associated with 12 species. Five species responded strongly to basal area of deciduous trees (*P. leucopus* and *P. m. gracilis*, positively; *I. tridecemlineatus*, *M. pennsylvanicus*, and *P. m. bairdii*, negatively) and *B. brevicauda* had a moderately positive response. Four species had strong occupancy responses to basal area of coniferous trees (*Glaucomys volans*, *M. gapperi*, and *P. m. gracilis*, positively; *M. pennsylvanicus*, negatively) and 2 species had moderate responses (*S. cooperi*, positively; *Sorex arcticus*, negatively). High shrub (2–10 m) was strongly associated with presence of 3 species (*B. brevicauda* and *M. gapperi*, positively; *M. ochrogaster*, negatively) and *G. volans* and *Mustela erminea* had moderate positive responses.

We described ground cover in terms of low shrub (≤ 2 m), vegetative cover, coarse woody debris, and leaf litter. Nine species had moderate to strong responses to these variables. *M. gapperi* and *Sorex cinereus* had a strong positive occupancy response to low shrub and *S. arcticus* had a moderately positive response. Vegetative cover was strongly associated with positive occupancy rates of *S. arcticus* and *S. cinereus* and moderately associated with presence of *M. pennsylvanicus* (positively) and *P. m. bairdii* (negatively). *P. m. gracilis* had a strong positive response to coarse woody debris and *P. leucopus* and *T. striatus* had a moderate positive response. Leaf litter was the only variable without a strong species response and had a moderate negative influence on occupancy of *P. m. bairdii* and *Sorex hoyi*.

Edaphic moisture represented by soil drainage class was the 2nd most important predictor of presence with moderate to strong responses of 8 species. Six species had strong occupancy responses as soil moisture decreased (*I. tridecemlineatus* and *P. m. bairdii*, positively; *M. pennsylvanicus*, *M. erminea*, *S. arcticus*, and *S. cinereus*, negatively) and *M. ochrogaster* and *P. leucopus* had moderate positive occupancy responses.

We included average low winter temperature in occupancy models for 6 boreal species and 4 species with southern affinities. Three boreal species had a strong positive occupancy response with decreasing winter temperatures (*M. erminea*, *P. m. gracilis*, and *S. cooperi*) and *S. arcticus* had a moderate positive response. Paradoxically, *G. volans*, a southern species, also had a strong positive response to decreasing winter temperature. *P. m. bairdii* was the only southern species with occupancy rates that strongly increased with warmer winter temperatures.

Habitat associations.—On average, species occurred in 7.9 natural habitats (range 2–13 habitats). Occupancy was

TABLE 2.—Relative importance of habitat covariate importance based on cumulative Akaike information criterion with correction for small sample size (AIC_c) weights (w_{ij} s) and detection covariates used to predict occupancy of 16 Wisconsin small mammal species. Direction of a species occupancy response to habitat and detection covariates is denoted in parentheses. Habitat covariates with $w_{ij} \geq 0.8$ (boldface type) were considered strong predictors of species occupancy, $0.6 \leq w_{ij} < 0.8$ moderate, and $w_{ij} < 0.6$ weak predictors. Blank spaces indicate that a variable was not included in analysis for a given species. See “Materials and Methods” for description of how measurements were collected (CWD = coarse woody debris).

Species ^a	Habitat covariates										Detection covariates ^b							
	Forest structure			Ground cover				Edaphic moisture			Climate		Pitfall	Temp	Precip	JD	Trap Occ.	
	Deciduous basal area	Coniferous basal area	High shrub	Low shrub	CWD	Vegetative cover	Leaf litter	Soil drainage	Winter temperature									
<i>Blarina brevicauda</i>	0.701 (+)	0.357 (+)	0.812 (+)	0.511 (+)	0.239 (+)	0.171 (-)	0.048 (+)	0.026 (-)										
<i>Glaucomys volans</i> ^S	0.221 (+)	0.999 (+)	0.759 (+)	0.310 (+)										0.841 (-)				(+)
<i>Ictidomys tridecemlineatus</i>	0.996 (-)	0.246 (-)												0.264 (+)				(+)
<i>Microtus ochrogaster</i> ^S	0.340 (+)		0.945 (-)		0.000 (-)													(-)
<i>Microtus pennsylvanicus</i>	0.999 (-)	0.999 (-)																(-)
<i>Mustela erminea</i> ^N	0.176 (+)		0.719 (+)	0.015 (+)										0.957 (-)				(+)
<i>Myodes gapperi</i> ^N	0.119 (+)	1.000 (+)	0.882 (+)	0.873 (+)	0.119 (+)									0.242 (-)				(+)
<i>Peromyscus leucopus</i> ^S	0.894 (+)	0.109 (+)	0.013 (+)		0.602 (+)	0.106 (-)								0.305 (+)				(+)
<i>Peromyscus maniculatus gracilis</i> ^N	0.994 (+)	0.992 (+)			0.813 (+)	0.004 (-)	0.002 (-)							1.000 (-)				(+)
<i>Peromyscus maniculatus bairdii</i> ^S	0.999 (-)		0.019 (-)											0.981 (+)				(-)
<i>Sorex arcticus</i> ^N	0.687 (-)		0.005 (+)		0.689 (+)	0.749 (-)	0.749 (-)	0.999 (+)						0.693 (-)				(-)
<i>Sorex cinereus</i>	0.021 (-)	0.583 (+)			0.884 (+)	0.995 (+)	0.307 (+)	1.000 (-)										(+)
<i>Sorex hoyi</i> ^N	0.143 (-)	0.103 (-)	0.356 (+)		0.288 (+)	0.275 (+)	0.232 (-)	0.822 (-)										(+)
<i>Synaptomys cooperi</i> ^N	0.729 (+)				0.438 (+)	0.012 (-)	0.711 (-)	0.111 (+)						0.403 (-)				(-)
<i>Tamias striatus</i>	0.519 (+)	0.380 (+)	0.392 (+)		0.619 (+)	0.340 (-)		0.224 (+)						0.999 (-)				(+)
<i>Zapus hudsonius</i>	0.380 (+)		0.547 (+)			0.448 (+)	0.386 (-)	0.436 (-)										(+)

^a A superscript N denotes species that primarily occur in northern Wisconsin and a superscript S denotes southern species. Species with no superscript are ubiquitous in their distributions.
^b Cumulative AIC_c w_{ij} values are not provided for detection covariates because they occurred across all models (Pitfall = pitfall trap nights, Temp = high temperature, Precip = precipitation, JD = Julian day, Trap Occ. = trap occasion).

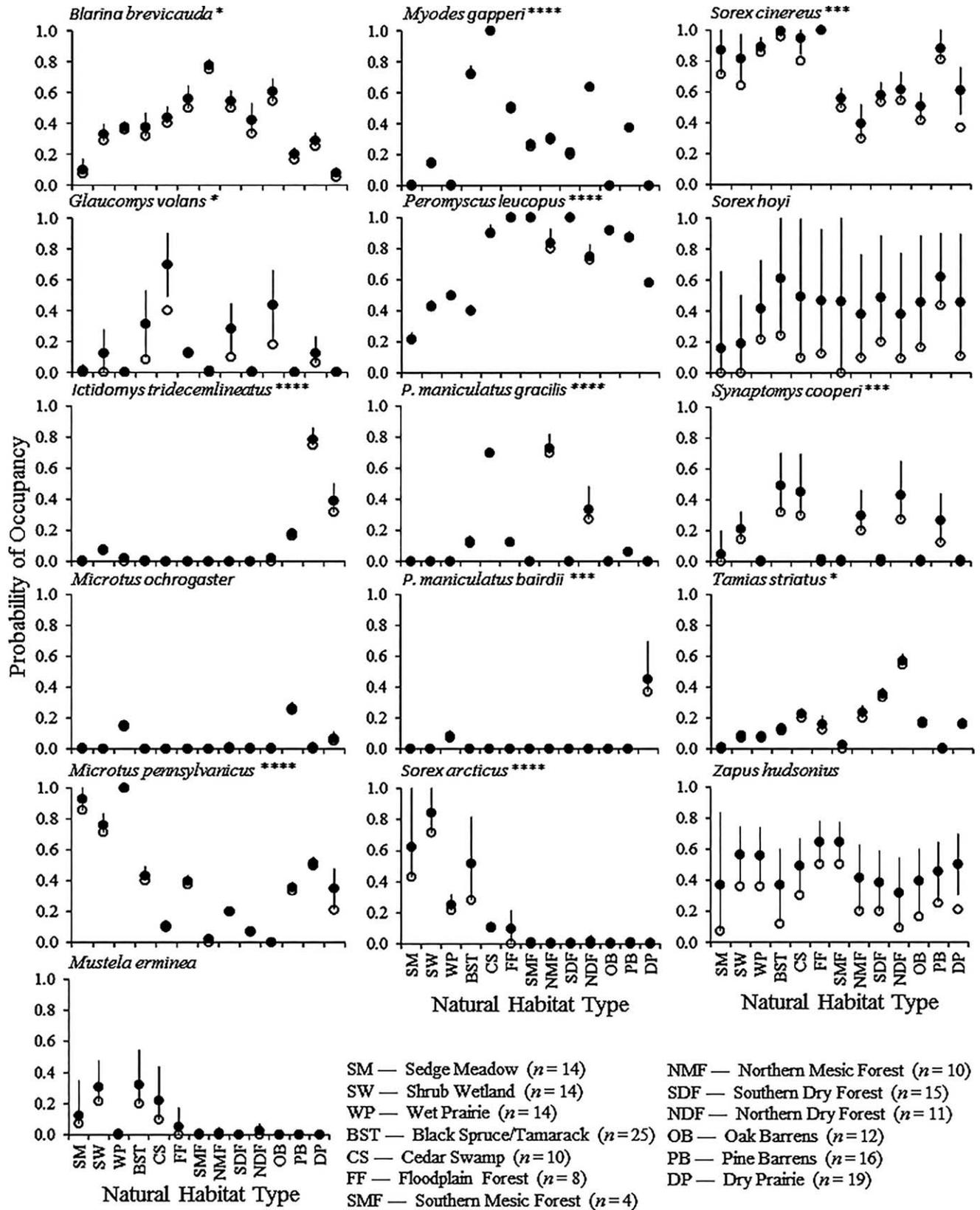


FIG. 3.—Naïve site occupancy estimates (○) as the percentage of sites with ≥ 1 detection(s) and estimated probability of occupancy (●) derived from the most-parsimonious model of occupancy for 16 small mammal species within Wisconsin natural habitats. Vertical lines represent 95% confidence intervals. Asterisks denote species with site occupancy rates explained better by habitat type over a null model as evidenced by results of a likelihood ratio test (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$) comparing an occupancy model using natural habitats as a categorical variable and detection covariates against a model using only detection covariates. Habitats are arranged from wet to dry (left to right) and from open communities on the peripheries to habitats with many trees toward the middle.

explained better by habitat than a null model for 12 of 16 species. Lack of habitat fit for *M. ochrogaster* and *M. erminea* was likely a function of relatively few captures because both species were narrowly distributed, occurring in only 3 and 4 habitats, respectively (Fig. 3). By contrast, *Z. hudsonius* occurred in every habitat and *S. hoyi* in all but 3 habitats and compared to other species both had extremely wide confidence intervals around derived occupancy estimates across all habitats (Fig. 3). The most narrowly distributed species, *P. m. bairdii*, was only found in wet and dry prairies.

Although *P. leucopus*, *S. cinereus*, and *B. brevicauda* were captured in all habitats, their occupancy rates differed across habitats (Fig. 3). *B. brevicauda* reached its highest occupancy rates in forested habitats and had occupancy rates of nearly 0 in habitats without trees or shrubs (Figs. 2 and 3). *S. cinereus* had occupancy rates of 1 or approaching 1 in all wetland habitats, whereas probability of occupancy was approximately 0.6 for other habitats. Probability of occupancy for *P. leucopus* increased in habitats with well-drained soil and was 1 or nearly 1 in forested habitats. *G. volans*, *M. gapperi*, *P. m. gracilis*, and *S. cooperi* reached their highest occupancy rates in northern forest habitats. *I. tridecemlineatus* and *P. m. bairdii* occurred almost exclusively in well-drained open habitats, whereas *S. arcticus* was present exclusively in wetland habitats. *M. pennsylvanicus* and *T. striatus* were found in all but 2 habitats; nevertheless, *M. pennsylvanicus* had greater occupancy rates in habitats without trees and reached its highest occupancy rates in wetland habitats, whereas *T. striatus* had higher occupancy rates in dry forested habitats, although the trend was weak.

Community composition.—The nonmetric multidimensional scaling ordination of small mammal community data was best fit by a 3-dimensional solution as determined by a Monte Carlo randomization test ($P < 0.05$) and visual examination of the scree plot. The first 3 axes accounted for 75.6% of the variability in the data (axis 1 = 26.6%, axis 2 = 33.3%, and axis 3 = 15.7%) and the final solution had a stress of 12.296. The ordination showed marked compositional separation among habitats and was supported by the multiresponse permutation procedure test (multiresponse permutation procedure statistic = -25.62 , $P < 0.0001$), although there was considerable variation within a habitat type as indicated by the multiresponse permutation procedure A -statistic ($A = 0.13$). A strong gradient of forested habitats, associated with increased basal area and coarse woody debris, to open habitats, associated with vegetative cover and low shrub, occurred from left to right across axis 1 (Figs. 4a and 4c). Another gradient of habitats with poorly drained soils to well-drained soils occurred from top to bottom along axis 2 (Figs. 4a and 4c). Finally, northern habitats and colder winter temperatures were positively associated along axis 3 and southern communities and warmer winter temperatures were negatively associated along axis 3 (Figs. 4b and 4d). Numerous individual species also responded to the same gradients in the nonmetric multidimensional scaling ordination (Figs. 4a and 4b). Open wetland associates such as *M.*

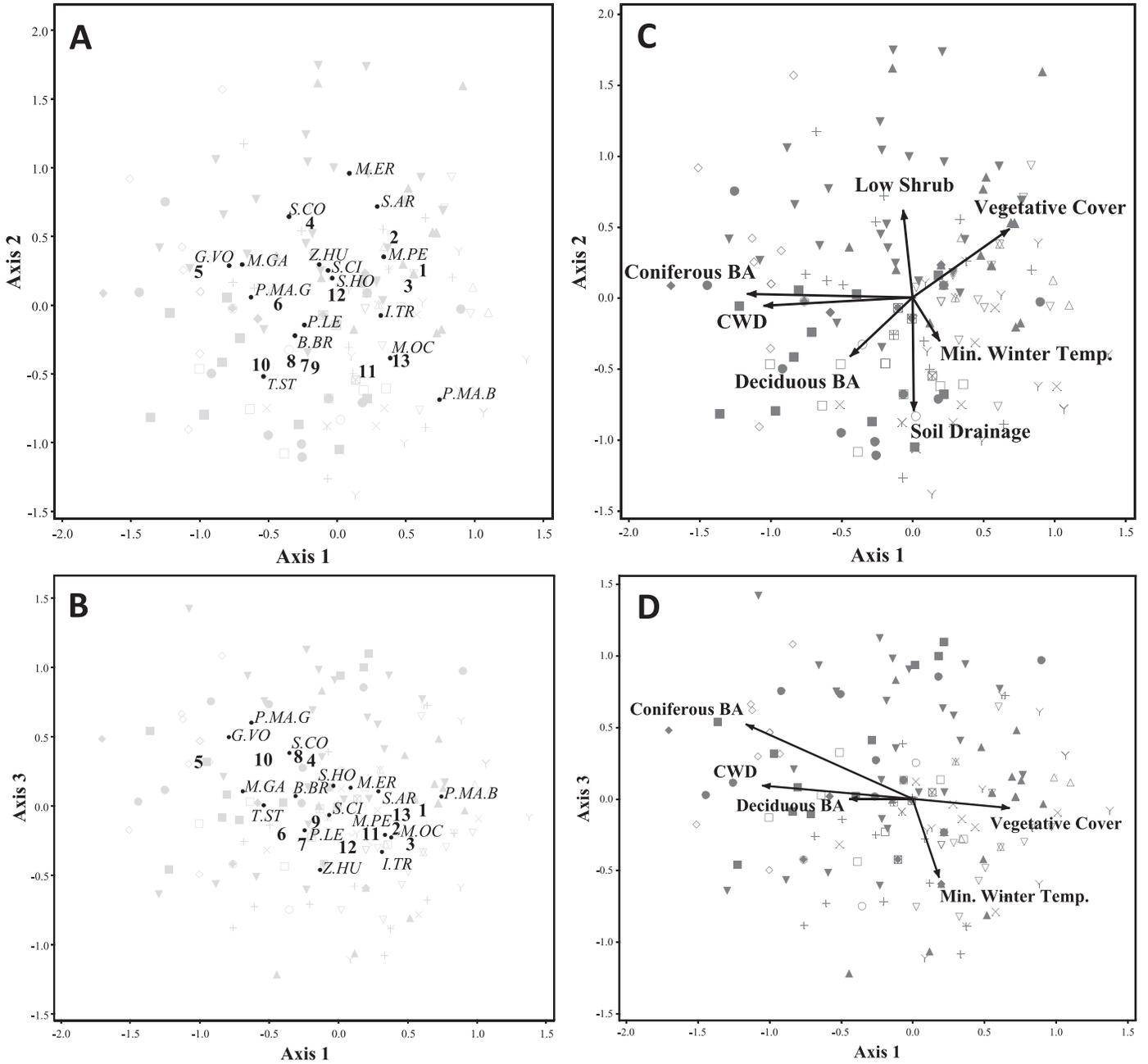
pennsylvanicus and *S. arcticus* correlated with reduced basal area, wetter soils, and increased vegetative cover, whereas forest associates such as *B. brevicauda*, *G. volans*, *P. leucopus*, and *P. maniculatus gracilis* responded positively to the basal area gradient (Figs. 4a and c). Prairie associates such as *I. tridecemlineatus*, *M. ochrogaster*, and *P. maniculatus bairdii* responded positively to drier soils and lack of basal area (Figs. 4a and 4c). Northern species such as *P. maniculatus gracilis* and *S. cooperi* were associated with colder winter temperatures, whereas southern species such as *P. maniculatus bairdii* and *M. ochrogaster* were associated with warmer winter temperatures (Figs. 4b and 4d). Together, these results closely mirrored those found from single-species occupancy modeling, indicating that idiosyncratic species responses were driving trends of community organization.

DISCUSSION

The strength of this study derives from the broad geographical range and diverse plant communities that were sampled. A variety of factors were shown to influence the probability of detection and occupancy of species, producing characteristic small mammal communities across Wisconsin.

Variation in species detection.—Raw field counts provided reliable estimates of occupancy for half of the species; for the remainder, survey specific covariates (weather conditions, seasonality, trap effort, and trap occasion) enhanced estimates. In particular, those species most effectively captured in pitfall traps, including *Sorex* spp., *S. cooperi*, and *Z. hudsonius*, were predicted to be much more prevalent than naïve occupancy estimates indicated. This is despite using more and larger pitfall traps than most studies that investigate small mammal communities. Urban and Swihart (2011) noted similar trends with *Sorex* spp. even though they too used considerable pitfall effort, reemphasizing that studies failing to account for imperfect detection of *Sorex* spp. likely have occupancy estimates that are biased low. Our ability to detect *G. volans* and *M. erminea* also was poor; however, this is not surprising because both species require specialized trapping techniques, including elevated traps for *G. volans* (Risch and Brady 1996) and specialized bait for *M. erminea* (King 1975).

Drivers of species occupancy.—Overall, characteristics describing forest structure helped explain occupancy rates for all but 4 species. Basal area, a measure of the area dominated by trees, was important for separating forest associates such as *B. brevicauda*, *G. volans*, *M. gapperi*, *P. leucopus*, and *P. maniculatus gracilis* from grassland species such as *I. tridecemlineatus*, *M. pennsylvanicus*, and *P. m. bairdii*. These designations are likely related to differential structural complexity between forested and open habitats affecting species-specific resource selection of nesting sites, food requirements, and competitive interactions with heterospecifics (Getz 1961c; Bowker and Pearson 1975; Manson et al. 1999; Williams et al. 2002). With the exception of *P. m. bairdii*, basal areas of coniferous and deciduous trees were included in model sets for the aforementioned species, yet only *P. m. gracilis* and



- △ (1) Sedge Meadow, *n* = 14
- ▲ (2) Shrub Wetland, *n* = 14
- ▽ (3) Wet Prairie, *n* = 14
- ▼ (4) Black Spruce/Tamarack, *n* = 25
- ◇ (5) Cedar Swamp, *n* = 10
- ◆ (6) Floodplain Forest, *n* = 8
- (7) Southern Mesic Forest, *n* = 4
- (8) Northern Mesic Forest, *n* = 10
- (9) Southern Dry Forest, *n* = 15
- (10) Northern Dry Forest, *n* = 11
- × (11) Oak Barrens, *n* = 12
- +
- (12) Pine Barrens, *n* = 16
- ∩ (13) Dry Prairie, *n* = 19

FIG. 4.—Nonmetric multidimensional scaling ordination of Wisconsin small mammal communities in 3-dimensional space with overlays representing the relationship of A) and B) the location of the centroid of a given habitat (represented by numbers) and small mammal species (●) and C) and D) habitat variables having an r^2 -value of 0.13–0.33 with 1 or more axes. Various shapes indicate natural habitat type in which a given community occurred. Vectors are scaled in proportion to r^2 . Small mammal abbreviations are as follows: *Blarina brevicauda*, B.BR; *Glaucomys volans*, G.VO; *Ictidomys tridecemlineatus*, I.TR; *Microtus ochrogaster*, M.OC; *Microtus pennsylvanicus*, M.PE; *Mustela erminea*, M.ER; *Myodes gapperi*, M.GA; *Peromyscus leucopus*, P.LE; *Peromyscus maniculatus bairdii*, P.MA.B; *Peromyscus maniculatus gracilis*, P.MA.G; *Sorex arcticus*, S.AR; *Sorex cinereus*, S.CI; *Sorex hoyi*, S.HO; *Synaptomys cooperi*, S.CO; *Tamias striatus*, T.ST; *Zapus hudsonius*, Z.HU.

M. pennsylvanicus responded moderately to strongly to both variables. The remaining species responded moderately or strongly to either coniferous or deciduous trees, indicating that in addition to forest structure, the type of trees present also was important. The strong positive association of *G. volans* to coniferous basal area and a weak relationship to deciduous basal area was surprising and at odds with most studies that find *G. volans* to preferentially inhabit deciduous forests (Dolan and Carter 1977; Weigl 1978). Our results may indicate a seasonal preference or use of more terrestrial resources in coniferous forests by the generally arboreal *G. volans* during summer before mast fall in deciduous stands. High shrub was important for *B. brevicauda*, *G. volans*, *M. erminea*, and *M. gapperi*. Specifically, both *B. brevicauda* and *M. gapperi* have high metabolic water requirements (Chew 1951; Pruitt 1953; Getz 1961b, 1968) and high shrub cover may help moderate both temperature and humidity, creating suitable microclimates (Yahner 1986; Bellows et al. 2001).

Ground cover in the form of vegetation and shrubs was important for occupancy of *M. pennsylvanicus*, *M. gapperi*, *S. arcticus*, and *S. cinereus*. This low structure is likely important for covering runways and constructing nests, and when in herbaceous form can provide a food resource for herbivores. Coarse woody debris was important for *P. leucopus*, *P. maniculatus*, and *T. striatus* and may provide nesting sites and travel corridors for safe passage from predators (Barry and Francq 1980; Zollner and Crane 2003). Ground cover also may prohibit occupancy by species that require open habitats (Snyder and Best 1988). Considering that leaf litter is positively associated with abundance of many species (Morris 1979), it is surprising that in this study, compared to other variables, it was relatively unimportant for predicting site occupancy of most species. However, this finding may be a result of identifying factors responsible for occupancy versus abundance. Leaf litter may be important for higher abundance but not necessarily for the presence of a species.

One-half of the species tested showed marked responses to soil moisture, with species present either under xeric or hydric conditions. Although physiological processes may limit some species from drier sites while giving a competitive advantage to others (Chew 1951; Getz 1963), it is more likely that for these species food resources are tied to edaphic moisture. Mesic conditions often have high abundances of invertebrates, an important food source for insectivorous mammals (Getz 1961b), and *S. arcticus* and *S. cinereus* are commonly associated with wetter soils (Wrigley et al. 1979). Mesic soils often support lush vegetation, particularly graminoids that are important to herbivores such as *M. pennsylvanicus* (Getz 1961a). *M. pennsylvanicus* is known to occupy areas that have standing water, as long as sufficient herbaceous cover is available for nests and food (Getz 1961a). The high occupancy rates of *M. erminea* in poorly drained soil may be a function of high prey density, including *M. pennsylvanicus*, *M. gapperi*, and *S. cinereus* (Aldous and Manweiler 1942; King 1983). *I. tridecemlineatus*, *M. ochrogaster*, and *P. maniculatus bairdii* are all prairie species that nest underground and this may

explain their association with well-drained soils (Streubel and Fitzgerald 1978; Getz and Hofmann 1986; Weber and Hoekstra 2009).

Winter temperature was important in predicting occupancy of 6 small mammal species and may impact small mammals directly and indirectly. Physiological limitations to temperature may directly limit distributions for some species. Although we failed to detect any temperature threshold for the distributions of *P. leucopus* and *G. volans* (see Myers et al. [2009] for possible reasons), the northward distributions of these species are known to be limited by cold winter temperatures (Weigl 1978; Wolff 1996; Bowman et al. 2005). Temperature thresholds also indirectly influence species occurrence by restricting competing species. Where *P. leucopus* and *P. maniculatus gracilis* are sympatric, variation in winter temperatures may facilitate syntopic coexistence of these congeners (Wolff 1996). However, consistently warm winters favor *P. leucopus*, leading to reduced abundance or extirpation of *P. maniculatus gracilis*, a species behaviorally and physiologically adapted to tolerate cold temperatures but behaviorally subordinate to *P. leucopus* (Long 1996; Wolff 1996; Myers et al. 2005). Other indirect effects include accumulation of snow in areas with cooler winter temperatures, creating subnivean habitat important for predator evasion and thermoregulation (Merritt et al. 2001). Lastly, temperature may limit the range of plant species or communities important for a given small mammal species.

Species habitat associations.—Although natural habitats (macrohabitats) are qualitatively designated, they form under a relatively narrow set of circumstances and embody an amalgam of abiotic and biotic environmental characteristics. Macrohabitat selection occurs when a specific combination of these characteristics important to a species comes together and is of greater quality than combinations found in adjacent habitats (Stevens and Tello 2009). Often differences in resources can vary more among macrohabitats than within and studies have found that abundance of a species sometimes can be explained better by macrohabitat associations than by microhabitat affinities (Morris 1987; Coppeto et al. 2006). We did not directly compare these 2 scales; nevertheless, occupancy responses of species at the macrohabitat level closely mirrored observed individualistic responses to abiotic and biotic site characteristics. These complementary perspectives offer insight into the underlying mechanisms driving a species' distribution across habitats and a region (Stevens and Tello 2009).

Only 2 (*S. hoyi* and *Z. hudsonius*) of the 16 species were identified as habitat generalists. Despite being uncommon, *S. hoyi* was characterized as a habitat generalist occurring in nearly all habitats. The generalist nature of this species has been noted elsewhere (Wrigley et al. 1979; Nagorsen and Peterson 1981; Bellows et al. 2001). In contrast, *Z. hudsonius* is often classified as being associated with grassland habitat and moist soils (Hamilton 1935; Getz 1961c; Whitaker 1972; Bellows et al. 2001), although some studies have found it with equal probability in grasslands and forested areas and even in

dry habitats (Whitaker 1963; Urban and Swihart 2009). We found occupancy rates of *Z. hudsonius* to be similar across natural habitats, from wetlands to dry habitats and from open habitats to well-forested ones. Their ubiquity does not mean that their abundance is not greater in more mesic and open habitats; nonetheless, Getz (1961c) did not capture *Z. hudsonius* under xeric conditions. This is a species that can be difficult to capture, particularly in Sherman traps (Boonstra and Hoyle 1986), and also is more active on nights that are cloudy and rainy (Quimby 1951). We found that probability of detection increased with precipitation and the use of pitfall traps. Given the difficulty in capturing *Zapus* and that trap effort and local weather can cause considerable heterogeneity in detection of *Z. hudsonius*, studies addressing occupancy should strongly consider using analysis that can incorporate imperfect detection (Urban and Swihart 2009).

Small mammal communities.—Within natural habitats of Wisconsin, idiosyncratic responses of small mammal species to abiotic and biotic characteristics create regular and predictable community organization across a heterogeneous landscape. We found that small mammal communities vary substantially among natural habitats and are structured primarily by differences in forest stand density, soil moisture regimes, and to a lesser extent, temperature and understory cover. Although many natural habitat types are adjacent, there is often little gradation between them. This marked boundary is particularly apparent at the interface of upland and lowland habitats or between open and forested habitats and creates dissimilar small mammal assemblages within a relatively small spatial area. The greatest changes arise as small mammal communities shift from those dominated by *M. pennsylvanicus* and *S. arcticus* in open wetland habitats to forested habitats with *P. leucopus*, *M. gapperi*, and *B. breviceauda*. Despite having substantial differences in small mammal community composition, communities such as sedge meadows and southern mesic forest are separated by only a few meters in some cases. Such proximity of dissimilar habitats creates a heterogeneous landscape with high β -diversity and may be important for enhancing foraging opportunities for predators but also can create issues for recolonization when the habitat fragments are isolated and small.

Sampling over a broad geographic area allowed us to integrate climate variables with biotic site characteristics and thus examine relationships that would not be possible if we only sampled at a local scale. Such comparisons are important for understanding proximal reasons for distributions of species, but also for predicting distributional changes as climates shift. We found that temperature was strongly associated with the presence of 5 common species. Based on museum records in Michigan, Myers et al. (2009) concluded that many northern species have recently suffered distributional contractions northward and decreased in relative abundance, whereas southern species have extended their ranges northward and increased in relative abundance. Our results suggest that continued climate warming could substantially change northern small mammal community composition. In particular, *P. m.*

bairdii may increase, whereas *M. erminea*, *S. cooperi*, *P. m. gracilis*, and *S. arcticus* may decline. Predicting impacts, however, is difficult because changes in precipitation also may complicate interactions. If abundance also is affected by climate change it could substantially alter the small mammal community structure.

The use of occupancy analysis allowed us to simultaneously account for imperfect detection while modeling the response of individual small mammal species to environmental variables across a range of natural gradients in Wisconsin. Occupancy modeling is robust to temporal variation, allowing us to sample more sites and include more species than would have been otherwise possible using analysis based only on abundance or density data (Kallies et al. 2012). However, studies on abundance will likely provide important insight into the role species interactions play on community composition, which is difficult to assess with the broader occupancy modeling approach presented here. Additionally, it is likely that combinations of environmental variables lead to habitat-mediated coexistence of species, creating natural habitats with high α -biodiversity. Indeed, we noted considerable variation in site richness, with between 1 and 9 species (average 3.8 species) present at a given site. Investigating the complex species interactions and examining combinations of environmental variables that allow for habitat-mediated species coexistence would further build on the ecological understanding of how small mammal communities structure around environmental characteristics in the Great Lakes region.

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APPENDIX I

Names and number of transects trapped in natural plant communities in Wisconsin during the summers of 2009 and 2010. Nomenclature follows that of Curtis (1959). Natural plant communities were placed into 13 aggregated groups, referred to as natural communities.^a

Natural community	Transects (<i>n</i>)
Black spruce–tamarack	
Black spruce bog	10
Muskeg	7
Tamarack rich swamp	5
Tamarack poor swamp	3
Cedar swamp	
Northern wet mesic forest	10
Northern mesic forest	
Northern mesic forest	10
Northern dry forest	
Northern dry mesic forest	10
Northern dry forest	1
Southern dry forest	
Southern dry mesic forest	8
Southern dry forest	5
Central sands pine–oak forest	2
Southern mesic forest	
Southern mesic forest	4
Floodplain forest	
Floodplain forest	8
Shrub wetlands	
Shrub carr	6
Alder thicket	5
Bog relict–open bog	3
Sedge meadows	
Southern sedge meadow	7
Central poor fen	4
Northern sedge meadow	3
Wet prairies	
Wet mesic prairie	10
Mesic prairie	3
Calcareous fen	1
Dry prairies	
Dry mesic prairie	8
Dry prairie	7
Dry sand prairie	4
Oak barrens	
Oak barrens	10
Oak opening	2
Pine barrens	
Pine barrens	16

^a Eight transects were not used in groupings because they did not have the required ≥ 4 transects: hardwood swamp ($n = 3$), old meadow–prairie ($n = 2$), white pine–red maple swamp ($n = 2$), and southern hardwood swamp ($n = 1$).

APPENDIX II

Summary of Akaike's information criterion with correction for small sample size (AIC_c) model selection for 16 Wisconsin small mammal species using single-season occupancy models. Models are ranked for each species by relative difference in AIC_c (ΔAIC_c); AIC model weights are denoted by w_i and number of parameters by k . Occupancy covariates (ψ) are as follows: BA Hard (deciduous basal area), BA Soft (coniferous basal area), ShrubH (high shrub), ShrubL (low shrub), CWD (course woody debris), Veg (vegetative cover), Litter (leaf litter), SOIL (soil drainage), and WTemp (winter temperature); and detection (p) covariates (indicated in a footnote for each species) are Pitfall (pitfall trap nights), Temp (high temperature), Precip (precipitation), JD (Julian day), and Trap Occ (trap occasion).

Model	ΔAIC_c	w_i	k
<i>Blarina brevicauda</i> ^a			
ψ (BA Hard+BA Soft+ShrubH+ShrubL) p	0.000	0.329	6
ψ (BA Hard+ShrubH) p	0.473	0.260	4
ψ (ShrubH+ShrubL+Veg) p	1.729	0.139	5
ψ (BA Hard+CWD) p	2.573	0.091	4
ψ (ShrubH+CWD) p	2.713	0.085	4
ψ (ShrubL+CWD+Litter) p	4.069	0.043	5
ψ (BA Hard+Veg+SOIL) p	5.449	0.022	5
ψ (BA Soft+CWD) p	5.533	0.021	4
ψ (BA Soft+Veg) p	7.723	0.007	4
ψ (Veg+Litter+SOIL) p	8.799	0.004	5
ψ (ShrubL+Litter+SOIL) p	12.819	0.001	5
ψ (BA Soft+Litter+SOIL) p	15.309	0.000	5
<i>Glaucomys volans</i> ^b			
ψ (BA Soft+ShrubH+WTemp) p	0.000	0.468	6
ψ (BA Soft+ShrubH+CWD+WTemp) p	1.836	0.187	7
ψ (BA Hard+BA Soft+WTemp) p	2.090	0.165	6
ψ (BA Soft+ShrubH+CWD) p	3.040	0.102	6
ψ (BA Hard+BA Soft) p	4.229	0.056	5
ψ (BA Soft+CWD+WTemp) p	6.300	0.020	6
ψ (ShrubH+CWD+WTemp) p	12.420	0.001	6
ψ (BA Hard+WTemp) p	15.149	0.000	5
ψ (BA Hard+ShrubH+CWD) p	20.240	0.000	6
ψ (BA Hard+CWD) p	20.529	0.000	5
ψ (BA Hard+ShrubH) p	21.409	0.000	5
<i>Ictidomys tridecemlineatus</i> ^c			
ψ (BA Hard+SOIL) p	0.000	0.621	5
ψ (BA Hard+BA Soft+SOIL) p	1.851	0.246	6
ψ (BA Hard+Veg+Litter+SOIL) p	3.146	0.129	7
ψ (Veg+Litter+SOIL) p	10.191	0.004	6
ψ (BA Soft+SOIL) p	19.280	0.000	5
ψ (SOIL) p	20.044	0.000	4
ψ (BA Soft+BA Hard+Veg) p	32.361	0.000	6
ψ (BA Hard+Veg+Litter) p	32.901	0.000	6
ψ (BA Soft+Veg+Litter) p	41.351	0.000	6
ψ (BA Soft+Litter) p	43.040	0.000	5
<i>Microtus ochrogaster</i> ^d			
ψ (BA Hard+ShrubH+SOIL) p	0.000	0.226	6
ψ (ShrubH+Litter+SOIL) p	0.010	0.225	6
ψ (ShrubH+SOIL+WTemp) p	0.090	0.216	6
ψ (ShrubH+Veg+Litter) p	0.440	0.181	6
ψ (BA Hard+ShrubH+Litter) p	1.690	0.097	6
ψ (Veg+SOIL+WTemp) p	3.990	0.031	6
ψ (BA Hard+Veg+SOIL+WTemp) p	5.736	0.013	7
ψ (Veg+Litter) p	6.879	0.007	5
ψ (BA Hard+WTemp) p	8.809	0.003	5
ψ (BA Hard+Veg+Litter+WTemp) p	10.506	0.001	7

APPENDIX II

Continued.

Model	ΔAIC_c	w_i	k
<i>Microtus pennsylvanicus</i> ^e			
ψ (BA Soft+BA Hard+Veg+SOIL) p	0.000	0.708	9
ψ (BA Soft+BA Hard+SOIL) p	2.353	0.218	8
ψ (BA Soft+BA Hard+Litter+SOIL) p	4.560	0.072	9
ψ (Veg+Litter+SOIL) p	14.973	0.000	8
ψ (Veg+Litter) p	15.242	0.000	7
ψ (BA Soft+BA Hard+CWD) p	18.013	0.000	8
ψ (Veg) p	19.917	0.000	6
ψ (BA Soft+CWD) p	23.952	0.000	7
ψ (CWD+Litter) p	33.422	0.000	7
ψ (BA Hard+CWD) p	34.012	0.000	7
ψ (SOIL) p	49.787	0.000	6
ψ (Litter) p	52.687	0.000	6
<i>Mustela erminea</i> ^f			
ψ (ShrubH+SOIL+WTemp) p	0.000	0.379	7
ψ (ShrubH+Veg+SOIL+WTemp) p	0.371	0.314	8
ψ (BA Soft+SOIL+WTemp) p	1.990	0.140	7
ψ (Veg+Litter+SOIL+WTemp) p	2.331	0.118	8
ψ (BA Soft+ShrubH+Litter) p	5.970	0.019	7
ψ (BA Soft+Veg+SOIL) p	6.450	0.015	7
ψ (ShrubL+Litter+WTemp) p	8.170	0.006	7
ψ (ShrubH+ShrubL+Veg) p	8.420	0.006	7
ψ (BA Soft+ShrubH+ShrubL) p	11.310	0.001	7
ψ (ShrubL+Litter) p	12.334	0.001	6
ψ (BA Soft+ShrubL) p	13.354	0.000	6
ψ (Veg+Litter) p	14.704	0.000	6
<i>Myodes gapperi</i> ^g			
ψ (BA Soft+ShrubH+ShrubL) p	0.000	0.741	7
ψ (BA Soft+ShrubH+ShrubL+WTemp) p	3.461	0.131	8
ψ (BA Soft+BA Hard+CWD+SOIL+WTemp) p	3.808	0.110	9
ψ (BA Soft+BA Hard+ShrubH) p	8.850	0.009	7
ψ (BA Soft+CWD) p	9.064	0.008	6
ψ (ShrubH+ShrubL+CWD+SOIL) p	17.241	0.000	8
ψ (BA Hard+CWD+WTemp) p	27.910	0.000	7
ψ (CWD+SOIL) p	31.404	0.000	6
ψ (BA Hard+ShrubL+WTemp+SOIL) p	38.941	0.000	8
ψ (ShrubL+WTemp+SOIL) p	44.860	0.000	7
ψ (BA Hard+ShrubH) p	65.124	0.000	6
<i>Peromyscus leucopus</i> ^h			
ψ (BA Hard+CWD+SOIL) p	0.000	0.396	6
ψ (BA Hard+SOIL) p	0.719	0.276	5
ψ (BA Hard+BA Soft+WTemp) p	2.600	0.108	6
ψ (BA Hard+CWD+WTemp) p	2.680	0.104	6
ψ (CWD+Veg+WTemp) p	2.890	0.093	6
ψ (BA Hard+ShrubH) p	7.209	0.011	5
ψ (CWD+Veg) p	7.399	0.010	5
ψ (ShrubH+Veg) p	10.809	0.002	5
ψ (BA Soft+Veg) p	11.249	0.001	5
ψ (ShrubH+SOIL+WTemp) p	21.770	0.000	6
ψ (BA Soft+SOIL) p	24.899	0.000	5
ψ (BA Soft+ShrubH) p	34.899	0.000	5
<i>Peromyscus maniculatus gracilis</i> ⁱ			
ψ (BA Soft+BA Hard+CWD+WTemp) p	0.000	0.805	9
ψ (BA Soft+BA Hard+WTemp+SOIL) p	2.960	0.183	9
ψ (BA Hard+CWD+WTemp) p	9.723	0.006	8
ψ (BA Soft+Veg+WTemp+SOIL) p	10.540	0.004	9
ψ (CWD+Litter+WTemp) p	12.493	0.002	8
ψ (BA Soft+CWD+Veg) p	43.223	0.000	8
ψ (BA Soft+Veg+Litter) p	44.543	0.000	8

APPENDIX II

Continued.

Model	ΔAIC_c	w_i	k
$\psi(\text{BA Soft}+\text{SOIL}) p$	49.072	0.000	7
$\psi(\text{Veg}+\text{Litter}+\text{Soil}) p$	54.993	0.000	8
$\psi(\text{CWD}+\text{SOIL}) p$	57.902	0.000	7
$\psi(\text{BA Hard}+\text{Veg}+\text{Litter}) p$	59.623	0.000	8
$\psi(\text{BA Hard}+\text{Litter}) p$	67.322	0.000	7
<i>Peromyscus maniculatus bairdii</i> ⁱ			
$\psi(\text{BA Hard}+\text{Veg}+\text{Litter}+\text{SOIL}+\text{WTemp}) p$	0.000	0.749	8
$\psi(\text{BA Hard}+\text{SOIL}+\text{WTemp}) p$	2.343	0.232	6
$\psi(\text{BA Hard}+\text{ShrubH}+\text{SOIL}) p$	7.513	0.017	6
$\psi(\text{BA Hard}+\text{ShrubH}) p$	13.693	0.001	5
$\psi(\text{SOIL}+\text{WTemp}) p$	15.763	0.000	5
$\psi(\text{ShrubH}+\text{Litter}) p$	17.153	0.000	5
$\psi(\text{ShrubH}+\text{Veg}+\text{WTemp}) p$	18.023	0.000	6
$\psi(\text{BA Hard}+\text{Veg}+\text{Litter}) p$	18.083	0.000	6
$\psi(\text{ShrubH}+\text{Veg}) p$	20.663	0.000	5
$\psi(\text{Veg}+\text{Litter}+\text{SOIL}) p$	23.313	0.000	6
$\psi(\text{Litter}+\text{WTemp}) p$	25.673	0.000	5
<i>Sorex arcticus</i> ^k			
$\psi(\text{BA Soft}+\text{Veg}+\text{ShrubL}+\text{SOIL}+\text{WTemp}) p$	0.000	0.687	8
$\psi(\text{Veg}+\text{Litter}+\text{SOIL}) p$	1.643	0.302	6
$\psi(\text{ShrubH}+\text{Litter}+\text{SOIL}) p$	9.923	0.005	6
$\psi(\text{Veg}+\text{SOIL}+\text{WTemp}) p$	10.033	0.005	6
$\psi(\text{ShrubL}+\text{Veg}+\text{SOIL}+\text{WTemp}) p$	12.179	0.002	7
$\psi(\text{Veg}+\text{Litter}+\text{WTemp}) p$	22.003	0.000	6
$\psi(\text{Veg}+\text{Litter}) p$	27.093	0.000	5
$\psi(\text{ShrubH}+\text{ShrubL}+\text{Litter}) p$	30.593	0.000	6
$\psi(\text{BA Soft}+\text{WTemp}) p$	41.013	0.000	5
$\psi(\text{BA Soft}+\text{ShrubH}+\text{ShrubL}) p$	42.763	0.000	6
$\psi(\text{BA Soft}+\text{ShrubH}) p$	45.503	0.000	5
$\psi(\text{ShrubH}+\text{ShrubL}) p$	48.533	0.000	5
<i>Sorex cinereus</i> ^l			
$\psi(\text{BA Soft}+\text{ShrubL}+\text{Veg}+\text{SOIL}) p$	0.000	0.571	9
$\psi(\text{ShrubL}+\text{Veg}+\text{Litter}+\text{SOIL}) p$	2.600	0.156	9
$\psi(\text{ShrubL}+\text{Veg}) p$	2.612	0.155	7
$\psi(\text{Veg}+\text{Litter}+\text{SOIL}) p$	4.113	0.073	8
$\psi(\text{SOIL}) p$	6.507	0.022	6
$\psi(\text{BA Hard}+\text{CWD}) p$	8.452	0.008	7
$\psi(\text{BA Hard}+\text{CWD}+\text{Litter}) p$	10.233	0.003	8
$\psi(\text{BA Soft}+\text{BA Hard}+\text{CWD}) p$	8.362	0.009	7
$\psi(\text{BA Soft}+\text{ShrubL}) p$	10.882	0.002	7
$\psi(\text{CWD}+\text{Litter}) p$	17.352	0.000	7
<i>Sorex hoyi</i> ^m			
$\psi(\text{ShrubH}+\text{Litter}) p$	0.000	0.201	5
$\psi(\text{Litter}+\text{WTemp}) p$	0.220	0.180	5
$\psi(\text{ShrubL}+\text{Litter}+\text{WTemp}) p$	0.461	0.160	6
$\psi(\text{Veg}+\text{Litter}) p$	0.330	0.170	5
$\psi(\text{BA Hard}+\text{ShrubH}) p$	2.250	0.065	5
$\psi(\text{ShrubH}+\text{ShrubL}+\text{Veg}) p$	2.691	0.052	6
$\psi(\text{ShrubL}+\text{SOIL}+\text{WTemp}) p$	2.951	0.046	6
$\psi(\text{BA Hard}+\text{BA Soft}+\text{ShrubH}) p$	3.371	0.037	6
$\psi(\text{BA Soft}+\text{ShrubL}+\text{Veg}+\text{SOIL}) p$	3.806	0.030	7
$\psi(\text{BA Hard}+\text{Veg}) p$	4.360	0.023	5
$\psi(\text{BA Hard}+\text{BA Soft}+\text{SOIL}) p$	4.801	0.018	6
$\psi(\text{BA Soft}+\text{SOIL}+\text{WTemp}) p$	4.931	0.017	6
<i>Synaptomys cooperi</i> ⁿ			
$\psi(\text{BA Soft}+\text{Shrub L}+\text{WTemp}) p$	0.000	0.517	6
$\psi(\text{ShrubL}+\text{WTemp}) p$	1.389	0.258	5
$\psi(\text{BA Soft}+\text{ShrubL}+\text{SOIL}+\text{WTemp}) p$	2.126	0.179	7
$\psi(\text{BA Soft}+\text{SOIL}+\text{WTemp}) p$	5.530	0.033	6

APPENDIX II

Continued.

Model	ΔAIC_c	w_i	k
$\psi(\text{Veg}+\text{SOIL}+\text{WTemp}) p$	7.500	0.012	6
$\psi(\text{ShrubL}+\text{CWD}) p$	13.369	0.001	5
$\psi(\text{ShrubL}+\text{Veg}+\text{CWD}) p$	16.639	0.000	5
$\psi(\text{BA Soft}+\text{CWD}) p$	20.759	0.000	5
$\psi(\text{BA Soft}+\text{Veg}+\text{SOIL}) p$	21.070	0.000	6
$\psi(\text{Veg}+\text{CWD}+\text{SOIL}) p$	27.250	0.000	6
$\psi(\text{Veg}+\text{CWD}) p$	27.979	0.000	5
<i>Tamias striatus</i> ^o			
$\psi(\text{BA Hard}+\text{CWD}) p$	0.000	0.208	7
$\psi(\text{ShrubH}+\text{CWD}) p$	0.360	0.174	7
$\psi(\text{BA Hard}+\text{BA Soft}+\text{CWD}) p$	1.451	0.101	8
$\psi(\text{BA Hard}+\text{BA Soft}+\text{SOIL}) p$	1.751	0.087	8
$\psi(\text{BA Soft}+\text{CWD}+\text{Veg}) p$	1.891	0.081	8
$\psi(\text{BA Soft}+\text{Veg}) p$	1.990	0.077	7
$\psi(\text{BA Hard}+\text{ShrubH}+\text{Veg}) p$	2.241	0.068	8
$\psi(\text{BA Hard}+\text{ShrubH}+\text{CWD}+\text{SOIL}) p$	2.608	0.056	9
$\psi(\text{ShrubH}+\text{Veg}+\text{SOIL}) p$	2.501	0.060	8
$\psi(\text{Veg}+\text{SOIL}) p$	2.660	0.055	7
$\psi(\text{BA Soft}+\text{ShrubH}+\text{SOIL}) p$	3.581	0.035	8
<i>Zapus hudsonius</i> ^p			
$\psi(\text{Veg}) p$	0.000	0.207	5
$\psi(\text{ShrubH}+\text{Litter}) p$	0.531	0.159	6
$\psi(\text{BA Hard}+\text{ShrubH}) p$	0.851	0.135	6
$\psi(\text{ShrubH}+\text{SOIL}) p$	0.891	0.132	6
$\psi(\text{BA Hard}+\text{Veg}+\text{SOIL}) p$	1.826	0.083	7
$\psi(\text{BA Hard}+\text{Litter}+\text{SOIL}) p$	2.206	0.069	7
$\psi(\text{ShrubH}+\text{Veg}+\text{Litter}) p$	2.346	0.064	7
$\psi(\text{Veg}+\text{Litter}+\text{SOIL}) p$	2.546	0.058	7
$\psi(\text{BA Hard}+\text{ShrubH}+\text{SOIL}) p$	2.576	0.057	7
$\psi(\text{BA Hard}+\text{Veg}+\text{Litter}+\text{SOIL}) p$	3.467	0.037	8

^a No detection covariates used.^b JD.^c JD.^d Trap Occ.^e Pitfall + Temp + Trap Occ.^f Temp + Precip.^g Precip + JD.^h Temp.ⁱ Temp + Precip + JD.^j Precip.^k Precip.^l Pitfall + Temp + Precip.^m Pitfall.ⁿ Trap Occ.^o Temp + Precip + JD.^p Pitfall + Precip.