

## **Comparisons of intermediately ranked species in avian rank-abundance distributions from four California forests**

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Biodiversity indices, such as those that measure species richness or evenness, provide limited information about ecological communities. The species abundance distributions from which these indices are derived contain greater detail about community structure. For this reason conservation planners and land managers would benefit from methods that allow more informative comparisons of these distributions than offered by traditional indices. We used bird survey data from four research forests in California to construct rank-abundance distributions. Using bootstrap re-sampling, we created uncertainty bands associated with the empirical shapes of these curves, allowing identification of significant ( $P < 0.05$ ) differences between distributions over a portion of their ranks. We found higher abundances of intermediately ranked species on two of the forests, and ascribe this result to differences in forest productivity and habitat complexity leading to greater niche partitioning of resources. Diversity indices derived from these data were less informative.

Key words: bootstrap re-sampling, California, community ecology, diversity indices, forest birds, rank-abundance distributions, resource partitioning

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Many researchers have advocated diversity indices for quantifying and evaluating biodiversity. The simplest index, species richness, formed the basis of MacArthur and Wilson's (1967) landmark theory of island biogeography. Other indices (Simpson 1949, Shannon and Weaver 1963) furnish relative abundance-derived information on evenness (or dominance) among species in a community. These measures remain central to biodiversity assessment for conservation planning (Margules and Pressey 2000, Moilanen et al. 2009, Zipkin et al. 2009, Chandler et al. 2013, Iknayan et al. 2014).

Species abundance distributions (Motomura 1932, Fisher et al. 1943, Preston

1948, Hubbell 2001, Harte 2011) provide a richer source of information than indices for quantifying biodiversity. One way of displaying these data, known as a rank-abundance distribution (RAD), is to plot species abundances in rank order. Whittaker (1965) was one of the first to use the RAD to connect concepts of resource competition and ecological niche to differences in abundance for dominant, intermediately abundant, and rare species. Beedy (1981) applied this method to compare bird communities and forest structure in California. He drew RADs for different forest types, and concluded that the lognormal form (Preston 1948) of the associated species abundance distribution in structurally complex habitats was indicative of greater resource partitioning (and food availability) supporting greater numbers of intermediately ranked species. One shortcoming of Beedy's (1981) results was the lack of a formal test of differences in abundances for these ranks.

We modified Beedy's approach, comparing the avian communities from four montane conifer forest locations in California. Rather than using indices, we evaluated empirical shapes of RADs and their sampling errors by means of bootstrap re-sampling (Efron 1982). Instead of evaluating entire curves, we focused attention on intermediate ranks because the amount of niche partitioning among these species may be demonstrative of differences between avian communities and the habitats that support them (Whittaker 1965, Beedy 1981, Lennon et al. 2004). Comparing pairs of forests, we estimated the percentage of intermediate ranks that supported higher abundances for one forest versus another. We compared these results with diversity indices of the data pertaining to species richness (alpha and gamma diversity) and evenness. To ascertain whether higher abundances in the intermediate ranks were associated with niche partitioning, we compared abundances of wood warblers (Parulidae) with the abundances of other species, because warblers provide a good avian example of niche differentiation in feeding habits (MacArthur 1958, Morse 1989, Lovette and Bermingham 1999).

The methods developed here offer an alternative to traditional diversity indices to assess differences among ecological communities. Bootstrap comparisons of RADs may be more useful than parametric approaches for estimating species diversity because they allow one to focus on a portion of ranks. Our evaluation of intermediately abundant species facilitates understanding of how niche partitioning differs among locations, habitats, and guilds of species, and this information may be of use to conservation planners and wildlife managers.

## MATERIALS AND METHODS

*Study areas.*— The avian survey data were from four research forests owned and managed by the University of California at Berkeley or the California Department of Forestry and Fire Protection (Figure 1). Management objectives for these forests included timber production and research.

The 3,650-ha Latour State Demonstration Forest (40° 38' N, 121° 42' W) is located 70 km east of Redding in the southern Cascade Mountains; elevations range from 1,200 to 2,050 m. Average annual precipitation was 117 cm on volcanic soils. The forest was predominantly mixed conifer and true fir (*Abies spp.*) forest punctuated by a few wet meadows and some post-fire brush fields. The forest was generally even-aged with sparse understory vegetation except along creeks and in brush fields. Average forest productivity was characterized as a low Dunning Site Class II (Dunning 1942, Ronald 1992, Barrett and Bise 1993).

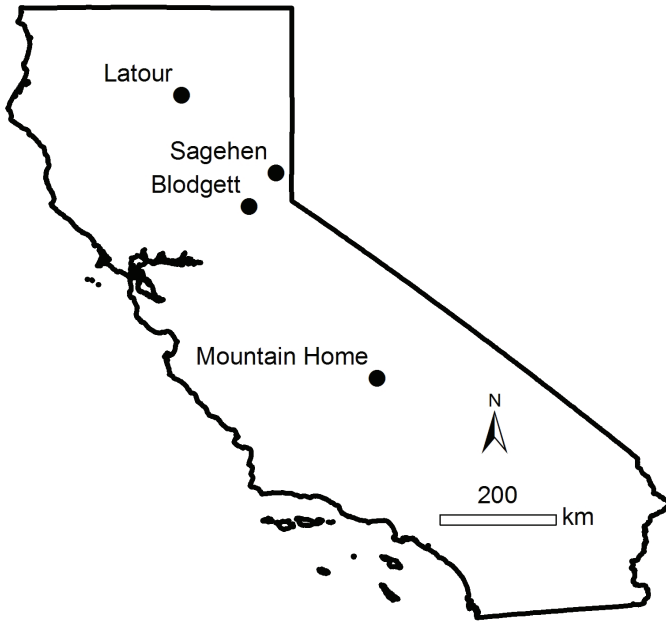


FIGURE 1.—California research forests where birds surveys occurred over the course of two breeding seasons at approximately 80 sites on each forest from 1979 to 1996.

The 1,175-ha Blodgett Forest ( $38^{\circ} 54' N$ ,  $120^{\circ} 39' W$ ) is located 18 km east of Georgetown in the central Sierra Nevada. Elevations range from 1,200 m to 1,500 m across gently rolling, highly productive terrain. Average annual precipitation was 166 cm. The forest was primarily mixed conifer with some oak (*Quercus spp.*) stands and brush fields. Average forest productivity was characterized as a high Dunning Site Class I (R. York, UC Berkeley, personal communication).

The 3,280-ha Sagehen Experimental Forest ( $39^{\circ} 35' N$ ,  $120^{\circ} 14' W$ ) is located 16 km north of Truckee in the central Sierra Nevada. Elevations range from 1,450 to 2,300 m. Average annual precipitation was 85 cm. The forest was a mosaic of mixed conifer and white fir (*Abies concolor*) stands, post-fire plantations, grassy meadows, and rocky shrublands. Average forest productivity was characterized as Dunning Site Class III or IV (S. Conway, US Forest Service, personal communication).

The 1,870-ha Mountain Home State Demonstration Forest ( $36^{\circ} 14' N$ ,  $118^{\circ} 41' W$ ) is located 35 km northeast of Porterville in the southern Sierra Nevada. Elevations range from 1,450 to 2,300 m. Average annual precipitation was 102 cm. The forest was predominantly mixed conifer forest with approximately 5,000 giant sequoia (*Sequoiadendron giganteum*) trees in excess of 1 m in diameter spread across half of the property. The forest was generally uneven-aged with more understory vegetation than at Latour. Springs supporting wet meadows occurred at numerous locations. Average forest productivity was characterized as a high Dunning Site Class II (Ronald 1992, Barrett and Bise 1993).

*Bird surveys.*—Breeding bird surveys were part of a comprehensive wildlife and wildlife habitat inventory undertaken by the University of California throughout the State

beginning in 1977 (Dedon and Barrett 1982). We limited this study to those locations from this inventory that occurred in coniferous forests and for which approximately 80 sites were surveyed at each forest over the course of more than one year. At Sagehen, 80 sites were surveyed in 1979 or 1981. At Latour and Mountain Home, 80 sites and 79 sites, respectively, were surveyed in 1993 or 1994. At Blodgett, 81 sites were surveyed in 1996 or 1997. Those sites were distributed evenly across each forest using a systematic design (Thompson 2002), and they were generally spaced at least 400 m apart. Each survey consisted of 20 consecutive 10-minute point counts (Ralph et al. 1995, Bibby et al. 2000) beginning 30 minutes after sunrise on a single morning, by a single surveyor during the breeding season, from the middle of May through the middle of July (Dedon and Barrett 1982, Barrett and Bise 1993).

*Abundance estimation.*—For analyses we limited detections to those birds the surveyor judged to have breeding territories intersecting at least half of the 30-m radial area surrounding the point count site. As surveys at each site occurred on a single day, we did not attempt to address detection probability via a model-based approach (Royle 2004). Instead, we used the highest count from the 20 consecutive survey replicates to approximate the true abundance of each species at the site. Counts were converted into densities (birds/ha) by dividing by area of the 30-m circle to which surveys applied. We assumed each naïve estimate of density to represent an index of abundance for use in our RADs.

*Rank-abundance distributions.*—We rank-sorted and then plotted point estimates of species densities in descending order. Considering the small survey area (0.28 ha) of the point counts and because most counts were unitary, we did not log-transform our densities as is usually done for these distributions (Whittaker 1965). We constructed RAD curves for each forest. As an exact distinction between dominant, intermediate and rare species is arbitrary, we chose a conservative definition of intermediate ranks that was less likely to unintentionally include species that might be considered dominant or rare. For the four forests we evaluated we defined intermediate species as ranks 6 to 20. Following the same reasoning we defined rare species at ranks > 25.

To assess differences between RADs we used bootstrap re-sampling (Efron 1982). We randomly sampled with replacement from the set of ~80 sites where surveys occurred at each forest and calculated an average density for each species. By repeating this process 10,000 times and rank-sorting the abundances each time, we created a sampling distribution for our index of abundance for each rank for each forest. By disregarding changing species identities within these ranks, we took a neutral theory (Hubbell 2001, Harte 2011) approach to evaluate ranks within RADs. Lastly, we estimated the uncertainty of the RAD curves using the 2.5th and 97.5th percentiles for each rank corresponding to a 95% confidence interval. Each upper confidence interval bound was connected by rank for graphing an uncertainty band associated with each RAD. Each lower confidence band was connected similarly. Pairs of forest-level RADs were considered significantly ( $P < 0.05$ ) different over a portion of their ranks as indicated by the bootstrapped uncertainty bands. We rejected the null hypothesis that both forests had the same avian abundance at a particular rank if each point estimate was outside of the confidence interval of the other forest.

To evaluate differences among the avian communities for pairs of forests, we calculated the percentage of intermediate ranks that had significantly ( $P < 0.05$ ) higher abundances for one forest versus the other. We repeated these comparisons for all 6 combinations of forest pairs. We applied hierarchical cluster analysis (Sharma 1996, McCune et al. 2002) to these results because the sample size of forest pairs was too small for

a parametric test, and we used this technique to assign the forests to two groups representing higher and lower abundances in the intermediate ranks.

To evaluate how well the uncertainty band technique worked with respect to traditional diversity indices, we computed average site-level species richness (alpha diversity; Whittaker 1960), forest-level species richness (gamma diversity; Whittaker 1960), and Simpson's measure of evenness (Smith and Wilson 1996). We used the same bootstrap re-samples to create 95% confidence intervals for these indices.

Our *a priori* hypotheses about differences in RADs for intermediately abundant species were based on niche and resource partitioning concepts (Grinnell 1917, MacArthur 1958, Hutchinson 1959, Whittaker et al. 1973, Schoener 1974, Chesson 2000). We hypothesized that higher forest productivity at the Blodgett and Mountain Home would lead to higher abundances of intermediately ranked species than at Sagehen and Latour, because larger trees, taller forests and greater structural complexity should lead to an increased potential for resource partitioning with respect to nesting and foraging habitat. We also believed that wood warblers (Parulidae) would rise to higher abundances in the intermediate ranks with respect to other species, because this taxon is well known to partition foraging resources in forests (MacArthur 1958, Morse 1989, Lovette and Bermingham 1999). Our expectation was that the percentage of individual birds within a community that was warblers would be higher for intermediate versus rare ranks and that this pattern would be more pronounced on higher productivity forests (Blodgett and Mountain Home). We estimated these percentages as the total densities of warblers in either the intermediate or rare ranks multiplied by 100 divided by the total densities of all birds in these ranks. We used the bootstrap samples to construct 95% confidence intervals about those percentages.

## RESULTS

*Abundance estimation.*—A total of 47 species was detected at least once at Latour, 57 at Blodgett, 62 at Sagehen, and 62 at Mountain Home. A total of 91 species was detected at least once for at least one of the forests. Species in the top five abundance ranks for at least one of the forests were American robin (*Turdus migratorius*), black-headed grosbeak (*Pheucticus melanocephalus*), dark-eyed junco (*Junco hyemalis*), golden-crowned kinglet (*Regulus satrapa*), mountain chickadee (*Poecile gambeli*), Nashville warbler (*Oreothlypis ruficapilla*), pine siskin (*Spinus pinus*), red-breasted nuthatch (*Sitta canadensis*), red crossbill (*Loxia curvirostra*), spotted towhee (*Pipilo maculatus*), Steller's jay (*Cyanocitta stelleri*), western tanager (*Piranga ludoviciana*), and yellow-rumped warbler (*Setophaga coronata*). Dark-eyed junco was the only species in the top five ranks for all forests.

Species in the intermediate ranks (6 to 20) for at least one of the forests were American robin, band-tailed pigeon (*Patagioenas fasciata*), black-headed grosbeak, brown-headed cowbird (*Molothrus ater*), Brewer's blackbird (*Euphagus cyanocephalus*), brown creeper (*Certhia americana*), Calliope hummingbird (*Selasphorus calliope*), Cassin's finch (*Haemorhous cassinii*), Cassin's vireo (*Vireo cassinii*), chipping sparrow (*Spizella passerina*), common raven (*Corvus corax*), dusky flycatcher (*Empidonax oberholseri*), fox sparrow (*Passerella iliaca*), golden-crowned kinglet, hairy woodpecker (*Picoides villosus*), Hammond's flycatcher (*Empidonax hammondi*), hermit thrush (*Catharus guttatus*), hermit warbler (*Setophaga occidentalis*), house wren (*Troglodytes aedon*), MacGillivray's warbler (*Geothlypis tolmiei*), mountain chickadee, Nashville warbler, northern flicker (*Colaptes*

*auratus*), purple finch (*Haemorhous purpureus*), red-breasted nuthatch, red-breasted sapsucker (*Sphyrapicus ruber*), Steller’s jay, warbling vireo (*Vireo gilvus*), western tanager, white-headed woodpecker (*Picoides albolarvatus*), Wilson’s warbler (*Cardellina pusilla*), yellow warbler (*Setophaga petechia*), and yellow-rumped warbler. Brown creeper and fox sparrow were the only species in the intermediate ranks of all forests, despite the fact that 24 of the 33 intermediately ranked species listed above were detected at least once at every forest. A full reporting of densities by forest is provided in Appendix I.

*Rank-abundance distributions.*— Visual inspection of RADs without the aid of uncertainty bands suggested differences in abundances among the four research forests we studied (Figure 2). The bootstrap method provided a quantitative description of those differences for pairs of forests (see Figures 3 and 4 as examples). In summary, we demonstrated significant ( $P < 0.05$ ) differentiation between a majority of intermediate ranks (6 to 20) for the Blodgett and Mountain Home forests versus Latour and Sagehen (Figure 5).

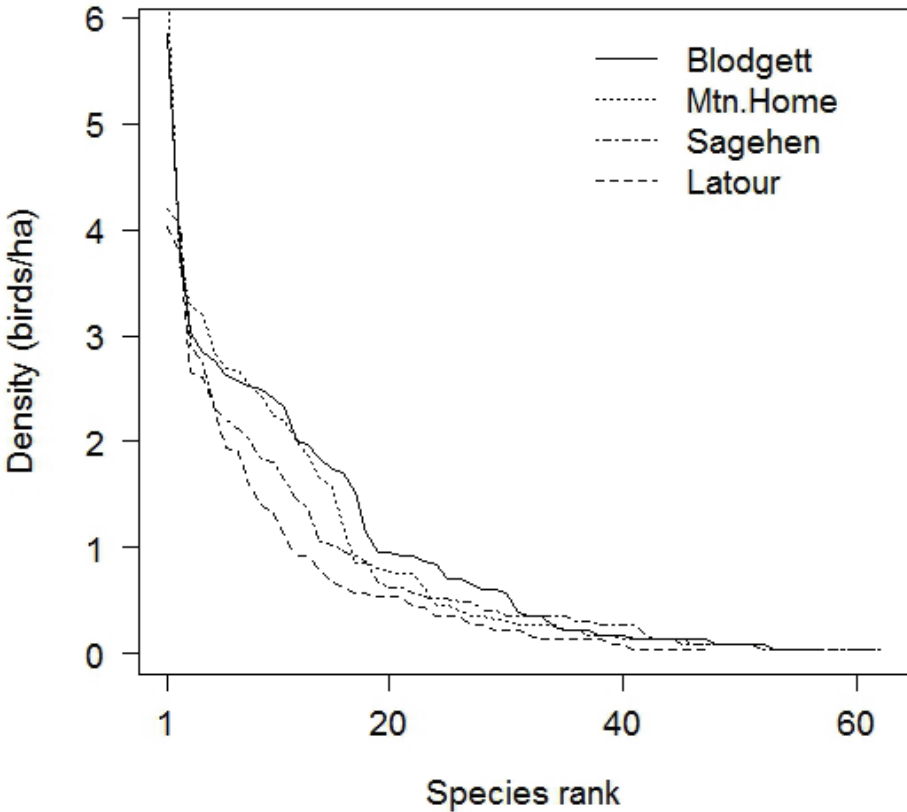
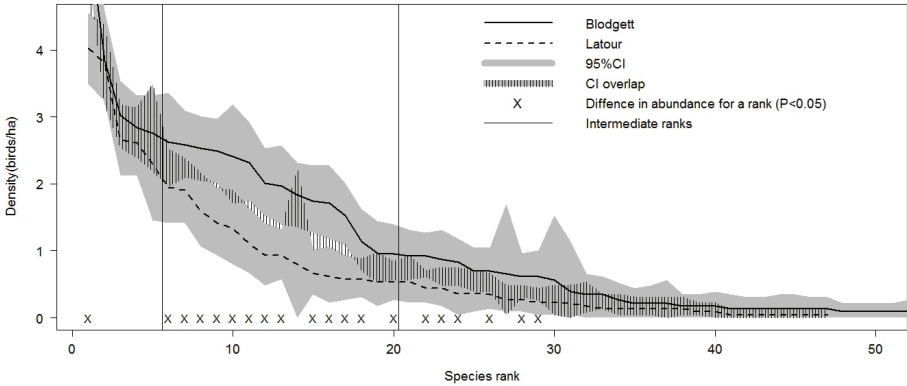
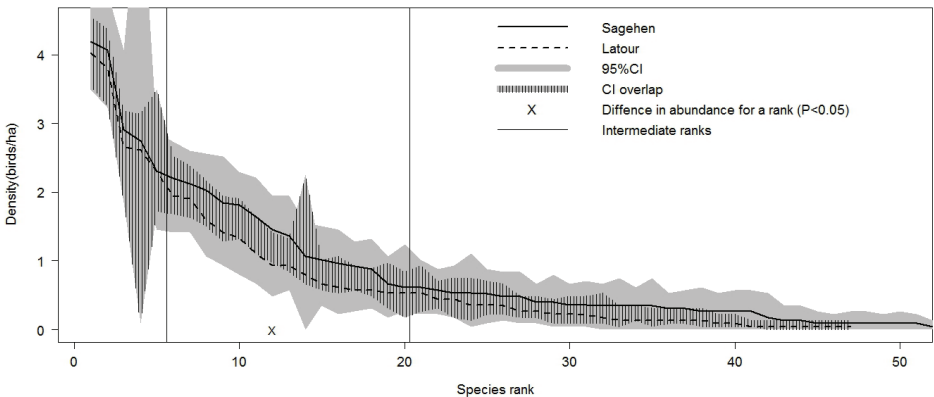


FIGURE 2.— Avian rank-abundance distributions from four research forests in California based on point count surveys.



**FIGURE 3.**—Pairwise of comparison of avian rank-abundance distributions from the Blodgett and Latour research forests in California. Using bootstrap re-sampling we created 95% confidence intervals for each rank. We identified differences in abundance for intermediate ranks (6-20) in cases where the point estimates for each forest lay beyond the confidence interval of the other. For this comparison 13 of 15 intermediate ranks had higher abundances at Blodgett than at Latour.



**FIGURE 4.**—Pairwise of comparison of avian rank-abundance distributions from the Sagehen and Latour research forests in California. Using bootstrap re-sampling we created 95% confidence intervals for each rank. We identified differences in abundance for intermediate ranks (6-20) in cases where the point estimates for each forest lay beyond the confidence interval of the other. For this comparison only 1 of 15 intermediate ranks had higher abundances at Sagehen than at Latour.

The exception to this pattern was the comparison between Mountain Home and Sagehen. Nevertheless, hierarchical cluster analysis split the forests into two groups (Blodgett and Mountain Home versus Latour and Sagehen) based on their differences in abundances in the intermediate ranks. These groups coincide with differences in soil productivity (Dunning Site Classification) among the forests.

*Diversity indices.*—Differences in diversity indices for the six pairwise combinations of forests varied considerably and this result did not appear to be associated with results of the bootstrap method (Figure 5). There was always a difference ( $P < 0.05$ ) in alpha diversity between forests. All three indices were different ( $P < 0.05$ ) for two of the four comparisons

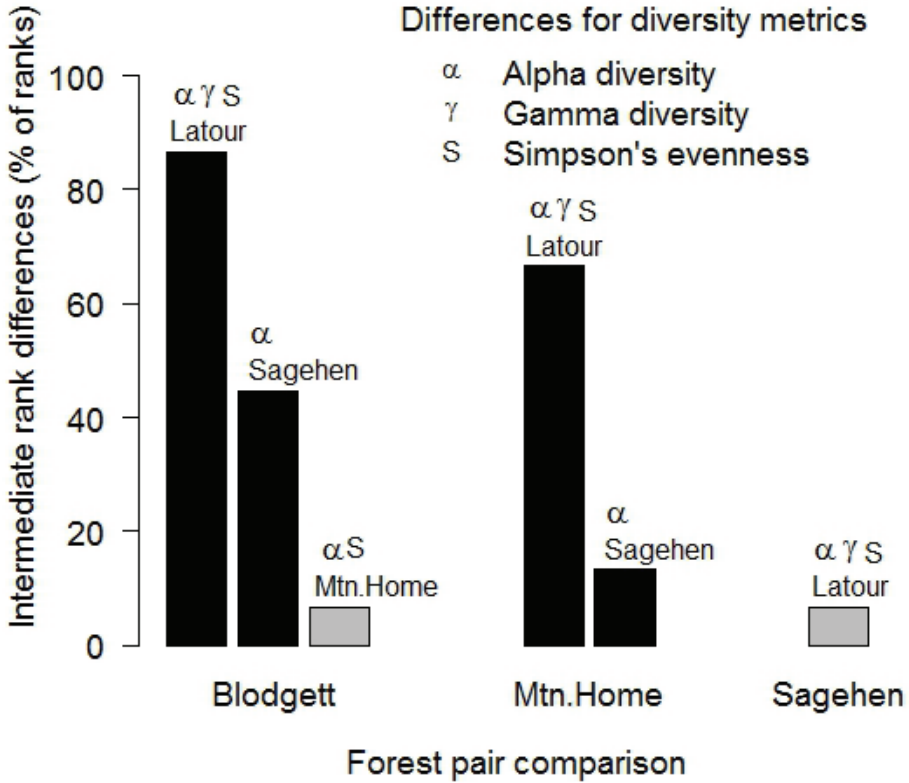
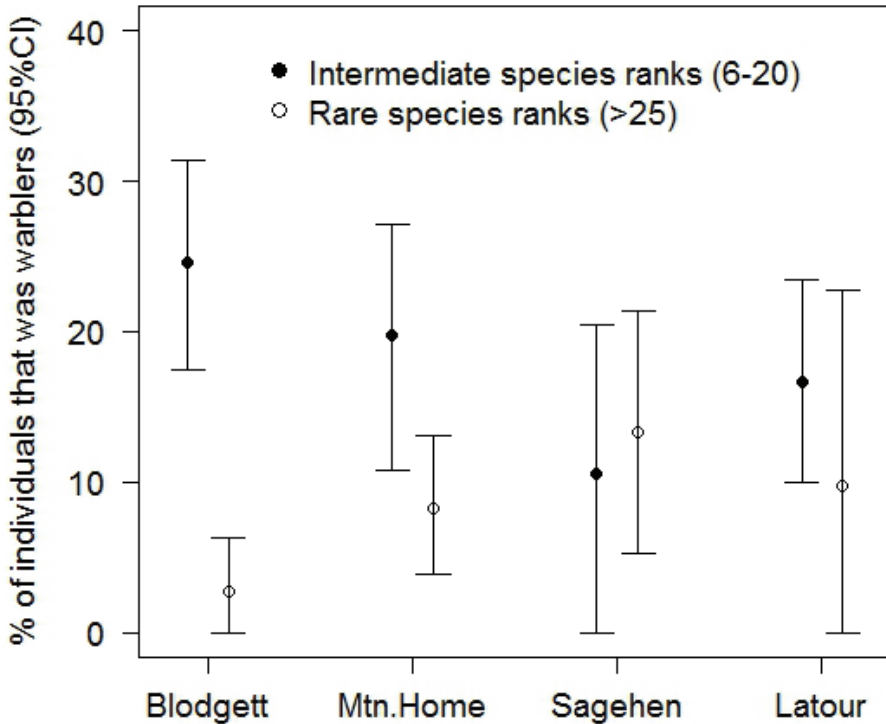


FIGURE 5.—Summary of all pairwise comparisons of avian rank-abundance distributions among four research forests in California. Forests listed at the bottom represent those that had higher abundances of intermediately ranked species compared to the forests listed above. Using bootstrap re-sampling we created 95% confidence intervals for each rank. For each pair of forests we identified differences in abundance for intermediate ranks (6-20) in cases where the point estimates for each forest lay beyond the confidence interval of the other. The dark colored bars represent comparisons between high and low abundance forests as confirmed by hierarchical cluster analysis. There was no consistency between the percentage of intermediate rank differences between forests and significant ( $P < 0.05$ ) differences in diversity indices between forests.

between the higher and lower abundance forests we identified, but they were also all different ( $P < 0.05$ ) for one of the two comparisons between lower abundance forests.

*Wood warblers.*— As expected, our estimates of the percentages of individual birds that were warblers were higher ( $P < 0.05$ ) for intermediate versus rare ranks on the more productive forests (Blodgett and Mountain Home, Figure 6). In contrast, our estimates of the percentages of individual birds that were warblers were not higher ( $P > 0.05$ ) for intermediate versus rare ranks on the less productive forests (Sagehen and Latour).





**FIGURE 6.**—Warblers abundances at four research forests in California. To identify evidence of resource partitioning within this taxon, we calculated the percentage of individuals of all birds surveyed that were wood warblers (Parulidae). We made this calculation separately with respect to intermediately abundant and rare species. The results show that warblers rose to higher abundances in the intermediate ranks at two of the forests. This finding supports the idea that higher productivity forests with greater structural complexity of habitats provide more opportunities for niche partitioning among avian species.

## DISCUSSION

Ecologists have proposed a confusing variety of biodiversity indices over the past century (Magurran and McGill 2011), and those indices have been accompanied by some criticism of their usefulness (Hurlbert 1971, Schwartz et al. 2000). Others have focused on the mathematical forms of species abundance distributions (Fisher et al. 1943, MacArthur 1957, Wilson 1991, Flather 1996). Rather than computing indices or fitting mathematical forms, we directly compared the empirical shapes of RADs using a bootstrap method to differentiate pairwise combinations of avian communities. This method provided greater information than indices about how abundances varied for dominant, intermediate, and rare species, a distinction that allowed us to explain results in terms of competition among species. Instead of making a measure of the entire RAD, we directly evaluated those intermediate ranks believed by plant and bird ecologists to be strongly associated with resource partitioning and the structural complexity of habitats (Whittaker 1965, Beedy 1981). In this regard, our method is similar to the approach taken by those researchers; however, we did so without

needing to make complicated assumptions about the mathematical properties of different classes of RADs.

Our results suggest that the avian communities at Blodgett and Mountain Home had higher abundances of intermediately ranked species than at Sagehen and Latour. These findings are consistent with the hypothesis that higher productivity forests provide the potential for greater structural diversity and enable more intermediately common species to rise to higher abundances, because niche partitioning reduces interspecies competition for resources. Blodgett and Mountain Home occurred on more productive soils (Dunning Site Class I and high II) than the other forests.

There was no consistency between the values of 3 commonly used diversity indices and our findings on how middle ranks were differentiated among forests. This discrepancy suggests that our bootstrap method may illuminate different community properties than traditional diversity indices do. These indices might not be optimal for isolating competitive effects over a portion of ranks or for a guild of species within a community. This distinction is important because resource partitioning does not occur to the same extent for all species in a community. For example, we used a comparison of abundances between intermediate and rare species to show how warblers rose to higher relative abundances on forests with more productive soils.

Results from this study are qualified by some limitations related to study design. First, these data reflected avian community structure over 2-year timeframes, and the survey years were different by forest. However, only one of the survey years was preceded by a strong El Niño or La Niña event that might have confounded results (Silllett et al. 2000). Second, we used raw survey data to which we were unable to apply hierarchical modeling to address heterogeneity in survey detection probability (Royle 2004) beyond taking the maximum count during a single day. It is possible that systematic differences in detectability (e.g., different surveyors, years, habitat conditions) confounded the conclusion that apparent differences in RADs were due to differences in forest productivity. This problem was compounded by the small sample size ( $n=4$ ) of the comparison among forests. Despite these study limitations, the RAD bootstrapping has diverse applications for evaluating and comparing communities.

Scale is another issue to be considered. The point counts used for estimating density covered a small area (0.28 ha), leading to generally small survey counts. In particular, 89% of non-zero counts per species per survey period were = 1, and 99% were  $\leq 2$ . It is unclear whether the rank differences reported here would have been the same for larger survey units. Nevertheless, the methodological advantages of bootstrapping, as discussed above for comparing a portion of ranks, are not especially related to scale. Furthermore, considering the dominance of ones and zeros in the data we used, the RAD bootstrap approach may also be appropriate for application to rank-occupancy distributions derived from presence-absence data.

In conclusion, methods that look at differences in abundances for individual ranks within RADs have advantages over diversity indices. By evaluating finer distinctions between dominant, intermediate, and rare species, there is greater potential for drawing ecological inferences, particularly with respect to resource partitioning. This approach may be especially relevant to biodiversity monitoring and conservation planning. Declines of individual species may be better understood in context of their relationship to other species, or niches, within the community. Segments of RADs could be monitored for changes in composition over time (Collins et al. 2008).

Multi-species abundance models (MSAMs; Yamaura et al. 2012, Chandler et al. 2013, Iknayan et al. 2014) that address heterogeneity in detection probability may offer a more sophisticated means of evaluating niche partitioning using RADs than provided by our bootstrapping method. We would have taken this approach if our surveys had been repeated on different days for estimating detectability of point counts. The hierarchical structure of MSAMs could be used to keep track of abundances of dominant, intermediate, and rare species separately as derived quantities in the model. The Bayesian algorithm for solving this model generates posterior distributions for all parameters (Link et al. 2002) which eliminates the need for additional bootstrapping to describe the uncertainty of abundance estimates for each rank. However, all of the other elements of our approach for quantifying and contrasting the intermediate ranks of RADs could be readily incorporated into a MSAM.

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## APPENDIX I. DENSITY ESTIMATES FOR AVIAN SPECIES SURVEYED AT FOUR RESEARCH FORESTS IN CALIFORNIA

Common Name	Scientific Name	Density (birds/ha)			
		Latour	Blodgett	Sagehen	Mt. Home
Acorn Woodpecker	<i>Melanerpes formicivorus</i>	0.000	0.217	0.000	0.000
American Dipper	<i>Cinclus mexicanus</i>	0.000	0.000	0.044	0.000
American Kestrel	<i>Falco sparverius</i>	0.000	0.131	0.089	0.000
American Robin	<i>Turdus migratorius</i>	0.221	3.843	2.032	2.013
Anna's Hummingbird	<i>Calypte anna</i>	0.044	0.176	0.000	0.268
Ash-throated Flycatcher	<i>Myiarchus cinerascens</i>	0.000	0.000	0.045	0.091
Band-tailed Pigeon	<i>Patagioenas fasciata</i>	0.533	0.218	0.355	0.756
Bewick's Wren	<i>Thryomanes bewickii</i>	0.000	0.351	0.000	0.045
Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>	0.044	2.836	0.000	2.688
Black-backed Woodpecker	<i>Picoides arcticus</i>	0.000	0.000	0.089	0.000
Brown-headed Cowbird	<i>Molothrus ater</i>	0.220	0.698	1.367	0.179
Brewer's Blackbird	<i>Euphagus cyanocephalus</i>	0.000	0.000	0.000	1.664
Brewer's Sparrow	<i>Spizella breweri</i>	0.000	0.000	0.353	0.000
Brown Creeper	<i>Certhia americana</i>	1.902	2.011	1.809	2.195
Blk.-throated Gray Warbler	<i>Setophaga nigrescens</i>	0.000	0.133	0.000	0.044
Bullock's Oriole	<i>Icterus bullockii</i>	0.000	0.000	0.000	0.447
Bushtit	<i>Psaltriparus minimus</i>	0.000	0.390	0.000	0.178
Calliope Hummingbird	<i>Selasphorus calliope</i>	0.000	0.000	2.123	0.000
California Towhee	<i>Melospiza crissalis</i>	0.000	0.000	0.000	0.045
Cassin's Finch	<i>Haemorrhous cassinii</i>	0.356	0.131	1.849	1.566
Cassin's Vireo	<i>Vireo cassinii</i>	0.223	2.579	0.000	0.000
Chestnut-backed Chickadee	<i>Poecile rufescens</i>	0.000	0.660	0.000	0.000
Chipping Sparrow	<i>Spizella passerine</i>	0.000	0.831	0.665	0.314
Clark's Nutcracker	<i>Nucifraga columbiana</i>	0.089	0.000	0.528	0.000
Common Nighthawk	<i>Chordeiles minor</i>	0.132	0.000	0.000	0.045
Common Raven	<i>Corvus corax</i>	0.440	0.000	0.000	0.849
Cooper's Hawk	<i>Accipiter cooperii</i>	0.132	0.043	0.044	0.000
Dark-eyed Junco	<i>Junco hyemalis</i>	4.022	5.844	4.068	6.309
Downy Woodpecker	<i>Picoides pubescens</i>	0.132	0.131	0.000	0.089
Dusky Flycatcher	<i>Empidonax oberholseri</i>	1.594	0.918	0.881	0.764
Evening Grosbeak	<i>Coccothraustes vespertinus</i>	0.134	0.350	0.616	0.357
Forster's Tern	<i>Sterna forsteri</i>	0.044	0.000	0.000	0.000
Fox Sparrow	<i>Passerella iliaca</i>	0.930	1.137	1.637	2.548
Green-tailed Towhee	<i>Ardea herodias</i>	0.045	0.000	0.308	0.224
Golden-crowned Kinglet	<i>Pipilo chlorurus</i>	2.610	2.489	2.204	3.673
Great Blue Heron	<i>Regulus satrapa</i>	0.000	0.088	0.000	0.000
Hairy Woodpecker	<i>Picoides villosus</i>	0.531	0.955	0.967	0.629
Hammond's Flycatcher	<i>Empidonax hammondi</i>	1.108	0.612	0.926	0.312
Hermit Thrush	<i>Cathartes guttatus</i>	0.929	0.611	0.576	0.267
Hermit Warbler	<i>Setophaga occidentalis</i>	1.413	1.832	0.044	1.211
House Wren	<i>Troglodytes aedon</i>	0.000	0.173	0.000	0.807
Hutton's Vireo	<i>Vireo huttoni</i>	0.044	0.130	0.000	0.045
Lazuli Bunting	<i>Passerina amoena</i>	0.000	0.000	0.132	0.136
Lincoln's Sparrow	<i>Melospiza lincolni</i>	0.000	0.000	0.044	0.134
MacGillivray's Warbler	<i>Geothlypis tolmiei</i>	0.265	2.317	0.132	1.880
Mountain Bluebird	<i>Sialia currucoides</i>	0.133	0.000	0.351	0.000
Mountain Chickadee	<i>Poecile gambeli</i>	3.798	2.405	4.194	2.683
Mourning Dove	<i>Oreortyx pictus</i>	0.000	0.087	0.000	0.090
Mountain Quail	<i>Zenaidura macroura</i>	0.089	0.088	0.043	0.045
Nashville Warbler	<i>Oreothlypis ruficapilla</i>	0.577	1.746	0.353	2.824
Northern Flicker	<i>Colaptes auratus</i>	0.531	1.528	0.309	0.762
Northern Goshawk	<i>Accipiter gentilis</i>	0.000	0.000	0.045	0.000
Olive-sided Flycatcher	<i>Contopus cooperi</i>	0.264	0.918	0.088	0.134
Orange-crowned Warbler	<i>Oreothlypis celata</i>	0.000	0.000	0.267	0.178
Pacific-slope Flycatcher	<i>Empidonax difficilis</i>	0.000	0.000	0.000	0.135
Pileated Woodpecker	<i>Dryocopus pileatus</i>	0.045	0.263	0.045	0.045
Pine Grosbeak	<i>Pinicola enucleator</i>	0.000	0.000	0.089	0.000
Pine Siskin	<i>Carduelis pinus</i>	0.000	0.087	2.913	0.000
Plumbeous Vireo	<i>Vireo plumbeus</i>	0.000	0.000	0.088	0.000
Purple Finch	<i>Haemorrhous purpureus</i>	0.796	0.000	0.000	0.449
Pygmy Nuthatch	<i>Sitta pygmaea</i>	0.000	0.000	0.176	0.000
Red-breasted Nuthatch	<i>Sitta canadensis</i>	2.298	1.967	1.062	2.416
Red-breasted Sapsucker	<i>Sphyrapicus ruber</i>	0.354	0.962	0.484	0.401
Red Crossbill	<i>Loxia curvirostra</i>	0.177	0.000	2.746	0.000

**APPENDIX I (CONTINUED). DENSITY ESTIMATES FOR AVIAN SPECIES  
SURVEYED AT FOUR RESEARCH FORESTS IN CALIFORNIA**

Red-tailed Hawk	<i>Buteo jamaicensis</i>	0.000	0.044	0.000	0.224
Rock Wren	<i>Salpinctes obsoletus</i>	0.000	0.000	0.089	0.000
Ruby-crowned Kinglet	<i>Regulus calendula</i>	0.000	0.000	0.267	0.000
Rufous Hummingbird	<i>Selasphorus rufus</i>	0.000	0.000	0.268	0.000
Sharp-shinned Hawk	<i>Accipiter striatus</i>	0.000	0.000	0.088	0.000
Song Sparrow	<i>Melospiza melodia</i>	0.000	0.000	0.266	0.000
Sooty Grouse	<i>Dendragapus fuliginosus</i>	0.000	0.088	0.000	0.088
Spotted Towhee	<i>Pipilo maculatus</i>	0.133	3.018	0.000	0.044
Steller's Jay	<i>Cyanocitta stelleri</i>	1.327	2.620	0.616	3.187
Swainson's Thrush	<i>Catharus ustulatus</i>	0.000	0.131	0.044	0.000
Townsend's Solitaire	<i>Myadestes townsendi</i>	0.443	0.131	0.485	0.090
Townsend's Warbler	<i>Setophaga townsendi</i>	0.000	0.044	0.000	0.045
Tree Swallow	<i>Tachycineta bicolor</i>	0.000	0.000	0.044	0.000
Warbling Vireo	<i>Vireo gilvus</i>	0.618	1.709	0.399	0.357
Western Bluebird	<i>Sialia mexicana</i>	0.000	0.000	0.000	0.091
Western Tanager	<i>Piranga ludoviciana</i>	1.946	2.531	1.457	3.272
Western Wood-Pewee	<i>Contopus sordidulus</i>	0.000	0.174	0.355	0.270
White-breasted Nuthatch	<i>Sitta carolinensis</i>	0.045	0.000	0.526	0.134
White-crowned Sparrow	<i>Zonotrichia leucophrys</i>	0.000	0.044	0.044	0.000
White-headed Woodpecker	<i>Picoides albolarvatus</i>	0.573	0.699	0.352	2.241
Willow Flycatcher	<i>Empidonax traillii</i>	0.000	0.219	0.000	0.045
Williamson's Sapsucker	<i>Sphyrapicus thyroideus</i>	0.000	0.000	0.400	0.000
Winter Wren	<i>Troglodytes hiemalis</i>	0.000	0.872	0.000	0.270
Wilson's Warbler	<i>Cardellina pusilla</i>	0.664	0.044	0.533	0.135
Wrentit	<i>Chamaea fasciata</i>	0.000	0.566	0.000	0.000
Yellow Warbler	<i>Setophaga petechia</i>	0.353	0.000	1.016	0.089
Yellow-rumped Warbler	<i>Setophaga coronata</i>	2.653	2.755	2.301	0.851