

BIRD COMMUNITIES OF NORTHERN FORESTS: ECOLOGICAL CORRELATES OF DIVERSITY AND ABUNDANCE IN THE UNDERSTORY¹

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Abstract. The bird community of the understory in far northern forests is markedly more diverse and abundant in deciduous than coniferous forests. Avian species richness within each vegetation type did not increase with size of source fauna, which can be interpreted as indicating that these communities are “saturated.” However, the communities may not be saturated either in the long-term view (post-Pleistocene lag) or in the short-term view (because marked population fluctuations may constrain diversity short of saturation). Differences in species diversity were not readily attributable to geographic barriers such as the coastal mountain ranges or to metapopulation dynamics. Local ecological factors that may contribute to avian abundance and diversity included density of litter invertebrates and understory vegetation structure, and possibly foliage invertebrate abundance and nest safety. Some typically understory birds in coastal conifer forests often shifted nest sites to moss wads in the canopy and subcanopy.

Key words: Bird community; species diversity; rainforest; understory; Alaska; Yukon; British Columbia; saturation; species richness; nest sites.

INTRODUCTION

The regulation of diversity and abundance in animal communities has fascinated ecologists for many years, but the study of diversity and abundance has evoked perhaps as much controversy as consensus. An early approach focused on food resources, examining foraging behavior, direct and indirect indices of competition for food, and comparisons of morphological features associated with foraging and food handling. Many of these studies assumed that the community was in equilibrium, and many of them sought to support some favored ecological process rather than weighing several to determine their relative importance. In part for these reasons, this approach has received heavy criticism (Wiens 1984, 1989). Yet many ecologists still feel that food-related ecology—or availability of usable energy and/or rates of energy acquisition—at least sets some boundaries on diversity and abundance (Turner et al. 1988, Currie 1991, Wiens 1991, Wright et al. 1993).

For a number of years following the early work of Robert MacArthur 1961, it was popular to measure (in various ways) vegetation structure

and attempt to relate some measure of structural complexity to avian diversity, primarily in wooded habitats (e.g., Karr and Roth 1971, many others). Although it is probably often true that there is some relationship between vegetation complexity and avian diversity, the nature of and basis for the relationship is unclear (Willson 1974)—early studies emphasized food and foraging, but other factors such as nest-site availability must also be considered (Martin 1988d, 1993; Steele 1993). The risk of nest predation may provide selection for diversification of nest sites, thus creating a direct link between vegetation structure and avian diversity (Martin 1988a, 1988c).

Ecologists have recently argued for the nonequilibrium status of many communities (Wiens 1984, 1989, Price 1984, Schluter and Ricklefs 1993). Nonequilibrium conditions may prevail if populations are subject to fluctuations caused by any of a myriad factors, including severe weather in various manifestations, disease, invasion of new or more predators and competitors, or insufficient time for equilibrium to be established. The role of historical and biogeographic factors in community ecology has also received increasing attention in recent years (Karr 1976, 1980, Ricklefs 1987, Cornell and Lawton 1992, Schluter and Ricklefs 1993).

Except for the addition of the historical/re-

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gional considerations, this litany sounds much like Andrewartha and Birch's (1954) four "components of the environment" (weather, food, other organisms, and a place to live) needed to explain the distribution and abundance of animals. Indeed, the four components, acting on separate species, have a cumulative effect on the structure of the entire assemblage. Andrewartha and Birch (1954:4) discarded the possibility of studying whole communities, even if taxonomically circumscribed, "because the enormous task of unraveling the ecological relationships in even a simple community has usually proved impracticable." However, the gulf between the population-level approach and community ecology is not as deep as may have been perceived, and the task, although enormous, is not intractable.

Factors that contribute to determining avian diversity and abundance can be sorted into two levels, which are not entirely independent (Brown and Maurer 1987). The geographic level includes regional biogeography (and hence history), landscape configurations, and metapopulation structure. At the local level are ecological characteristics of the occupied site, including food resources and nest sites. We assess, in a necessarily preliminary way, the relationship of factors at these two levels to diversity and abundance in understory bird communities of northern forests. No assumptions are made initially about the equilibrium status of the community. We limit our study to the understory sub-community, because it is accessible to field examination of local factors.

Specifically, we addressed the following questions of the understory bird community in Southeast Alaska and neighboring Yukon/British Columbia forests. The first three questions are at the geographic level, the second three at the local level: 1) Is the diversity (species richness) of the understory bird community correlated with the size of the source fauna? 2) Are the coastal mountains a barrier to colonization, especially for birds of conifer understory? 3) Is there evidence that the understory bird community in coastal forests has such low reproductive success that only continual immigration can maintain the populations? 4) Is understory diversity and abundance related to vegetation structure, and thence to cover and potential availability of nest or foraging sites? 5) Is understory diversity and abundance related to potential prey density or abundance? 6) Is under-

story diversity and abundance related to nest safety (or, conversely, to the risk of nest predation)? These questions are considered in a comparison of the understory bird community in deciduous and coniferous forests and within each forest type.

STUDY SITES AND METHODS

Our study sites were located in coastal forest near Juneau and Haines, Alaska, and in interior forest near Atlin, British Columbia. At all three locations, both coniferous and deciduous vegetation types were sampled. Brief descriptions of the study sites and census methods and comparisons of the avian assemblages can be found in a companion paper (Willson and Comet 1996).

This study emerged from the results of some preliminary sampling with mist nets, showing that many more birds were caught in the understory of deciduous stands than in coniferous stands. We therefore present results from more extensive mist-net samples as well as visual/auditory point-count censuses (see details in Willson and Comet 1996). Mist-net sampling used 12 m nets with 30 and 36 mm mesh size. Nets were operated from one half hour before sunrise to mid-late morning. At our latitude, sunrise occurs at about 02:30 Alaska Standard Time on 1 June.

"Understory species" were defined as those that use the understory (defined as the first 3 m above ground) heavily for either foraging or nesting, judging from published information on nest sites and our experience. They included six thrushes, seven warblers, eight sparrows, and five others. Many species use the understory to some extent, but we tried to identify those that are characteristic of the understory. Analyses of census data refer to this set of species, but comparisons of mist-net catches utilize all species caught in standard nets set at ground level. Site diversity is the number of regularly occurring (in >1 census) understory species per site in the census data, point diversity is the average number of regularly occurring understory species per point, and relative abundance is the average number of birds of understory species/point/day.

Vegetation structure profiles were assessed using a 0.015 × 5 m sampling pole, which was placed vertically at 10 m intervals along a haphazardly-located transect through each study site ($n = 50-60$ points in 1992, $n = 100$ points in 1993). We counted the number of "hits" (foliage-

bearing branches that touched an imaginary cylinder of radius 4 cm around the pole) in meter intervals. This is an index of the quantity of vegetation present in each height interval; for this study, we used this measure as an index of vegetation density for the first 3 m above the ground.

Foliage invertebrates on understory vegetation were sampled by enveloping an undisturbed branch or stem in a large cloth bag (1×1 m square), cutting the branch, fogging the interior of the bag with Ortho indoor fogger for 10–15 sec and setting the bag aside for at least 20 min, shaking the bag to dislodge the invertebrates, and then opening the bag and counting all detectable invertebrates in the accumulated debris. Volume of foliage and woody material for each sample was measured by water displacement in the field. Shrub species to be sampled during each sampling period were determined randomly from a list of common species. This method of invertebrate sampling was extremely labor intensive and limited the number of samples that could be processed. In 1992, a total of 712 samples was taken, and in 1993, there were 597 samples from common understory trees and shrubs. We obtained dry weights of foliage insects in the laboratory, but the results were more ambiguous (more interaction terms in the anovas) than for density, and we do not present the results here.

We used three indices of potential prey availability in understory vegetation: 1) Prey density, which is number of invertebrates per unit volume of vegetation (either foliage and twiglets alone, or total volume both foliage and branch); 2) prey patchiness, measured as the standard error of prey density, and 3) estimated prey abundance, which was calculated as the prey density \times the average vegetative density for each site.

Litter invertebrates were sampled by a timed search: a 0.20×1.0 m quadrat was placed haphazardly on the ground between woody stems. The censuser carefully searched the litter or loose moss to a depth of about 4 cm for a period of three minutes. A total of 43 samples was taken, each sample consisting of six pooled replicates.

Invertebrates were usually recorded without taxonomic designations; caterpillars were recorded separately, as were earthworms and snails in the litter samples. Sampling was conducted periodically from late May to late July in 1992 and 1993, and all samples were used collectively to provide an estimate of potential prey density for each site; for present purposes, no attempt was made to discern temporal trends.

Studies of nest predation were done only in Juneau and Atlin. We examined natural nests at four sites in Juneau and two sites in Atlin in 1994 (total $n = 490$ nests of known fate). We also conducted experiments with artificial nests baited with quail eggs in Juneau (1993) and Juneau and Atlin (1994) (Sieving and Willson, unpubl.).

We constructed a potential source fauna in two ways. 1) Only birds known (from published or unpublished sources) to occur in or near each location were included. 2) We counted birds of appropriate habitat affinities whose range maps in standard field guides indicated occurrence within about 400 km of each location. Results from both methods were similar, and we present only from the first one here. Both methods are somewhat conservative in that many birds are known to stray far beyond their usual range. If we allowed for such vagrancy, all of North America and part of Asia should be included in the possible source fauna; this seemed excessive and would have made the source fauna the same for all three locations.

Three-way ANOVAs examined the differences between vegetation types, years, and locations (see Willson and Comet 1996 for details). The ANOVAs allowed us to discern whether or not the measures of avian diversity and abundance and of environmental factors varied in parallel (that is, whether or not the direction of difference was the same). We then more closely examined the relationship of local ecological variables to avian diversity and abundance in several ways: correlations between selected ecological variables (vegetation density, an array of estimates of prey density and abundance, nest safety) and average diversity or abundance for samples grouped by vegetation type, location, and year (called "group means" below), and correlations on data more finely divided across all sites within years (called "across sites" below). To examine the relationships of avian abundance to several environmental variables simultaneously, we used a stepwise multiple regression with three independent variables that showed up as significant (or nearly so) in the simple correlations or anovas previously described (litter invertebrates, foliage invertebrates [using density/total branch volume or estimated abundance], and vegetative density; added by the program in order of importance). A similar regression included size of source fauna as a fourth independent variable. All chi-square tests (when $df = 1$) for comparisons of frequencies used Yates' correction.

TABLE 1. Patterns of diversity (species richness per site and per point) and relative abundance of understory birds. C = coniferous, D = deciduous stands; acronyms for sites given in Willson and Comet 1996.

Location	Site	Veg. type	Site diversity		Point diversity		Relative abundance	
			1992	1993	1992	1993	1992	1993
Juneau	DACR	C	7	8	5.5	6.5	4.1	5.5
	HERV	C	8	9	5.3	5.2	5.9	4.6
	PECR	C	8	6	5.0	4.5	4.5	3.6
	Avg.		7.7	7.7	5.3	5.4	4.8	4.6
	BKLO	D	13	14	8.8	9.4	6.6	6.5
	SHCR	D	14	12	9.6	9.6	8.1	9.5
	Avg.		13.5	13.0	9.2	9.5	7.4	8.0
Haines	CHKO	C	5	8	3.6	6.8	2.3	3.2
	LASI	C	—	8	—	5.5	—	5.0
	Avg.		5.0	8.0	3.6	6.2	2.3	4.1
	COFP	D	11	13	9.1	9.7	8.1	7.7
	KLRI	D	12	12	7.4	7.8	8.3	7.4
	KLSL	D	10	—	7.5	—	6.2	—
	Avg.		11.0	12.5	8.0	8.8	7.5	7.6
Atlin	BCSP	C	7	6	4.4	3.6	1.8	1.9
	YUSP	C	6	6	4.6	3.6	2.1	2.0
	PCPI	C	4	4	2.4	3.0	0.8	1.1
	Avg.		5.7	5.3	2.3	3.4	1.6	1.7
	BCAS	D	7	7	5.8	4.5	3.1	1.4
	YUAS	D	7	8	5.2	4.9	2.8	1.8
	PCWI	D	9	11	6.8	8.0	4.5	3.5
Avg.		7.7	8.7	5.9	5.8	3.5	2.2	
ANOVA Summary (Model 1, 3-way)	veg F = 84.8, $P < 0.001$ loc F = 22.5, $P < 0.001$ veg \times loc F = 4.19, $P = 0.032$ D > C (11.1 > 6.6) J = H > A (10.5 = 9.1 > 6.8)		veg F = 68.6, $P < 0.001$ loc F = 18.7, $P < 0.001$ D > C (7.0 > 4.6) J = H > A (7.3 = 6.6 > 4.7)		veg F = 54.1, $P < 0.001$ loc F = 42.9, $P < 0.001$ veg \times loc F = 5.2, $P = 0.016$ D > C (6.1 > 3.1) J = H > A (6.2 = 5.4 > 2.3)			

RESULTS

PATTERNS OF AVIAN DIVERSITY AND ABUNDANCE

Site diversity in the understory differed significantly between vegetation types (deciduous, coniferous) and among locations (Juneau, Haines, Atlin) but not between years (1992, 1993). Overall, diversity was lower in Atlin than in Juneau and Haines, and higher in deciduous than coniferous stands (Table 1). There was a significant interaction term between vegetation type and location, but at all three locations the direction of the difference between the avian site diversity in the two vegetation types was Deciduous > Coniferous. Point diversity was uniformly greater in deciduous than coniferous vegetation types at all locations in both years (Table 1). Point diversity was lower in Atlin than in the two coastal locations.

Relative abundance differed significantly between vegetation types (deciduous > coniferous) and among locations (Atlin lower than Juneau

and Haines) but not between years (Table 1). There was a significant interaction term between vegetation type and location, but at all three locations, relative abundance in deciduous stands was greater than that in coniferous stands.

The greater number of species in deciduous understory could have been due to the greater abundance of birds there, because a larger sample increases the probability of finding more species. Rarefaction curves for each location and year showed that the contrast between deciduous and coniferous stands was maintained for Juneau in 1992 and 1993, Haines 1992, and Atlin 1993 (Fig. 1). In Haines 1993 the two sets of curves overlapped, although the composite curve for deciduous stands would be higher than that for coniferous stands. In Atlin 1992, the overlap was more extensive, although two of three curves for conifer stands were still slightly lower than the curves for deciduous stands. In most cases, then, standardizing the sample for the number of individuals did not erase the contrast between habitats, making it likely that some ecological dif-

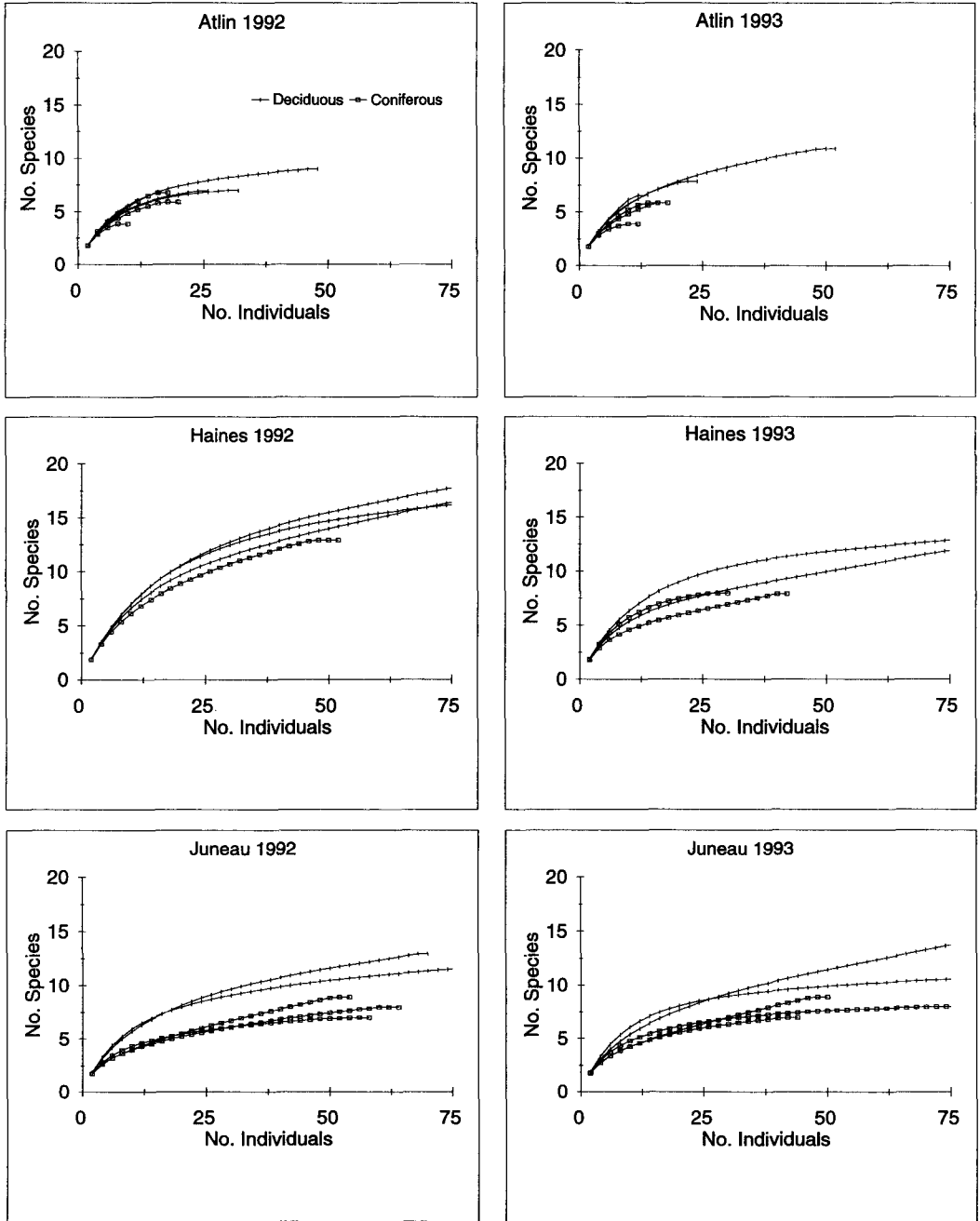


FIGURE 1. Rarefaction curves for understory bird communities in northern coniferous and deciduous forests. In most cases, the understories of deciduous forests contained more species for a given number of individuals than did conifer forests.

ferences are directly important in determining the contrast between bird communities of the different vegetation types.

In 1994 we recensused most of the sites in Atlin and Juneau, to see if patterns of diversity

and abundance were similar to previous years. Again, Atlin bird communities had lower site diversity, point diversity, and abundance than Juneau, and all three measures were greater in deciduous than coniferous stands.

TABLE 2. Mist-net captures in understory of deciduous and coniferous forests. Birds/mist-net hour (excluding recaptures) and total number of species/100 mist-net hours. D = deciduous, C = coniferous forest. Data cells with two entries represent two different study sites.

Year	Months	Net-hours (D; C)	Number of birds		Number of species	
			Deciduous	Coniferous	Deciduous	Coniferous
1991	July, Aug	221; 221	0.35	0.05	9.9	3.6
1992	May, June	527; 635	0.22	0.03	2.3	1.3
	July, Aug	752; 580	0.38, 0.90	0.07	4.6, 6.3	1.4
1993	July, Aug	1,386; 1,774	0.76, 0.78	0.07	3.6, 2.6	0.1

Mist-net capture rates in Juneau confirmed the between-vegetation contrasts seen in the census data, whether the netting activity occurred during the height of the breeding season (May and June) or later (Table 2). More individuals and species were observed in deciduous understory even when, as in 1991, the deciduous netting site was a small enclave within continuous conifer forest.

RELATIONSHIP TO SIZE OF SOURCE FAUNA

The size of the observed fauna was correlated with the size of the potential source fauna ($R = 0.556$, $F = 12.5$, $P = 0.001$), when both deciduous and coniferous stands are included (Fig. 2). Therefore, it is possible that the greater diversity in deciduous forest understory could be attributed to the greater size of the potential source fauna. However, within each vegetation type, the slope of the line was not significantly different from zero, so the actual fauna within each vegetation type was not a function of the potential source fauna.

The proportion of the understory source fauna actually recorded for each location in each vegetation type was higher, overall, in deciduous forests, but the contrast was significant or marginally so only in Haines and Atlin (Table 3). Two results stand out: the proportion was unusually high for Haines—deciduous, and the proportion for Juneau—coniferous was sufficiently high that it was similar to that in deciduous stands.

MOUNTAIN BARRIERS

The coastal mountains rise steeply from the coast in Southeast Alaska, and broad icefields occupy most of the width of the cordillera, possibly forming a physical barrier between populations on the east and west sides. This barrier is perforated at several places by major rivers that arise in the interior and penetrate the cordillera in wide valleys, and passes free of permanent ice

occur in a few places. A number of species found commonly in the interior east and north of the mountain range also have been recorded from Southeast Alaska, especially in such valleys (Kessel and Gibson 1978). In addition, a few species appear to replace each other geographically on the east and west sides of the mountains. For example, there are Steller's Jay (*Cyanocitta stelleri*), Blue Grouse (*Dendragapus obscurus*), and Red-breasted Sapsucker (*Sphyrapicus ruber*) on the west, but Gray Jay (*Perisoreus canadensis*), Ruffed Grouse (*Bonasa umbellus*), and Yellow-bellied Sapsucker (*S. varius*) on the east. This indicates that the mountains constitute a barrier of some kind.

However, many interior species occur in the extensive deciduous stands in Haines, as well as in Skagway, at the northern end of the Inside Passage, and in the Berner's Bay area north of Juneau (Willson, unpubl.). In these locations, interior species occur in the floodplains of broad rivers whether or not the rivers penetrate the coast range, suggesting that their presence is determined chiefly by the availability of riparian deciduous habitat. Birds may reach coastal locations by moving through the large river valleys or over the mountains, which are generally <1,300 m high, or through the mountain passes (Weeden 1960). In general, coastal forest understory supported more bird species than either coniferous or deciduous interior forests, strongly suggesting that the mountains do not limit access

TABLE 3. Average proportion of the understory source fauna (number of species) that is actually recorded for each location (using the narrow-sense construction of source fauna, see Methods). * indicates $P < 0.05$; (*) indicates $P < 0.10$, Mann-Whitney U test.

Location	Deciduous	Coniferous
Juneau	57%	56%
Haines	71	* 43
Atlin	45	(*) 39

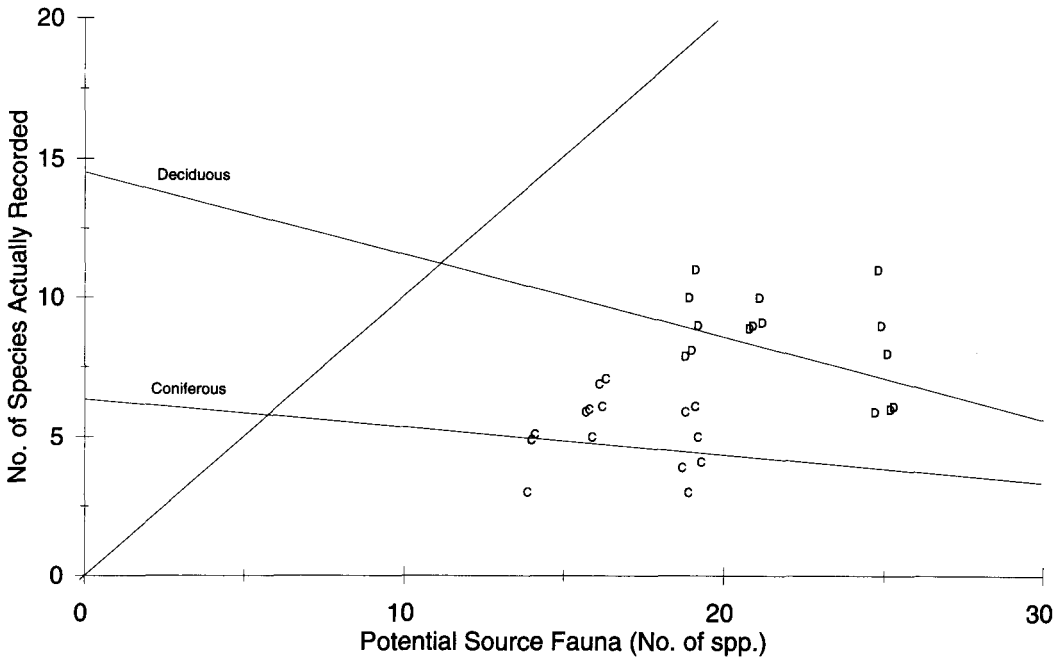


FIGURE 2. Number of species in observed avifauna vs. number of species in potential source fauna. D = deciduous forest, C = coniferous forest. The line through the origin indicates the relationship when observed equals potential (source). The other two lines are the calculated slopes for each type of forest separately (slopes = -0.32 [deciduous], -0.07 [coniferous]; neither is significantly different from zero).

to the coastal forests for most species in ecological time.

METAPOPULATION STRUCTURE

Portions of the species population might have such low reproductive success that they cannot sustain the local population density without considerable colonization from elsewhere. We lack the data to analyze this possibility in detail. However, our data on nesting success suggest that reproductive success was not unusually low on either side of the mountains or in either vegetation type (54–86% of nests successful per site in 1994, $n = 448$ nests at four sites near Juneau, 57–78% of nests successful per site near Atlin, $n = 42$, two sites). Predation was severe in some habitats (10–54% of nests in 1994) but no higher than recorded for many other places (Martin 1988b, 1993). More juveniles than adults were caught in post-breeding-season mist nets in Juneau in both years (ratio = 1.19:1.0). It is not likely that the coastal populations are maintained solely by recolonization.

VEGETATION DENSITY

The index of vegetation density in the first three meters above the ground at each site was con-

sistently greater on deciduous than on coniferous sites and, on average, understory vegetation was particularly dense in Juneau-deciduous sites (Table 4). Vegetation density across sites was correlated with both site diversity and bird abundance in both years (all Spearman r_s between 0.614–0.841, all $P < 0.05$); such correlations were also significant for group means (abundance: $r_s = 0.879$; diversity: $r_s = 0.866$, both $P < 0.01$). Thus, greater amounts of understory foliage tended to be associated with more species and individuals on a site.

Several species that are typically understory nesters often used other nest sites in Juneau spruce-hemlock stands. For example, the Dark-eyed Junco (*Junco hyemalis*), normally a ground nester, commonly nested in moss wads on dead and dying conifer branches (up to 14 m, at least) in some Juneau stands. Hermit Thrush (*Catharus guttatus*) nests ranged from 10 to 17 m (at least) in conifer stands. In addition, Winter Wrens (*Troglodytes troglodytes*), which commonly build covered nests in root wads or cut-banks, frequently used moss wads high in conifer trees (at least to 25 m).

An index of the magnitude of this microhabitat

TABLE 4. Summary of vegetation density index (average number of "hits"/point). D = deciduous, C = coniferous; Direction = direction of the difference.

Location	1992			1993		
	Decid.	Conif.	Direction	Decid.	Conif.	Direction
Juneau	9.0–10.3	2.7–5.7	D > C	10.5–11.5	2.7–5.7	D > C
Haines	4.9–7.8	3.4	D > C	4.4–6.1	2.5–2.9	D > C
Atlin	3.1–4.7	0.7–2.5	D > C	3.3–6.3	1.3–2.2	D > C

ANOVA: Vegetation type $F = 60.94$, $P < 0.001$, $D > C$; location $F = 37.64$, $P < 0.001$ Juneau > Haines = Atlin; interaction veg \times loc $F = 8.29$, $P = 0.003$.

shift can be obtained by comparing the number of nests of species that are typically considered to be understory species with the number of nests of such species that were actually discovered in the understory. Of 209 nests of "understory species" in deciduous forest, 25 (12%) were not actually placed in the understory. In contrast, of 38 nests of "understory species" in conifer forest, 23 (61%) were not actually placed in the understory ($\chi^2 = 45.4$, $P < 0.001$). Thus, the microhabitat shift was markedly greater for "understory birds" in conifer forest.

POTENTIAL PREY AVAILABILITY

Litter invertebrates were, on average, denser in deciduous than in coniferous stands, and in Juneau and Haines compared to Atlin (Table 5). Also, their density was higher in 1992 than 1993 at all locations. Overall, prey density on understory branches was somewhat higher in deciduous than coniferous stands for three of four indices (Table 5). Both measures of caterpillar density were higher in Atlin than in Juneau and Haines. Patchiness of prey density varied little, except that caterpillar density was patchier in Atlin than on the coast (per foliage volume, location $F = 9.75$, $P = 0.002$; per total volume, location $F = 11.04$, $P = 0.001$). Estimated foliage prey abundance was greater in deciduous than coniferous forest and greater in 1993 than in 1992 (Table 5). Significant interaction terms (especially for all invertebrates) showed that annual changes differed with vegetation type and location: foliage invertebrate abundance increased in 1993 only in deciduous forest and only in Juneau and Atlin. However, these interactions do not alter the contrasts between vegetation types or among locations. In general, the densities of litter and foliage invertebrates were not significantly correlated with each other. Thus, the average higher invertebrate density and abundance in understory foliage and the higher density in the

litter of deciduous stands broadly paralleled the average higher diversity and abundance of birds there. Although the low average density of litter invertebrates in Atlin matched the low average diversity and abundance of birds in that location, neither density nor abundance of foliage invertebrates was especially low in Atlin.

The only positive, significant correlation of avian abundance with prey variables was with litter invertebrate density (group means, Spearman rank correlation $r_s = 0.78$, $P = 0.01$; across sites, $r_s = 0.675$ in 1992, 0.620 in 1993, both $P < 0.01$). Group means for avian site diversity were correlated with litter invertebrates ($r_s = 0.54$, $P < 0.05$) and marginally with estimated foliage-invertebrate abundance (all invertebrates; $r_s = 0.543$, $P < 0.05$; caterpillars; $r_s = 0.448$, $P < 0.10$). However, when estimated prey abundances on foliage were compared across sites, the patterns among locations and between vegetation types or years disappeared (except with site diversity in 1993; $r_s = 0.628$, $P < 0.05$). Correlations of diversity across sites with litter invertebrates were significant or marginally significant ($r_s = 0.502$ in 1992, $P < 0.05$; 0.404 in 1993, $0.10 < P < 0.05$).

NEST SAFETY

Experimental, artificial nests were safer in deciduous than coniferous forest (overall, combining all data for open-cup nests by site, 31% vs. 59% depredated; Table 6, data from Sieving and Willson, unpubl.), corresponding to the lower abundances (0.09/point/day vs. 0.94/point/day) of the major nest predators (red squirrels [*Tamiasciurus hudsonicus*], Steller's and gray jays) in deciduous vegetation. Habitat differences in nest safety were especially marked in Atlin (Table 6). Furthermore, experimental nest safety was negatively correlated with the abundance of these predators (over all sites, both years, $r_s = -0.821$, $n = 11$, $P = 0.009$ and positively correlated with

TABLE 5. Summary of ANOVAs (Model 1, 3-way) on measures of prey density and abundance. Only those with some detectably significant (or marginally significant) effect are shown. Abbreviations: D = deciduous, C = coniferous, J = Juneau, H = Haines, A = Atlin. Prey densities for foliage invertebrates are per cc of branch; estimated prey abundances is an index (prey density \times vegetation density).

Measure	Factor	Main effects		Interactions		Density or abundance	Direction
		F	P	F	P		
Number/total vol.	veg	3.25	0.089			0.052 > 0.027	D > C
	veg	3.89	0.065			0.109 > 0.053	D > C
Caterpillar number/total vol.	veg	3.71	0.071			0.005 > 0.003	D > C
	location	9.68	0.002			0.008 > 0.002 = 0.002	A > H = J
Caterpillar number/fol. vol.	location	7.72	0.004			0.019 > 0.005 = 0.005	A > H = J
	veg	9.08	0.008			31.6 > 11.5	D > C
Caterpillar abundance	year	4.75	0.045			28.8 > 14.3	1993 > 1992
	veg	13.26	0.002	veg \times loc \times yr	0.097	308.6 > 80.8	D > C
Invertebrate abundance	year	3.33	0.087			251.8 > 137.6	1993 > 1992
	location	10.17	0.000	loc \times yr	0.074		
Litter inverts (per 0.25 m ²)	veg	8.89	0.005	veg \times yr	0.078	6.1 = 6.1 > 2.1	J = H > A
	year	11.87	0.002			6.0 > 3.6	D > C
				loc \times yr	0.08	6.2 > 3.4	1992 > 1992

vegetation density ($r_s = 0.783$, $P = 0.013$). However, natural open-cup nests of understory species may be even safer in conifer than deciduous forests (Juneau, 1994, 7% vs. 23% depredated; Willson, unpubl.), and the safety of natural nests was not correlated with the abundance of major nest predators, vegetation density, or the safety of artificial nests. Thus, the safety of experimental nests paralleled the contrast in understory bird diversity and abundance in conifer and deciduous stands, but that of natural nests did not. Overall safety of experimental nests, but not natural nests, was marginally significantly correlated with site diversity ($r_s = 0.560$, $P = 0.058$).

MULTIPLE REGRESSIONS

Group means of avian abundance were significantly correlated or nearly so with three variables ($R = 0.953$, $P < 0.001$; vegetation density $P < 0.001$, litter invertebrates $P = 0.001$, foliage invertebrate density $P = 0.066$). However, across sites, only vegetation density and litter invertebrates contributed significantly and consistently to the stepwise regression in both years (1992: $R = 0.848$, $P = 0.003$, vegetation density $P = 0.002$, litter invertebrates $P = 0.046$; 1993: $R = 0.851$, $P < 0.001$; vegetation density $P = 0.007$, litter invertebrates $P = 0.009$).

Avian site diversity (group means) was correlated with vegetation density and litter invertebrates ($R = 0.882$, $P = 0.001$, vegetation density $P = 0.002$, litter invertebrates $P = 0.018$), but not with any measure of foliage invertebrates. Stepwise multiple regressions across sites in each year, however, showed that only vegetative density contributed significantly to the relationship with avian site diversity (1992: $R = 0.866$; 1993: $R = 0.891$; both $P \leq 0.001$). Source fauna did not contribute to the multiple regressions.

Thus, vegetation density was the best predictor of bird species diversity at a site, but both vegetation density and the density of litter invertebrates predicted avian abundance per site. Foliage invertebrate density and estimated abundance differed between vegetation types in parallel with avian abundance and diversity but did not figure significantly in the multiple regressions, suggesting that their effects were relatively small and perhaps not independent of other factors. Nest safety was not included in the multiple regressions because too few sites were examined.

TABLE 6. Average proportions of experimental open-cup nests that were depredated in the understory of conifer and deciduous forests. Each cell has data for two sites.

Site, year	Deciduous	Coniferous
Juneau 1993	14%, 35%	51%, 21%
Juneau 1994	45%, 29%	54%, 61%
Atlin 1994	30%, 31%	82%, 82%

DISCUSSION

The understory of deciduous forest clearly harbored a greater diversity and abundance of birds than conifer forest in all our northern study locations. Coastal deciduous sites supported many species despite the small areas of suitable habitat and a Pleistocene history of habitat destruction throughout North America (Keast 1990). Local ecological factors appeared to be more important than regional factors in determining diversity and abundance. Local ecological factors with some consistent power for predicting avian diversity and abundance were density of understory vegetation and of litter invertebrates and, at least at the between-habitat level, perhaps foliage-invertebrate abundance and potential nest safety.

Although correlation of avian abundance or diversity with vegetation volume or complexity is common (Martin 1988d, Mills et al. 1991), it is not altogether clear why vegetation density is important: understory vegetation provides both foraging and nesting sites, as well as protective cover against predators and weather. The higher density of vegetation in the understory of deciduous stands might provide greater food abundance. Our mist-net data show that there were more understory birds in deciduous stands than in conifer stands even in the post-breeding season, when it is likely that food is a critical ecological resource. Two other studies have also found a higher density, but not necessarily biomass, of insects in deciduous-forest understory than in coniferous-forest understory (Schimpf and MacMahon 1985, Werner 1983). However, total abundance of foliage invertebrates may not reflect availability to foraging birds, because invertebrate density often varies among plant species, and birds forage differently on plants of differing characteristics (Holmes and Robinson 1981, Recher et al. 1991, Whelan 1989). In addition, many forest birds forage on the ground at least part of the time, and the density of litter

invertebrates was higher in deciduous than conifer understory (see also Hoff 1957) and contributed to most of the multiple regressions. Although aerial insects can be important for aerial foragers and for leaf-gleaners when low temperatures inactivate flying insects, the trend for flying insects did not parallel bird abundance and diversity (unpubl.).

Nesting sites and nesting cover strongly affect avian habitat use and, ultimately, diversity and abundance (Ricklefs 1989, Martin 1993). Differences in predation risks can be associated with differences in avian density and recruitment (George 1987, Sherry and Holmes 1992, Suhonen et al. 1994) and predation on nests may favor evolutionary divergence of nest sites and coexistence of bird species, thus influencing habitat selection (Martin 1988c, 1988d, 1993). Foliage density explained more variation of species richness in nesting than in foraging guilds in Arizona highlands (Martin 1988d) and patterns of habitat use often reflect nest-site requirements (MacKenzie et al. 1982, Steele 1993). Concealment of the nest itself may be directly important (but see Thurber et al. 1994), although vegetation configuration also diffuses predator searches (Holway 1991, Martin and Roper 1988, Martin 1992, Knopf and Sedgwick 1992, Kelly 1993). At least one study has reported greater nest safety in deciduous-forest understory (Seitz and Zegers 1993).

If vegetation density is an index of the availability of nest sites or nesting cover for open-nesting species, then there are more potential nest sites or more cover in the shrub stratum in deciduous stands. The contrast is probably even greater than indicated by the vegetation profile, because birds use some shrubs much more than others. For example, understory shrubs in coastal coniferous forest offer few places that will hold a nest, and those few are typically very exposed, such as in the fork of a *Vaccinium* or *Menziesia* shrub). No natural nests were ever observed in such sites.

The safety of artificial nests in our study was negatively correlated with the relative abundance of the major nest predators. However, the success of natural nests was not related either to the abundance of these predators or to the safety of experimental nests. We suggest that the experimental, artificial nests provided an index of potential risk of predation. The difference between experimental and natural nests has several possible explanations. Real birds, especially in

coniferous forest, often shifted their nests to sites above the understory, and those that did use the understory presumably concealed their nests more successfully and certainly nested at a lower density, which would reduce the risk of predation (Martin 1988d, Hoi and Winkler 1994). Furthermore, predators that key in on parental activity have additional clues to the locations of natural nests, which may decrease the habitat contrasts suggested by our experimental nests. We also suspect that estimates of predator abundance from the census data, which relied heavily on songs and calls, are too low, especially for deciduous sites. The major predators, primarily red squirrels and corvids, regularly foraged in deciduous vegetation, frequently >100 m from their home territories (K. E. Sieving, pers. comm., our observ.). If conifer-based predators such as red squirrels range several hundred meters from their normal habitat, none of the Juneau deciduous stands may have been large enough to diminish the risk of predation on natural nests.

Predator abundance also varies greatly from place to place, and different predators hunt in different ways, so the same availability of sites and cover may not suffice in all locales. Deciduous stands in our area do not seem to harbor major predators that are specific to those kinds of stands, so—to some extent—a habitat shift to deciduous stands might represent a shift toward greater nest safety. But in other areas, deciduous forests have their own array of predators so that deciduous stands do not necessarily offer a general haven from predation.

The contrast between the understory avifaunas of deciduous and coniferous forest described in this study is not universal although it appears to be fairly common: greater diversity has been observed in deciduous-forest understory in some studies (Salt 1957, Theberge 1976, Spindler and Kessel 1980) but not others (Erskine 1977, Finch and Reynolds 1988, Scott and Crouch 1988). Similarly, avian abundance was greater in deciduous-forest understory than in coniferous-forest understory in most of the studies just cited except for Erskine (1977). Furthermore, there is often variation within a general vegetation type: aspen stands may have lower diversity and abundance than willow/alder (Theberge 1976, Spindler and Kessel 1980, this study), and the understory of black spruce forest may have higher diversity and abundance than white spruce (Spindler and Kessel 1980).

Several authors have suggested that when the

diversity of a local fauna does not increase with increasing size of source fauna, the community may be "saturated" with species (e.g., Ricklefs 1987, Cornell and Lawton 1992), but the shape of the curve is not a definitive test of saturation (Cornell and Lawton 1992). We suspect that our communities are subject to population fluctuations related to weather (Wiens 1974) on and off the breeding grounds; to that degree, there may be changes in local colonization and extinction that are unrelated to species interaction and true saturation. Moreover, it is possible that the entire bird community lies below a potential saturation point simply because of a time lag following the pre-Quaternary glaciations (Willson and Comet 1996), or because climatic or other factors might limit the northward expansion of some populations irrespective of any conventional concept of saturation.

Conclusions based on correlations must be tentative, not least because there is always a risk that the critical variables remain unmeasured. In addition, logistics and funding may limit sample sizes, and small sample sizes, despite enormous effort in the field, can limit the ability to draw even correlational conclusions. Nevertheless, correlations at least can help sort out some factors that offer good prospects for further study. Experimental studies can often clarify the importance of various factors (Newton 1995) but are not always feasible, especially when interpretation of observed patterns depends on factors operating at different scales. Our study, based on correlations, has suggested that local ecological factors are important in determining diversity and abundance of birds in northern forests and some of these factors eventually might be amenable to experimentation.

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