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Geographic variation in habitat structure for the wood warblers in Maine and Minnesota

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Abstract. The habitats occupied by species of wood warblers (Emberizidae) were compared at two study areas, Itasca State Park, Minnesota and Mount Blue State Park, Maine. Univariate comparisons of each variable of habitat structure show geographic differences for each species of warbler. Habitats available were also different because small trees were always more dense in Maine than in Minnesota. The Black-throated Green Warbler had the most dissimilar habitat with 9 of 11 variables different at the two sites.

Cluster analysis identified four generalized habitat groups containing (1) species occupying territories with high percent shrub cover, (2) forest species from Maine, (3) forest species from Minnesota and (4) open country species. Reciprocal averaging ordination was used to identify habitat gradients at each site. The first axis of the Maine and Minnesota ordinations was a gradient from open country with dense ground cover to forest vegetation. The second axes differed, however. In Minnesota, the gradient separated medium deciduous trees from large conifers, whereas in Maine, vegetation graded from medium and large deciduous trees to coniferous habitats. Spearman rank correlation indicated that the warblers were similarly arranged along both habitat axes at each site despite differences in axis loadings of habitat variables.

A combined reciprocal averaging ordination separated forest and shrub-forest edge species in Maine from the same two species groups in Minnesota along a smaller to larger tree axis. The results clearly demonstrate that habitat structure is not consistent throughout the range of many widely distributed species. It is suggested that the similar arrangement of species along the habitat axes probably results from an individualistic distribution of opportunistic bird species. Variation is probably induced at a site level by intraspecific competition for territories, small-scale vegetation dynamics, and resource fluctuation that occurs both within and between seasons.

structure differ within the range of some breeding species. This contradiction may reflect the scope of each study since Noon et al. (1980) adopted a community level approach whereas the latter studies employed species-specific methodologies. In addition, several recent analyses have shown that breeding birds generally exhibit broad habitat preferences (Cody 1978, Rotenberry and Wiens 1980, Collins et al. 1982) which may contribute to the difficulty of producing accurate predictive generalizations concerning habitat structure.

Few geographic comparisons of bird habitat have been based upon the distribution of groups of breeding birds in relation to specific characteristics of vegetation structure (Noon and Able 1978, Cody 1978). Thus, the purpose of my research was to determine if habitat for breeding birds is consistent and therefore, predictable for a group of similar, broadly distributed, co-occurring species. The wood warblers (Emberizidae) are ideally suited for a study of habitat variability. This family is numerically dominant in the northcentral and northeastern United States (Wiens 1975) and many species co-exist at any given site. In addition, the foraging ecology of most eastern warblers is well known (MacArthur 1958, Morse 1980). Finally, the Emberizidae are similar both morphologically (Greenberg 1979) and genetically (Barrowclough and Corbin 1978). Thus, the wood warblers are an abundant and closely related group well suited for broad geographical comparisons.

Materials and methods

Study areas. The study areas were Itasca State Park, northern central Minnesota (Lat 47° N) and the vicinity of Mount Blue State Park, west-central Maine (Lat 44° N); a distance of 1960 kilometers separates the two sites. Both sites are within large areas of relatively continuous forest in the hemlock-white pine-northern hardwoods forest region defined by Braun (1950). This regional vegetation type consists of the pronounced alternation of coniferous, deciduous, and mixed forest types. Fires and logging have created stands of open, non-forest vegetation and dense coppice. Thus, each site supports vegetation that is compositionally and structurally heterogeneous. The major physiographic difference between the two regions is the flat topography of Minnesota versus the mountainous landscape in Maine. This topography affects both vegetation structure and habitat gradients.

Vegetation structure provides the primary background for the life history of many breeding birds. Noon et al. (1980) found that habitat structure was consistent and predictable throughout the range of several eastern United States breeding birds. In contrast, Cody (1978) and Collins (1983) have quantitatively demonstrated that aspects of habitat

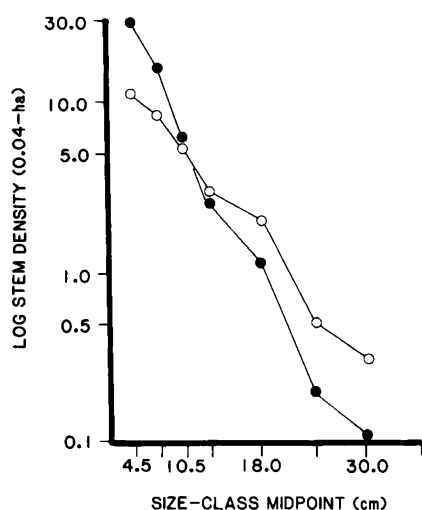


Fig. 1. A plot of the average number of stems within tree diameter size classes (cm) for all tree species in Maine (—●—) and Minnesota (---○---). Size classes are denoted by their midpoints

One estimate of the successional status of forest vegetation is the distribution of trees in several stem diameter classes (Goff and West 1975, Johnson and Bell 1975). Figure 1 shows that Minnesota vegetation contains more large trees and fewer small trees than Maine forest which yields a slightly flatter curve for Minnesota. This distribution implies that Maine vegetation is less mature than in Minnesota, a consequence of recent logging activity and elevation on forest population structure in Maine. Despite the geographic and topographic differences, these sites contain a similar warbler avifauna (Table 1).

Data collection. Habitat structure was determined by measuring 13 habitat variables (Table 2) in 0.04-ha circular plots (James and Shugart 1970) located within the territory

of singing male warblers (Table 1). Most circles were centered on song perches; however, some nest-site samples were recorded for most species (Collins 1981). In general, samples were located without regard to vegetation-type, topography, or elevation, and the number of circles per species reflects the relative abundance of that species at each study site. Sampling occurred after the leaves of all trees had fully expanded and territories were established. Therefore, measurements of cover for each stratum characterize aspects of habitat structure, but probably are not important when territories are selected by some individuals prior to leaf expansion. Sampling in Minnesota occurred from 1 June to 7 July 1978 (34 samples), and 1979 (173 samples); and from 28 May to 10 July 1980 (152 samples) in Maine. Unfortunately, both sites could not be sampled within one season, thus an effort was made to concentrate sampling over as short a time as possible. However, some differences in habitat between sites could result from year to year variation in warbler species populations (c.f. Wiens 1981a). The 0.04-ha sampling procedure was used in this study because it allows a quantitative comparison of habitat structure and relationships for different species on different study plots in forested regions (James 1978).

Data analysis. Statistical differences for each habitat variable for those species with at least five samples per site were determined using a non-parametric Mann-Whitney U-test. To compare community organization of the warblers in Maine and Minnesota, multivariate techniques were employed. To obtain general habitat categories, data for the 13 habitat variables for each species were averaged, standardized ($\bar{X}=0$, $s^2=1$) and subjected to an unweighted pair-group cluster analysis (UPGMA, Sneath and Sokal 1973) based upon an Euclidean distance resemblance matrix. UPGMA is an agglomerative, polythetic, hierarchical clustering procedure. Cluster analysis was performed on the combined Maine and Minnesota data sets. This analysis will produce groups of species with similar habitat prefer-

Table 1. Names, abbreviations, and number of samples for the 19 species of warblers breeding in Minnesota or Maine^a

Scientific name	Common name	Abbreviation	Number of samples	
			Minnesota	Maine
<i>Mniotilta varia</i>	Black and White Warbler	BW	10	10
<i>Vermivora chrysoptera</i>	Golden-winged Warbler	GW	11	
<i>V. ruficapilla</i>	Nashville Warbler	NA	13	10
<i>Parula americana</i>	Northern Parula	NP	16	9
<i>Dendroica petechia</i>	Yellow Warbler	YE	14	7
<i>D. magnolia</i>	Magnolia Warbler	MA	9	9
<i>D. caerulescens</i>	Black-throated Blue Warbler	BL		10
<i>D. coronata</i>	Yellow-rumped Warbler	YR	5	10
<i>D. virens</i>	Black-throated Green Warbler	BG	15	11
<i>D. fusca</i>	Blackburnian Warbler	BB	15	10
<i>D. pensylvanica</i>	Chestnut-sided Warbler	CS	16	10
<i>D. striata</i>	Blackpoll Warbler	BP		10
<i>D. pinus</i>	Pine Warbler	PI	15	
<i>Seiurus aurocapillus</i>	Ovenbird	OV	18	10
<i>Oporornis philadelphia</i>	Mourning Warbler	MO	15	5
<i>Geothlypis trichas</i>	Common Yellowthroat	CY	17	11
<i>Wilsonia canadensis</i>	Canada Warbler	CA	3	10
<i>Setophaga ruticilla</i>	American Redstart	AR	15	10

^a Coefficient of community = 84.5% (see Whittaker 1975:118)

Table 2. Univariate comparison of habitat structure by a Mann-Whitney U-test for each species with at least five samples at both sites

Habitat variable	Species												
	NA	YE	CS	CY	MO	YR	OV	AR	BW	BB	BG	MA	NP
Ground cover			*	*	*	*	*				*		
Shrub cover				*				*					
Canopy cover		*				*	*	*			*	*	
Canopy height		*									*		
Percent conifer		*					*				*		
Number of tree species	*	*		*			*	*	*		*		*
Trees 7.5–15 cm dbh ^a	*	*	*	*			*	*		*	*	*	*
Trees 15.1–23 cm dbh					*	*	*	*		*	*		*
Trees 23.1–30 cm dbh									*		*		
Trees 30.0–38 cm dbh									*				
Trees > 38 cm dbh ^b					*						*		

^a Diameter at breast height^b Includes tree sizes classes: 38.1–53 cm dbh, 53.1–68 dbh, and > 68 cm dbh used in ordination analyses* Indicates significantly different at $P < 0.05$. Yellow Warbler and Common Yellowthroat had all tree size classes combined for one analysis. Species abbreviations are given in Table 1

ences based upon vegetation structure, and it will allow a between-site comparison of species membership within the quantitatively defined habitat groups.

Recent analyses have indicated that bird species are not found in discrete communities as cluster analysis would imply; instead, birds tend to be independently dispersed along habitat gradients (Wiens and Rotenberry 1981, Collins et al. 1982). Therefore, reciprocal averaging ordination (RA, Hill 1973) was used to determine the distribution of species or species groups along derived habitat gradients. RA has been shown to provide reliable vegetation ordinations (Gauch et al. 1977) as well as bird habitat ordinations (Sabo and Whittaker 1979, Collins et al. 1982). This technique uses an iterative procedure to obtain species scores based upon habitat variables simultaneously with a habitat ordination based upon species scores. Between each iteration, the ordination scores are rescaled from 0 to 100. RA ordinations based on unstandardized average habitat variables were performed with the Maine species data set, the Minnesota species data set, and a combined Maine-Minnesota data matrix. Again, comparisons of community organization along with overall differences in a species habitat structure can be observed between the two sites. Unlike Mann-Whitney U-test, the multivariate procedures do not provide a quantitative statistical measure of between-site habitat differences; however, multivariate techniques have the advantage of reducing the data matrix complexity by combining all habitat variables into one analysis (Gauch 1982).

Results

Univariate comparisons. In all, 49 of 135 (36%) comparisons of habitat variables by the Mann-Whitney U-test were significantly different (Table 2). Of the eleven variables, small trees, number of species of trees, ground cover, and canopy cover were most frequently dissimilar and there is a distinct pattern to the differences. Values for T1, T2, SPT, and CC were always smaller for samples from Minnesota habitats when compared to habitat structure in Maine (Table 2).

Only ground cover was consistently higher in the Minnesota samples (Table 2). Thus, the overall pattern of habitat structure reflects differences in population age distribution of trees in the forests of Maine and Minnesota as noted earlier (Fig. 1).

All warblers had at least two ($\bar{X} = 3.8$) habitat variables that were significantly different in Maine and Minnesota (Table 2). The Black-throated Green Warbler and the Ovenbird, forest species, had the most dissimilar habitats. This partly reflects the fact that there is a greater potential for habitat differences in forest vegetation based upon this set of variables. It is tempting to suggest that variables that were not significantly different may be components or correlates of each species niche-gestalt. This is unlikely however, because of the high degree of within-site variation for each of the habitat variables, and cannot be conclusively determined without controlled manipulations of habitat structure.

Cluster analysis. The cluster analysis produced four habitat groups at a distance level of 46.0 (Fig. 2, Table 3). Group I contains six species found in forest habitats with high percent shrub cover, moderate canopy cover, and low percent conifer in the canopy. This vegetation structure represents forest edges and gaps. Group II is a forest and forest-edge group which can be divided into two subgroups. Subgroup IIA contains forest and edge species occupying habitats with high percent ground cover (70%) and moderate canopy cover. Group IIB contains five forest species from Minnesota. These species occur in habitats with tall canopies, moderate coniferous cover, few small trees and more larger trees. Group III represents forest species from Maine. These habitats have high percent canopy cover, variable coniferous cover and many trees in the smaller size classes. Finally, Group IV species are associated with open habitats characterized by few trees, and high percent ground cover. In general, the open country species of Maine and Minnesota clustered together. Forest species, on the other hand, were somewhat segregated between Group II mostly Minnesota and Group III (Maine).

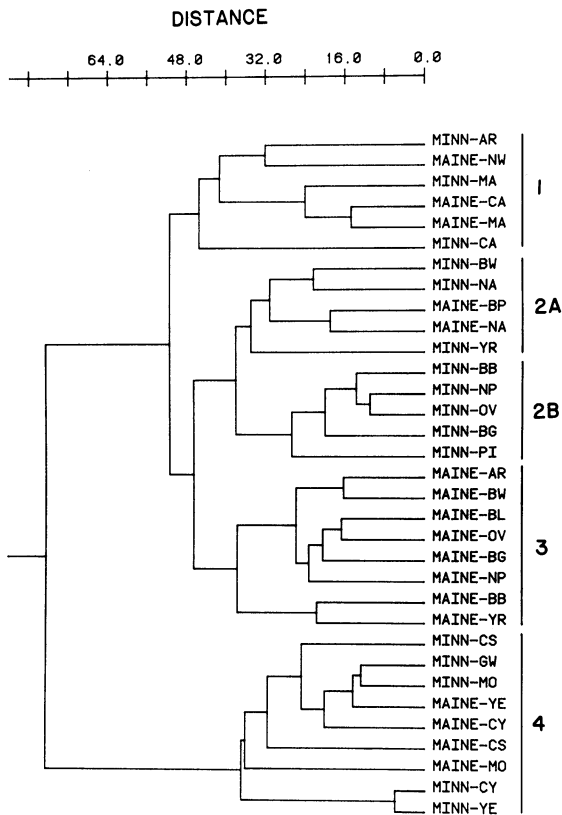


Fig. 2. Unweighted pair group cluster analysis for averaged habitat variables for the species in Maine and Minnesota. In the dendrogram, Group 1 represents forest species with high percent shrub cover, Group 2 contains primarily forest species from Minnesota, Group 3 contains forest species from Maine, and Group 4 combines open country species

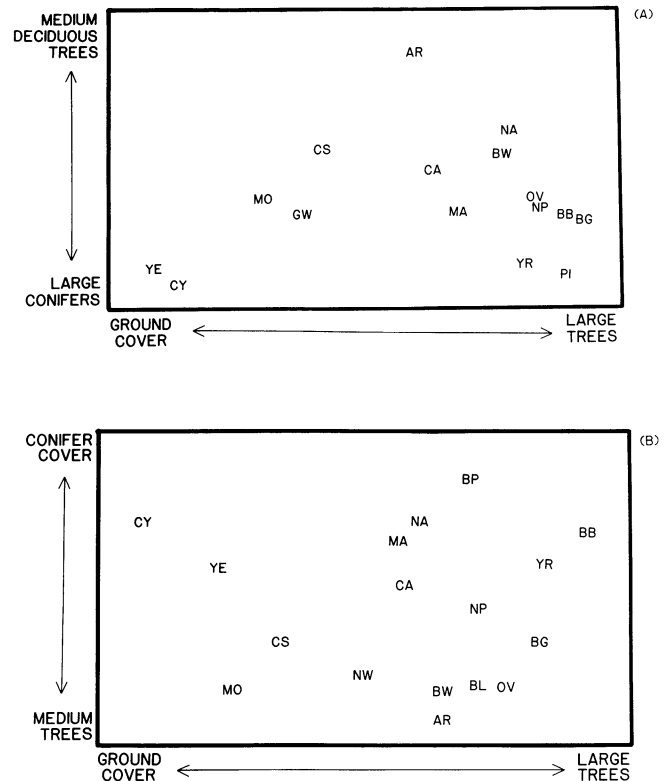


Fig. 3A, B. Reciprocal averaging ordination based upon averaged habitat variables. Species abbreviations are given in Table 1. **A** Minnesota, **B** Maine

Table 3. Means (\pm standard deviation) for each habitat variable for each group defined by the cluster analysis. Explanation of the habitat variables is given in Table 4

Variable	Group				
	I	IIA	IIB	III	IV
GC	65.7 \pm 15.7	72.5 \pm 10.3	59.8 \pm 5.2	48.4 \pm 6.7	88.2 \pm 9.9
SC	70.2 \pm 6.7	49.0 \pm 4.0	43.3 \pm 4.2	35.1 \pm 8.5	49.9 \pm 11.7
CC	64.2 \pm 8.4	65.9 \pm 4.7	78.4 \pm 3.4	84.3 \pm 5.4	27.2 \pm 12.1
CH	48.6 \pm 8.9	43.1 \pm 9.8	59.4 \pm 9.2	46.2 \pm 5.0	31.6 \pm 9.2
CO	24.7 \pm 13.4	42.3 \pm 10.8	53.6 \pm 7.9	30.6 \pm 16.0	6.5 \pm 3.5
SPT	6.7 \pm 2.3	5.0 \pm 0.8	5.6 \pm 0.5	8.0 \pm 1.0	3.1 \pm 1.4
T1	20.9 \pm 11.4	26.9 \pm 9.2	12.0 \pm 3.4	36.6 \pm 5.9	7.9 \pm 6.9
T2	12.8 \pm 2.7	12.5 \pm 3.8	10.8 \pm 1.6	21.4 \pm 4.4	4.2 \pm 2.2
T3	6.7 \pm 2.3	6.2 \pm 2.2	7.3 \pm 2.4	8.8 \pm 2.1	1.6 \pm 1.1
T4	2.7 \pm 1.5	2.9 \pm 1.7	4.4 \pm 0.6	4.0 \pm 0.7	0.5 \pm 0.5
T5 ^a	0.7 \pm 1.2	0.5 \pm 0.7	1.7 \pm 1.6	0.8 \pm 0.9	0.2 \pm 0.2

^a Includes all trees greater than 38.0 dbh

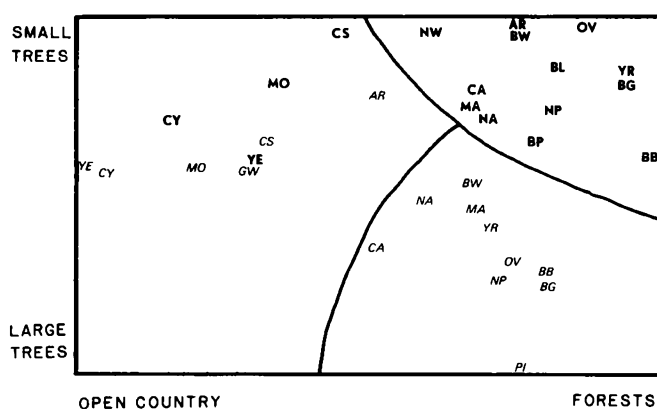
Ordination. The reciprocal averaging ordinations from averaged habitat variables for Maine warblers and Minnesota warblers were relatively similar (Table 4, Fig. 3a, b). In each case, RA axis I was a gradient from forest habitats with large trees and little ground cover to open areas with fewer trees and dense ground and shrub cover. These axes accounted for 71% and 74% of the variance in Maine and Minnesota data sets, respectively. The correlation of vari-

able loadings for Maine RA axis I and Minnesota RA axis I was highly significant ($r=0.944$, $P<0.001$; $df=2,11$). Therefore, the major habitat gradient, open country to forest, is essentially identical for the warblers at the two study sites.

Some differences occur in the variable scores along RA axis II (15% and 12% of the variance at Maine and Minnesota, respectively) of the Maine and Minnesota ordinations.

Table 4. Summary statistics for the three reciprocal averaging ordinations

Variable	Mnemonic	Maine		Minnesota		Both	
		Axis I	II	I	II	I	II
Ground cover	GC	0.0	53.5	0.0	40.9	0.0	71.0
Shrub cover	SC	5.6	58.0	24.7	84.6	19.8	73.2
Canopy cover	CC	52.7	32.2	76.2	69.6	82.6	75.4
Canopy height	CH	34.6	36.6	58.6	60.6	55.8	63.6
Percent conifer	CO	73.3	100.0	98.9	19.3	100.0	41.4
Number of tree species	ST	41.2	21.8	65.8	71.3	73.9	87.7
Trees 7.5–15 cm dbh	T1	57.7	50.1	77.9	57.8	99.3	100.0
Trees 15.1–23 cm dbh	T2	67.0	45.2	72.6	78.0	99.6	89.7
Trees 23.1–30 cm dbh	T3	72.6	47.0	80.4	100.0	96.7	71.9
Trees 30.1–38 cm dbh	T4	77.2	29.8	89.6	89.5	98.9	60.6
Trees 38.1–53 cm dbh	T5	74.2	0.0	100.0	40.3	95.9	34.4
Trees 53.1–68 cm dbh	T6	84.7	19.8	94.5	7.4	94.0	24.0
Trees > 68 cm dbh	T7	100.0	71.3	98.4	0.0	84.9	0.0
% Variance		71.6	15.4	73.8	12.3	63.3	18.2

**Fig. 4.** Reciprocal averaging ordination of the combined Minnesota and Maine data sets. The ordination clearly separates forest and shrub-forest edge birds in Maine from those in Minnesota along a gradient from small to larger trees. Italicized abbreviations = Minnesota species, Arabic letters = Maine species

Although both axes tended to separate deciduous from coniferous forests, the conifer forests of Minnesota contain larger trees than coniferous habitats in Maine. That is, the size differences between coniferous and deciduous forests at the two sites are reversed. This is reflected in the negative correlation of variable loadings for Maine RA axis II with Minnesota RA axis II ($r = -0.240$, NS); however, this relationship was not significant.

The distribution of warblers along the habitat gradients in Maine and Minnesota was also very similar (Fig. 3a, b). Axis I separated forest birds like the Blackburnian Warbler, Northern Parula, and Overbird from shrub-forest edge species (e.g. Canada and Nashville warblers) and open country species (e.g. Yellow Warbler and Common Yellowthroat). Coniferous forest species (Blackburnian and Yellow-rumped warblers) were segregated from deciduous forest dwellers (e.g. American Redstart) along the second RA axes. The Spearman rank correlation (based only on species occurring at both sites) of species along RA axis I of each ordination was highly significant ($r_s = 0.900$, $P < 0.01$). The RA axis II rank correlation was also significant, but the distribution of species along this habitat gradient was more variable between sites ($r_s = 0.56$, $P < 0.05$).

The combined RA ordination clearly demonstrates that differences in habitat structure exist for each species at the two sites (Table 4, Fig. 4). Axis I (63% of the variance) grades from open country to forest vegetation as in the previous ordinations (Fig. 3a, b). Axis II (18% of the variance) separates habitats with more smaller trees from areas with more larger trees. Ordinations in general do not depict local relationships as well as overall trends (Sneath and Sokal 1973). However, this can not account for the complete separation in Fig. 4 of forest species in Maine from those in Minnesota. This separation by a method which combines all habitat variables in one analysis corroborates the large number of differences noted among comparisons of individual habitat variables (Table 2). In addition, the open country species are separated in the ordination as well, with individuals from Maine having more smaller trees in their habitats than those species from Minnesota.

Discussion

The univariate and multivariate analyses have demonstrated that warblers in Maine occupy habitats that are different from those in Minnesota. These results contradict those of Noon et al. (1980) although the two species showing the most habitat variation in their study were warblers as well. The implications of the differences in habitat noted here are uncertain until the actual impact of each aspect of habitat structure on each species can be ascertained. Although dissimilarities in habitat structure can be demonstrated, this does not necessarily imply that species have different preferences in different portions of their range. Instead, birds may simply be selecting the most optimal habitat at each site from the total available. Also, the birds may be selecting consistent elements within their range and this is not being detected by the sampling technique. Unfortunately, it is difficult to distinguish between these alternatives. For instance, in a study of the habitat of the Black-throated Green Warbler, Collins (1983) found all structural features to be highly variable. It was suggested that much of a species niche-gestalt is based upon threshold values for features of the habitat above or below which, the habitat becomes suitable. Therefore, variance and differences may not be meaningful when analyzing occupied territories. This

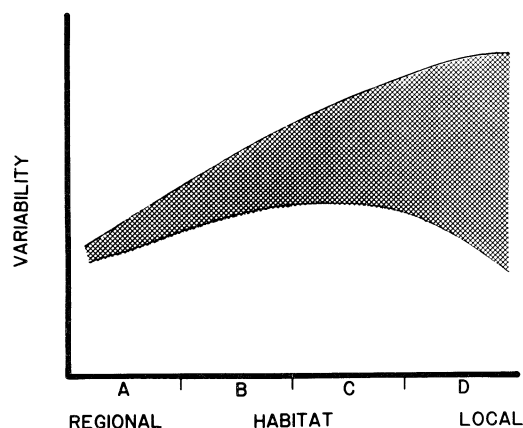


Fig. 5. A generalized model representing habitat variability in relation to scale of study. In general, as habitat is viewed along a continuum from regional to local levels, observable habitat variation increases. Level *A* represents regional habitat such as forest or grassland. Level *B* incorporates variation by differentiation among deciduous vs coniferous forest or tallgrass vs shortgrass prairie. At level *C* analysis is more localized focusing on structural variables such as stem density, shrub cover, etc. Changes in these factors occur due to the natural dynamics of the vegetation such as windthrow in forest or fires in grasslands. Finally, at a localized level (*D*), habitat structure may vary seasonally in response to seasonal patterns of prey abundance

can not always be resolved by comparing occupied versus unoccupied habitats (Johnson 1981) since the interpretation of absence is tenuous, at best.

An interesting feature of the between-site comparison was the similar arrangement of species along the derived habitat gradients (Fig. 3a, b). This is especially intriguing in light of the dissimilar habitats exemplified in the univariate comparisons of individual species (Table 2). Essentially, the habitat gradient in Maine is compressed in comparison to the gradient in Minnesota. The open country species in Maine had more small trees and greater shrub cover than in Minnesota. The forest habitats of Maine contain more small trees, fewer large trees (Fig. 4), and greater tree species richness than forests in Minnesota. Despite these differences, the warblers were similarly arranged along the first habitat axes derived for each site by the ordinations. Differences were evident along the second habitat axes where community structure was correlated yet habitat loadings were not.

The similar arrangement of species with regard to vegetation structure noted between sites suggests that some general organizing factor may exist in warbler habitat relationships. Competition for habitat could be the overriding organizing factor (e.g. Cody 1981). However, Wiens (1977) stated that because competition is a within-community phenomenon, geographic comparisons are not reasonable measures of competitive interactions. In addition, evidence from previous studies of warbler habitat relationships implied that interspecific competition for habitat was probably not a continuously important influence (Collins et al. 1982). Warbler habitats are highly variable and overlap considerably along derived gradients. This phenomenon has been noted for other groups of birds as well (Cody 1978, Wiens and Rotenberry 1981). Thus, birds probably select habitats based upon general features of vegetation structure (Hilden 1965, James 1971). This individualistic response to vegeta-

tion structure produces an independent distribution of bird species along habitat gradients (Rotenberry and Wiens 1980) resulting in repeatable patterns of species organization amongst this widely occurring group of warblers.

The habitat variability, structural dissimilar and similar species organization can be incorporated into a simple, hierarchical model of habitat selection (Fig. 5) similar to that suggested by Wiens (1981b) and Wiens and Rotenberry (1981). In a broad sense, birds select their habitat based upon general features such as forest versus grassland vegetation. Little variation is imposed at this level (Fig. 5, point A). At the next level, a species habitat may be more predictable or identifiable such as mixed coniferous forest or tall grass prairie (Fig. 5B). Variation at a local level (Fig. 5C) reflects short-term habitat fluctuations such as gap-phase dynamics or fire frequency. These events affect canopy cover, shrub cover, tree size class distribution, etc. Such disturbance phenomena occur at different frequencies and intensities for different vegetation (habitat) types (White 1979, Runkle 1982). Most comparative habitat studies are focused at this level (James 1971, Whitmore 1975, Smith 1977, Collins et al. 1982). Finally, if intraspecific competition for territories is severe, individuals may breed in a broad spectrum of vegetation structure (Svardson 1949). This is coupled with individualistic responses to aspects of territory use especially in relation to foraging and nest site selection. For instance, the availability of prey items changes between species of tree and time of season (Futuyama and Gould 1979). Birds have been shown to feed on trees with the greatest abundance of insect prey (Holmes and Robinson 1981). Prey populations will change seasonally and in response to predation intensity (Holmes et al. 1979). Birds may alter their foraging activities based on changes in search image reliability as prey populations vary seasonally (Heinrich and Collins 1983). Combined, these factors produce a high degree of intra-population variation in habitat (Fig. 5D). On a temporal scale, only habitat fluctuations at level D occur regularly within the life span of an individual bird. The overall impact of this spatial and temporal heterogeneity in habitat will be a limited ability to accurately predict specific features of habitat structure for many widely occurring species of birds. As Wiens (1981b) stated, however, despite this variation, the incorporation of time and space effects can lead to meaningful insights into community structure and relationships.

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