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Fitting species–accumulation functions and assessing regional land use impacts on avian diversity

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Abstract. As one samples species from a particular assemblage, the initial rapid rate with which new species are encountered declines with increasing effort. Nine candidate models to characterize species–accumulation functions were compared in a search for a model that consistently fit geographically extensive avian survey data from a wide range of environmental conditions. Landscape-specific species–accumulation curves generated under a bootstrap resampling plan were best described by a generalized Weibull cumulative distribution function. Traditional species–area models of cumulative species richness as a function of accumulated sample had notable functional bias. The Weibull model fitted species–accumulation data equally well among sixty-six forested landscapes in the eastern U.S. Landscapes with a greater proportion of agricultural and urban land uses accumulated species more slowly than landscapes which retained a greater proportion of natural habitats ($r = -0.64$, $P<0.001$). This finding supports predictions of ecosystem behavior under human land use. There was no evidence that intermediate levels of land use intensity maximized accumulation rates. The approach reviewed in this paper makes no assumptions about the form of the species–abundance distribution or how species are distributed in space, thereby offering some advantages over more conventional diversity indices for characterizing how species assemblages respond to anthropogenic disturbance. Investigation of how species accumulation varies over time in a given geographic area is needed to evaluate fully the potential application of this approach to regional land use planning.

Key words. Species–accumulation functions, species–area relations, birds, land use impacts, regional scale.

INTRODUCTION

A central question in ecology concerns the description and mathematical characterization of species–abundance frequencies (MacArthur, 1960; Brown, 1984; May, 1986). Typically, investigations of abundance distributions observe that species assemblages have many relatively rare species and few relatively common species (Hairston, 1959; Hughes, 1986). This qualitative description belies the extensive inquiry into theoretical derivation of mathematical forms and whether departure from derived forms is ecologically interpretable (Fisher, Corbet & Williams, 1943; Preston, 1948, 1962, 1980; Taylor, 1978; Kempton, 1979; Wilson, 1991). The interest in describing and explaining distributions of species abundance extends beyond a basic desire to understand factors influencing community structure. Increasing human populations and concomitant land use intensification have changed the amount, quality and distribution of habitats available to native biota. Consequently, conservationists, land managers and resource planners are concerned with anticipating how natural or human-induced disturbance to ecosystems affect the pattern of commonness and rarity of the inhabiting biota (Lubchenco *et al.*, 1991; Solbrig, 1991). Species diversity indices have commonly been used to summarize species occurrence and abundance data. However, combining information on occurrence and relative abundance for all species in an assemblage into a single number has been difficult to interpret (Peet, 1975). Consequently, the potential for diversity indices to provide useful resource conservation and management insights has been questioned (for review see Magurran, 1988). Discontent with such composite indices of community structure has led to the examination of a family of measures that are based more directly on empirical species–abundance relations (Hurlbert, 1971).

Regardless of the form of the species–abundance distribution as one samples from a large collection of species, new species are initially encountered rapidly. As samples accumulate, the rate of encounter declines and the total number of species in the collection is approached asymptotically (Pielou, 1966). This relation has been variously termed species–diversity curves (Sanders, 1968), species–richness curves (Hurlbert, 1971), collector's curve (Pielou, 1975; Clench, 1979), species–cover curves (Palmer, 1991), species–area curves (Miller & Wiegert, 1989; Solow & Smith, 1991), cumulative species–area curves (Quinn & Harrison, 1988; Beckon, 1993) and species–accumulation curves (Grassle & Maciolek, 1992). To distinguish species richness relations based on increasing area of similar habitat

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from those based on increasing area of potentially heterogeneous habitat, I have chosen to term the latter species–accumulation curves.

What is the value of fitting a model empirically to species number as a function of accumulated sample? If different environments tend to have '. . . characteristic rates of species increment' (Sanders, 1968:246), then quantifying accumulation patterns would facilitate comparison of species assemblages in different regions (Kilburn, 1966; Buys *et al.*, 1994) or in landscapes subject to different levels of natural or anthropogenic disturbance (see for example McNaughton & Wolf, 1970; Aspinall, 1988). Such comparisons, however, are contingent upon finding a model that consistently fits data from a wide range of environmental conditions (McGuinness, 1984).

The first objective of this study was to determine empirically if species–accumulation data from different geographic regions could be fit by a single functional form. Extensive avian surveys designed to monitor continental population trends were used to generate accumulation curves through statistical simulation procedures that randomly draw successively larger samples from the total regional sample. A second objective was to illustrate the potential utility of fitted species–accumulation functions by examining the ability of estimated parameters to distinguish avian community structure among landscapes with differing physiographies and land use histories. The asymptote of species–accumulation curves, an estimate of species number in a given collection, has been the focus in most studies (Miller & Wiegert, 1989; Palmer, 1990; Mingoti & Meeden, 1992; Bunge & Fitzpatrick, 1993; Soberón & Llorente, 1993). However, the rate of accumulation (i.e. the shape of the curve) is also of interest as it reflects the evenness of species abundances (James & Rathbun, 1981; Brewer & Williamson, 1994) and the spatial distribution of species (Peterson, 1975; Solow & Smith, 1991). Specifically, I tested the hypothesis that increased anthropogenic disturbance is associated with decreased rates of species accumulation. This hypothesis derives from the stress ecology literature (Barrett, Van Dyne & Odum, 1976; Odum, 1985; Rapport, Regier & Hutchinson, 1985), which predicts that conversion of natural habitats to human-dominated land uses results in an overall decline in diversity caused, in part, by increased dominance of opportunistic species associated with simpler, disturbed habitats (Urban, O'Neill & Shugart, 1987; Cotgreave & Harvey, 1994).

METHODS

My approach involved: (1) delineating landscapes and calculating an index of land use intensity for each landscape, (2) generating avian species–accumulation curves for each landscape and selecting a 'best' model fitting these data, and (3) correlating the estimated rates of species accumulation with the land use intensity index.

Landscapes and land use intensity

Landscape boundaries are defined by criteria that delineate ecologically distinct regions based on differences in climate, geomorphology and natural and anthropogenic disturbance regimes (Forman & Godron, 1986; Zonneveld, 1989). The U.S. Soil Conservation Service (1981) stratified the United States into Major Land Resource Areas (MLRAs) that define, in general, 10^4 km^2 regions of relatively homogeneous climate, physiography, soils and land use. MLRAs constituted the observation units (i.e. landscapes) for this study. The study area was limited to those MLRAs in the eastern United States that could potentially support forest vegetation as defined by Küchler (1964). A total of sixty-nine landscapes, ranging from 3000 to 285,000 km^2, comprised the region (Fig. 1, see also Appendix A).

There are numerous measures of landscape structure that reflect the composition and configuration of land uses (O'Neill *et al.*, 1988; Turner & Gardner, 1991), many of which may affect patterns of species diversity. For the purposes of initially examining the usefulness of quantifying species accumulation, I chose as a broad measure of land use intensity the proportion of cropland and urban land within each landscape. The National Resources Inventory (NRI) (U.S. Soil Conservation Service & Iowa State University Statistical Laboratory, 1987) was used to estimate the proportion of crop and urban land use. The NRI is a periodic inventory of soil and water resources, including land cover, land use and management activities, that occur on non-federal lands. In 1982, a stratified, two-stage, area sampling scheme involving approximately 365,000 primary sample units ($\approx 3\%$ sample of the total land and water area in the conterminous U.S.) were inventoried to provide areal estimates of major land uses for each MLRA.

Species–accumulation curves and candidate models

The North American Breeding Bird Survey (BBS, see Peterjohn & Sauer [1993] for details) was used to provide data on the occurrence of avian species based on randomly located roadside routes. Each route was comprised of fifty stops spaced at 0.8 km intervals and an attempt was made to survey each route annually. At each stop all birds seen or heard during a 3-min observation period were recorded. The location of the route centre was used to map and assign BBS routes to MLRA-defined landscapes.

A 5-year period of BBS data was chosen centred on the year of the NRI (i.e. 1982) to generate landscape-specific accumulation curves. A 5-year period was chosen to increase the detectability of rare species. Each route–year combination was treated as a separate observation. Routes identified by BBS administrators as incomplete, run by unacceptable observers, completed during inclement weather, or run late in the breeding season were eliminated. Species with marine affinities (as defined in American Ornithologists' Union [1983], and DeGraaf, Tilghman & Anderson [1985]) were excluded to eliminate incidental sightings. Birds that were not identified to species (e.g. Chickadee spp., unid. Accipiter) were also eliminated.

Because the shape of species–accumulation curves depends on the order in which samples are accumulated, a bootstrap resampling plan was used (Efron, 1982; Smith & van Belle, 1984; Verner & Ritter, 1986) to estimate the expected number of species for successively larger samples

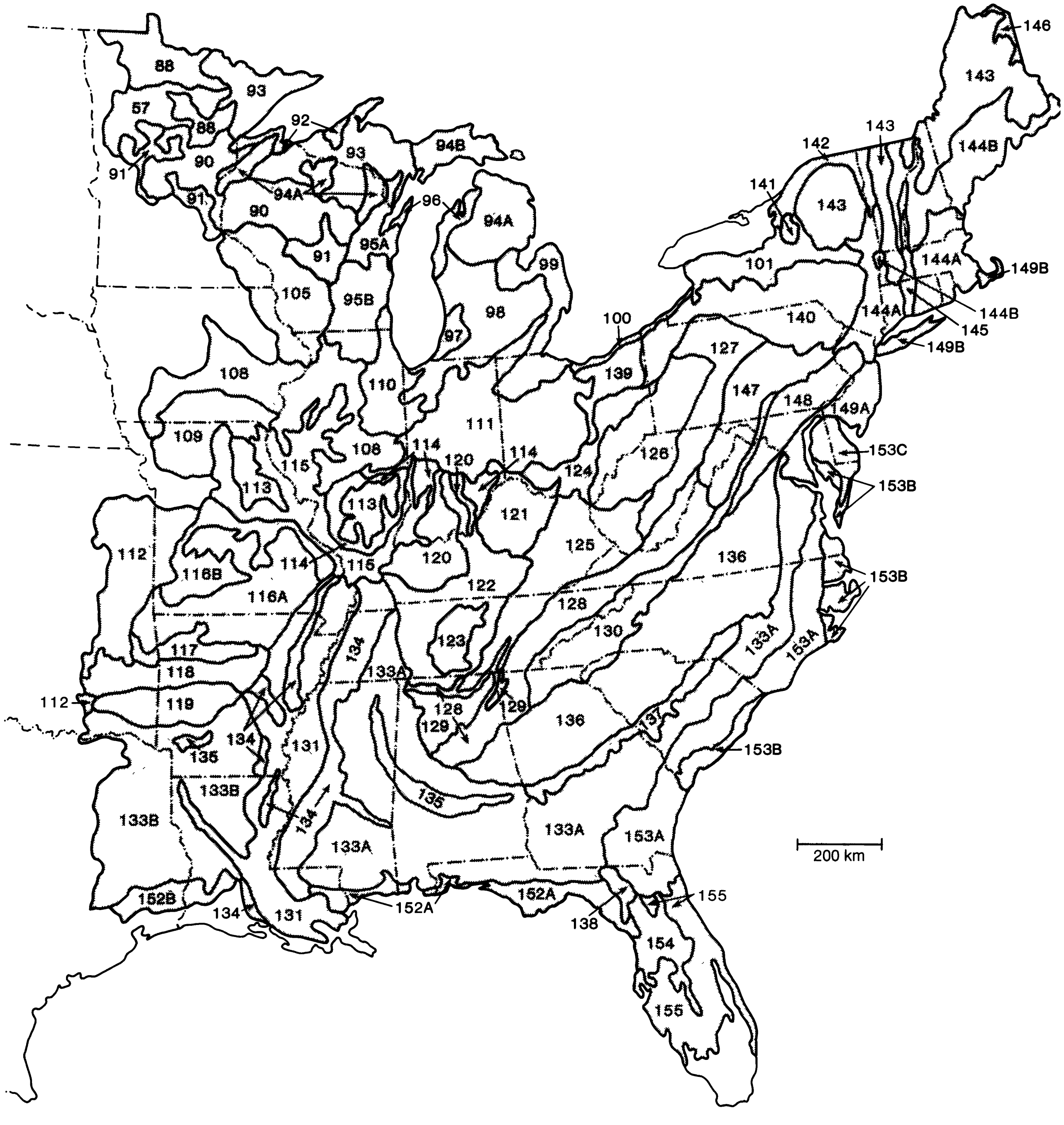

FIG. 1. MLRA-defined landscapes that could support eastern forest vegetation (numeric codes defined in Appendix A).

of routes. The approach follows that of Pielou (1966) for collections in which organisms are patchily distributed and sampled in a spatially random manner. Note that species are accumulated by routes, not individuals, and that presence of a species on a route, not its abundance, is all that is required to generate accumulation curves under this procedure. Curves were generated by tallying bird species occurrence in bootstrap subsamples of a size m for each n-tuple, where n varied from 1 to the total number of route-years sampled within each landscape. The bootstrap estimate of the number of species $B_n(S)$ observed in a sample of size n is given by:

$$B_n(S) = (1/m) \sum_{i=1}^{m} S_i,$$

where S_i is the observed richness in the i^{th} bootstrap subsample. A bootstrap subsample size of $m = 1000$ was chosen for analysis by empirically noting that m where $B_1(S)$ stabilized. All uniform random deviates were generated using an algorithm developed by L'Ecuyer (1988).

Candidate species–accumulation models (Table 1) were

TABLE 1. Candidate models for fitting species–accumulation data. Dependent variable is accumulated species, x is accumulated samples, and a, b, c and d are fitted coefficients.

Model	Parameters (n)	Description/source
1. ax^{b}	2	Power model proposed from species–area literature (Arrhenius, 1921; Preston, 1962)
2. $a+b\log(x)$	2	Exponential model proposed from species–area literature (Gleason, 1922; Fisher *et al.*, 1943)
3. $a(x/b+x)$	2	Monod function proposed from plant species–area literature (Monod, 1950) and used to fit butterfly collection curves (Clench, 1979)
4. $a(1-e^{-bx})$	2	Negative exponential model proposed for species–accumulation of rare plants (Miller & Wiegert, 1989)
5. $a-bc^{x}$	3	Asymptotic regression model used in fertilizer tests and to fishery growth (Ratkowski, 1983)
6. $(a+bx)/(1+cx)$	3	Rational function which has been used to approximate other mathematical functions when a theoretical basis for selecting an appropriate model is lacking (Ratkowski, 1990)
7. $a(1-e^{-bx})^{c}$	3	Modification of the negative exponential model (model 4), also appears as the Chapman–Richards model which has been used in forestry growth and yield research (Ratkowski, 1990)
8. $a(1-[1+(x/c)^{d}]^{-b})$	4	Cumulative distribution function of a beta-P distribution that has been used to to describe accumulated streamflow and precipitation amount data (Mielke & Johnson, 1974)
9. $a[1-e^{-(b(x-c))^{d}}]$	4	Cumulative distribution function of a Weibull distribution that has been used in engineering and in modelling cumulative germination (Brown & Mayer, 1988).

proposed from two sources. The first source was the species–area literature which has traditionally fit these data with power or exponential models. Because many investigators have noted that species accumulation becomes asymptotic for large areas (Kilburn, 1966; Connor & McCoy, 1979; Martin, 1981; Burgman, Akcakaya & Loew, 1988; Glenn & Nudds, 1989), the second source involved a broader search of the literature for models that increased monotonically to an asymptote.

Standard goodness-of-fit criteria including mean squared error (MSE), R^2, and a graphical examination of residuals were used to evaluate model performance (Draper & Smith, 1981). Because R^2 is expected to increase with the number of parameters, the adjusted coefficient of multiple determination R^2_a was used to account for a varying number of parameters in comparing performance among candidate models. In all but one case, non-linear regression models were fit using the Marquardt procedure (SAS Institute, Inc., 1985; Proc NLIN). A logarithmic transformation of the exponential model was fit using simple linear regression.

Association between accumulation rate and land use intensity

Because diversity covaries with sampling size (Peet, 1975) and species counts (Sheldon, 1969), the pattern of association between land use intensity and rate of species accumulation was examined after the sampling effort was fixed at 50 route-years and the effect of species counts was removed statistically. The routes comprising the sample pool (50 route-years) from which bootstrapped accumulation curves were generated were selected randomly. Partial correlation analysis (Draper & Smith, 1981:265) was used to statistically remove the influence of species richness on the rate of species accumulation. Species richness was estimated from the 'best-fitting' model to the accumulation curve generated under the random sample of 50 route-years.

The hypothesis that land use intensification is negatively associated with rates of species accumulation was tested in two ways. First, the Pearson product moment correlation between rate of accumulation and land use intensity index was estimated and tested for a simple linear negative relation ($P<0.05$). Because there is evidence that regional diversity may peak at intermediate levels of land use (Abugov 1982; Miller, 1982; Moore, 1983; Collins & Barber, 1985), a pattern formalized as the intermediate disturbance hypothesis (Connell, 1978), a second analysis tested if the simple linear model was improved by a second-order polynomial model specification.

RESULTS

Generating avian accumulation curves

Bootstrap estimated accumulation curves were constructed for sixty-six of the sixty-nine landscapes. Three relatively small (<3500 km^2) landscapes lacked BBS routes of adequate quality based on criteria previously specified. Avian species–accumulation curves varied both in their shape and in the relative completeness of the breeding avian community that was sampled (Fig. 2). There were many cases in which the cumulative number of species observed within a landscape did not approach an asymptote (e.g. MLRA 88: Northern Minnesota Glacial Lake Basins).

Apart from the ecological implications of an incompletely described avifauna, there were also implications for assessing the relative merits of candidate species–accumulation models. Landscapes with accumulation curves that terminated while still rising relatively rapidly may be fit equally well by non-asymptotic and asymptotic models (see

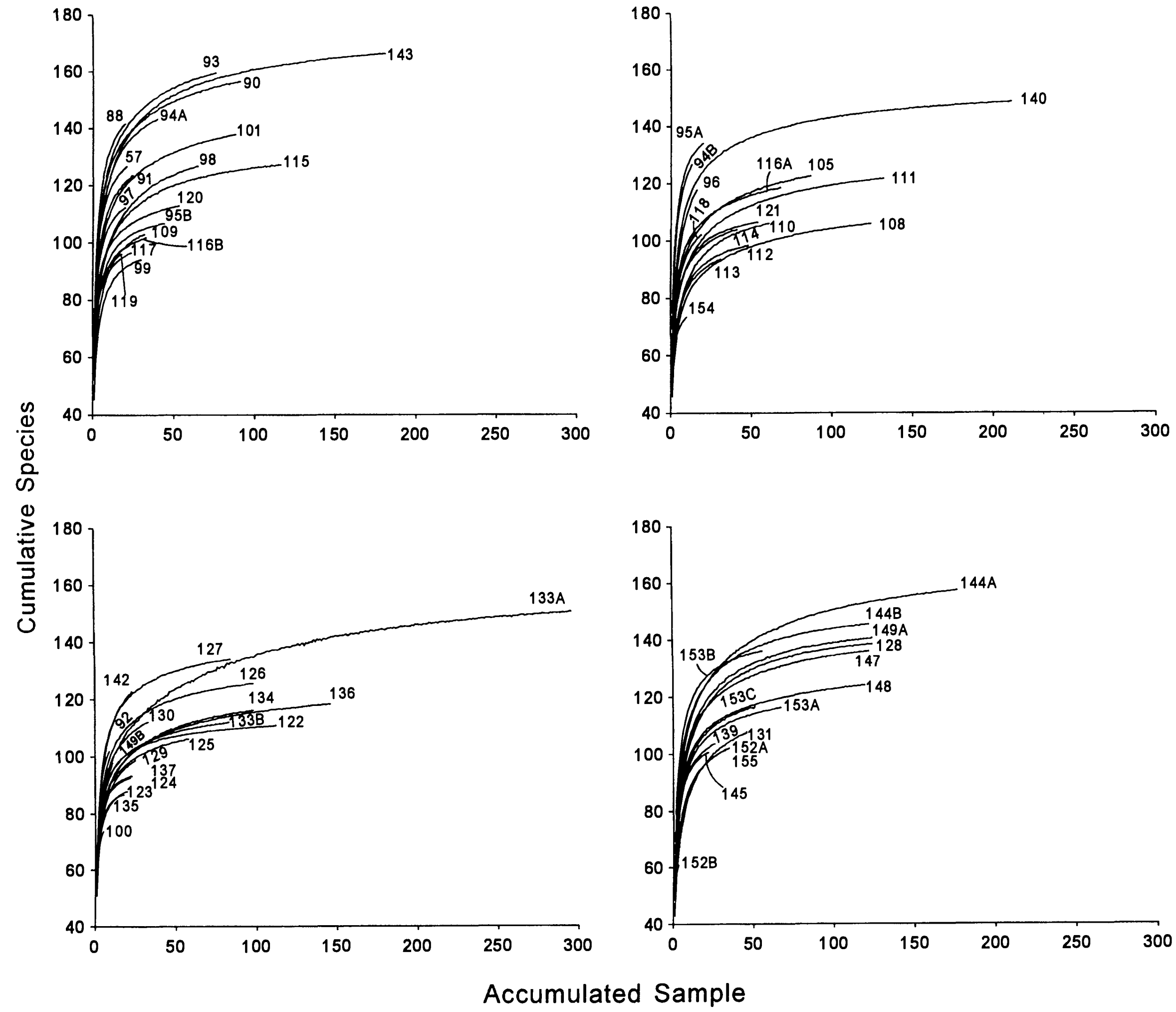

FIG. 2. Avian species–accumulation curves for 66 MLRA-defined landscapes in the eastern United States (numeric codes defined in Appendix A).

Soberón & Llorente, 1993). Therefore, a single landscape (MLRA 111: Indiana and Ohio Till Plain) whose accumulation curve implied a relatively complete representation of the avifauna was arbitrarily chosen to initially evaluate candidate models.

Choice of species–accumulation model

Candidate models differed in goodness-of-fit (Table 2). Traditional species–area models (power and exponential) appeared to fit the data well ($R_a^2>0.96$), with the exponential model providing a slightly better fit than the power model—a pattern expected with large-scale area relations (Gleason, 1922; Martin, 1981). The negative exponential model exhibited the least explanatory power, accounting for only 63% of the variance in the cumulative number of observed species.

With the exception of the negative exponential, all models accounted for >90% of the variance in accumulated species richness. However, because there are cases in which the 'wrong' model can give high coefficients of determination (Ekbohm, 1990), residuals were examined to explore lack-of-fit patterns among candidate models. Graphical display of the residuals as a function of accumulated observations revealed marked differences among competing models (Fig. 3). As expected from the R_a^2 and MSE statistics, the negative exponential exhibited the greatest lack-of-fit (Fig. 3d). For all models that exhibited obvious systematic pattern in their residuals (Fig. 3a–g), the lack-of-fit was most pronounced along the lower portions of the accumulation curve, indicating difficulty fitting the initial rapid rise in cumulative species observed on BBS routes.

The beta-P and Weibull models were exceptions to the general patterns noted among other candidate models. Although the residuals for the beta-P model still showed a systematic pattern (Fig. 3h), the magnitude of the residuals was small (<1.0) over the entire range of accumulated samples. The Weibull model lacked any apparent functional bias, but a mild heteroscedastic scatter in the residual plot was indicated (Fig. 3i). This condition violates the homogeneity of variance assumption of least-squares regression; however, weighted regression can be used to

TABLE 2. Goodness-of-fit characteristics among candidate models.

Model		MLRA 111 (Indiana and Ohio Till Plain)		Among all MLRA-defined landscapes	
		Mean square error	R^2_a	Mean rank R^2_a	Range of rank R^2_a
1. Power	ax^b	5.44	0.962	7.4	5–8
2. Exponential	$a+blog(x)$	1.94	0.986	5.5	3–7
3. Monod function	$a(x/b+x)$	13.80	0.903	5.8	4–7
4. Negative exponential	$a(1-e^{-bx})$	53.45	0.624	9	—
5. Asymptotic regression	$a\text{-}bc^x$	5.65	0.960	7.1	5–8
6. Rational function	$(a+bx)/(1+cx)$	1.49	0.989	3.4	1–5
7. Chapman–Richards	$a(1-e^{-bx})^c$	0.70	0.995	3.6	2–8
8. beta-P	$a(1-[1+(x/c)^d]^{-b})$	0.04	0.999	1.8	1–7
9. Weibull	$a[1-e^{-(b(x-c))^d}]$	0.01	0.999	1.3	1–2

provide minimum variance estimates of the coefficients (Draper & Smith, 1981). Weighting factors that are proportional to the inverse of the variance in accumulated species for each sample size could be estimated from the bootstrapping procedure used to generate the accumulation curves. Consequently, a heteroscedastic condition was of little consequence in selecting the 'best' fitting model.

This initial comparison among candidate models indicated that the Weibull formulation offered the best description of species accumulation in this particular landscape. These results were interpreted to offer only preliminary evidence in support of an appropriate model of species accumulation. There was no guarantee that the Weibull model would consistently characterize species accumulation well in different landscapes.

Fitting candidate models to avian accumulation data across all landscapes provided additional evidence that the Weibull formulation offered a sufficiently general description of species accumulation for use in a comparative study. The average rank R^2_a indicated that the negative exponential always performed poorly relative to the other candidate models (Table 2). Traditional species–area models had high ranks as well with the exponential model fitting accumulation data better than the power model. The Weibull and beta-P consistently performed better (i.e. lowest average rank) than other specifications. However, the beta-P model failed to converge in twenty-four of the sixty-six cases and was also characterized by a high degree of parameter correlation when compared with the Weibull model—attributes indicative of model overspecification (Ratkowski, 1990). Despite failure to achieve convergence in all landscapes the beta-P model explained much of the variation in accumulated species, with a median MSE of 0.03 (range 0.004–0.149). The Weibull formulation converged in all but one landscape and typically explained a greater proportion of the variance in species number, with a median MSE of 0.02 (range 0.002–0.095). Comparing the two models in only those cases where convergence was achieved showed that the Weibull had a lower MSE in twenty-two of the forty-one cases, although the MSE between models were not shown to be different (Wilcoxon signed rank test; Conover [1971]:206; $T=-10.5$; $P=0.89$).

Of the candidate models considered, the Weibull was chosen as the most suitable formulation for quantifying and comparing species–accumulation curves. Traditional specifications (power, exponential, and negative exponential models) were inadequate because of notable functional bias. Although both the beta-P and Weibull models had similar MSEs, the beta-P showed high correlation among parameters and failed to converge in more than a third of the MLRA-defined landscapes.

Interpretation of model parameters is an important issue for comparative studies (Connor & McCoy, 1979; Martin, 1981; McGuinness, 1984; Brown & Mayer, 1988). For the Weibull model, the total number of species in the avian assemblage is estimated by a, the asymptote; the rate of species accumulation is fixed by b; c is a scaling factor that determines the x-axis intercept; whereas d is a shape parameter. Accumulation rate (b) is affected by both the relative abundance and the spatial distribution of species. As the proportion of relatively rare species increases, the rate of accumulation is expected to decline (Fig. 4, compare log normal and log series). Similarly, as the clumping of individuals among sample locations increases, accumulation rate declines (Fig. 4, compare log normal and clumped distribution).

As expected, species–accumulation rate (b) covaried with sampling effort ($r=-0.57$; $P<0.001$) and species richness as estimated by a ($r=-0.69$; $P<0.001$) among MLRAs. To control for the confounding effects of these relations, the sampling effort was fixed at 50 route-years and partial correlation analysis was used to statistically remove the influence of species richness on accumulation rate. Correlation analysis on accumulation rate and other Weibull parameters did not indicate that higher order partials were warranted ($P>0.1$), once variation is sample size and species richness has been factored out statistically. The residuals from first-order partial correlation analysis were then used to examine the association between species–accumulation rate and land use intensity.

Patterns of association with land use intensity

Fixing the sampling effort resulted in a total of thirty-one landscape units with a sufficient number of routes (i.e. $\geqslant 50$ route-years) to explore relations between rate of species

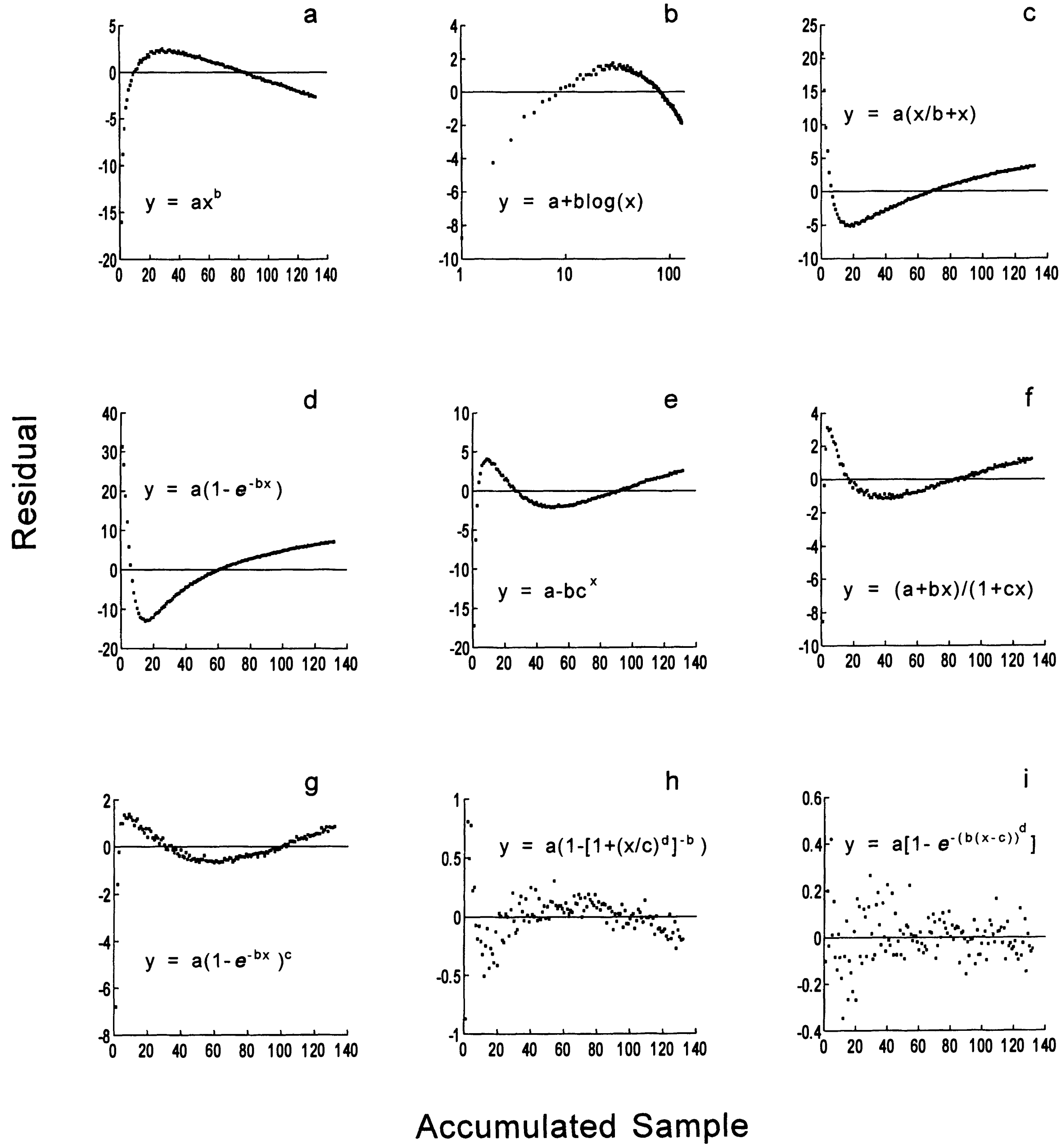

FIG. 3. Candidate species–accumulation model residuals plotted against accumulated samples for MLRA 111 (Indiana and Ohio Till Plain). Note that the range of values on the ordinate varies among plots. (a) power model, (b) exponential model, (c) Monod function, (d) negative exponential, (e) asymptotic regression, (f) rational function, (g) Chapman–Richards model, (h) beta-P, (i) generalized Weibull.

accumulation and land use intensity. The only portion of the eastern study region that was not represented in this subset of landscapes was peninsular Florida. Although similar sample sizes are recommended for among-site comparisons of diversity (Magurran, 1988), there is concern that rate of accumulation may vary with total landscape area and therefore potentially confound relations with land use intensity. The correlation between accumulation rate (*b*) and total landscape area did not indicate an area effect ($r=0.02$; $P=0.93$). Because routes sampled during a 5-year window were treated as separate observations, there is also a potential confounding effect if the number of years/route varied substantially among landscapes. The average number of years/route in the random sample of 50 route-years was 2.3 (range 1.3–3.8) and this did not covary with accumulation rate among landscapes ($r=0.11$; $P=0.56$).

The rate of species accumulation was lower in landscapes with a higher proportion of intensive land use ($r=-0.64$; $P<0.001$) as predicted by the stress ecology literature (Fig. 5). Those landscape units with the lowest rates of species accumulation (lower right in Fig. 5) are found primarily in the eastern portion of the U.S. corn belt including the

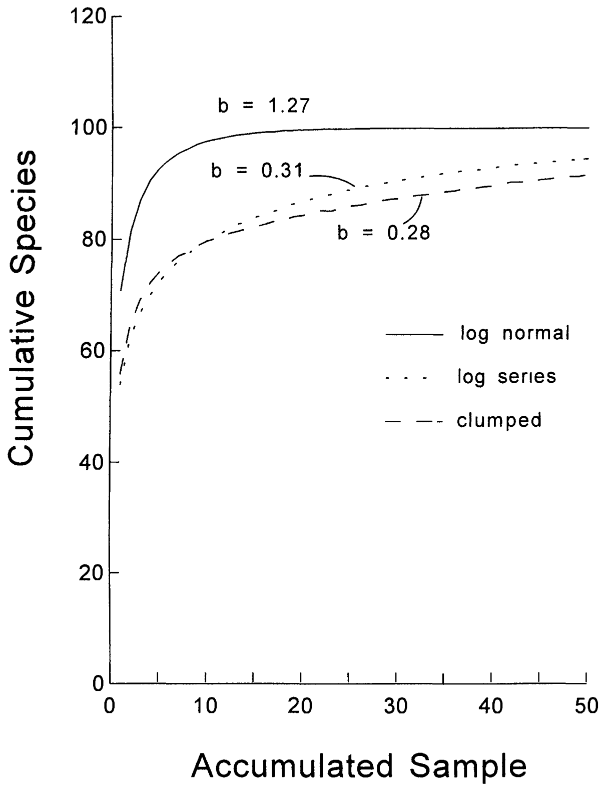

FIG. 4. Species–accumulation curves for a hypothetical species assemblage comprised of 100 species, 50,000 individuals, distributed among fifty sample locations. In both the log normal (ten species with <ten individuals) and log series (thirty-two species with <ten individuals), individuals were distributed randomly among sample locations. In the case of a spatially clumped occurrence of individuals, species abundances were distributed log normally, and all individuals of twenty-five species (selected randomly) were assigned to occur on a single route (selected randomly). Log normal and log series species–abundance distributions were generated as described by Magurran (1988: 132–138). The number of individuals in the most abundant class was altered to guarantee 50,000 individuals.

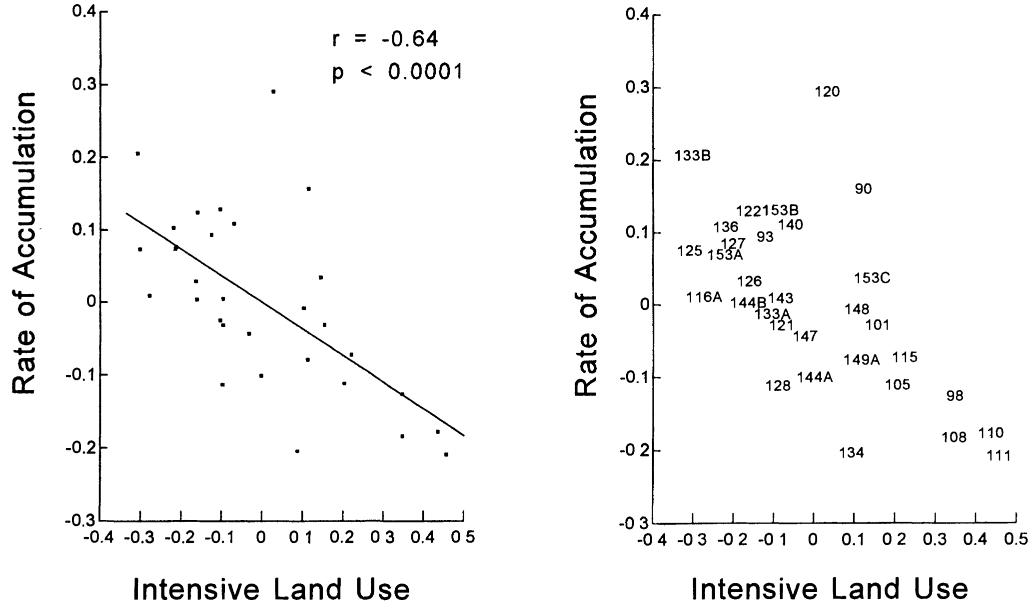

FIG. 5. Relation between proportion of the landscape in intensive land use and the rate of accumulation. Note that axes reflect the residuals from first-order partial correlation analysis (controlling for variation in species count).

Indiana and Ohio Till Plain, the Northern Illinois and Indiana Heavy Till Plain, and the Illinois and Iowa Deep Loess and Drift. Although these landscapes are important centres for agriculture, they are also heavily urbanized. Higher rates of species accumulation were not as clustered geographically and included the Western Coastal Plain (133B), the Southern Piedmont (136) and the Highland Rim and Pennyroyal (122).

One landscape that accumulated species at a rate much greater than expected given the proportion of land under crop and urban development was MLRA 120 (Kentucky and Indiana Sandstone and Shale Hills and Valleys). The extreme value of species–accumulation rate for MLRA 120 may be attributable to chance associated with the random selection of routes used in the generation of accumulation curves. However, a more probable explanation is that this landscape includes federally managed National Forest land. The greater than expected accumulation rate cannot be attributed entirely to the presence of federal land. The contrast between land use on private and federal land may also be a factor. Although there are eight MLRA-defined landscapes with an equal or greater proportion of federal land than MLRA 120, the proportion of intensive land uses was >2.5 times less in these landscapes.

There was no evidence of a convex relation between accumulation rate and land use intensity as suggested by the intermediate disturbance hypothesis. Specifying a second-order polynomial did not significantly improve on a simple linear regression ($t=0.56$; $P=0.58$). Failure to detect a quadratic relation does not appear to be related to the relatively high anthropogenic disturbance characteristic of the eastern U.S. The proportion of intensive land uses within landscapes ranged from 0.06 to 0.88.

DISCUSSION

There is a growing recognition that biogeographic-scale studies are needed to gain a more comprehensive assessment of faunal response to anthropogenic disturbance. Because it is often impractical for individual investigators to collect the necessary biogeographic data (Kodric-Brown & Brown, 1993), one must rely on the independent efforts of others to infer relations. As noted by Martin (1981), attempts to identify generalizations from the works of others are hindered by the heterogeneous nature of independent studies. It is difficult to determine whether synthesized results have an ecological interpretation or are an artefact of combining studies with varying objectives, sampling approaches, taxa and analysis methodologies.

Although a comprehensive inventory to support macroecology is indeed lacking (Brown & Roughgarden, 1990), large-scale monitoring efforts do exist, primarily in government agencies with natural resource stewardship responsibility. In this study, consistent methodologies were applied in surveying both avian assemblages and land use and a single model specification for species accumulation was found to be robust to fitting data from many different landscapes. Consequently, variation in avian species–accumulation patterns could not be attributed to properties of varying methodology.

Species–accumulation patterns generated under a bootstrap resampling plan were best described by a generalized Weibull cumulative distribution function. Models that have been used in the past to describe the monotonic increase in species number with increasing area sampling had notable functional biases despite accounting for a substantial portion of the variation in cumulative species richness as a function of accumulated sample. The Weibull model did not exhibit such functional bias and fit species–accumulation data equally well among landscapes comprising the study region, and thereby afforded a consistent methodology for exploring correlates between species–accumulation rates and landscape structure attributes.

The relation between land use intensity and species–accumulation rate was consistent with predictions of ecosystem behaviour under anthropogenic land use stress. Rapport *et al.* (1985) noted that physical restructuring associated with land use conversion from natural habitats (e.g. forest and wetland) to human-dominated land uses (e.g. agriculture and urban land) is associated with a degradation of species diversity. The reduced rate of species accumulation under land use intensification is indicative of a disparate species–abundance distribution, with the avian assemblage being comprised of a greater proportion of rare and distributionally restricted species.

An advantage of the approach used here is that assumptions concerning the form of the species–abundance distribution or how individuals interact (i.e. how they are distributed in space) are not required. More conventional diversity indices (e.g. H', H'/H_{max}) assume that the probability of encountering individuals depends only on their relative abundances (Smith & van Belle, 1984; Magurran, 1988), which will hold if individuals are randomly distributed in space. Rarefaction (Sanders, 1968; Simberloff, 1972), which also has been used to generate curves of species accumulation (see Siegel & German, 1982) except that species accrual is interpolated rather than fit empirically, also assumes a random distribution of individuals in space (Tipper, 1979). At regional scales, spatial heterogeneity of species occurrences is expected (Sousa, 1984:353), and Grassle & Maciolek (1992:326) have demonstrated the inappropriateness of conventional diversity indices at this scale. If one is interested in comparing community structure in homogeneous habitat, where a random distribution of individuals could be expected, then conventional indices may suffice.

An additional advantage to the approach proposed here is that only presence/absence data is required to empirically generate species–accumulation curves. Therefore, the difficulties and expense of estimating species abundances can be avoided. This is particularly important in the analysis of BBS data because many of the problems surrounding its use have focused on estimating avian abundance trends (for review see Sauer & Droege, 1990).

It could be argued that the approach used here is limited in not being able to attribute changes in species–accumulation rates to change in spatial clumping or change in abundance (see Fig. 4). This is a valid criticism and one that has important conservation implications. A relatively well dispersed species that becomes 'rarer' may do so by a uniform reduction in abundance or by expressing a more clumped occurrence pattern—two scenarios that have varying susceptibilities to local extinction. However, there is widespread evidence that distribution and abundance are correlated—species widely distributed tend to be more abundant locally than species with limited distributions (Hanski, 1982; Bock & Ricklefs, 1983; Brown, 1984: Gaston & Lawton, 1988; Lawton, 1994). If, as species become rarer, there are both a reduction in abundance and an increase in aggregation, then assessing their separate effects may not be possible or necessary.

Another potential criticism of the approach taken in this study is that selection of a species–accumulation model was based on purely empirical criteria and therefore lacks a theoretical basis. Although species–abundance distributions and species–accumulation curves are expected to be associated, it has become untenable to argue that the former determines the latter except under a limited set of conditions. A mathematical link between the two relations is prevented by the fact that species accumulation is not solely a function of species abundances, but is also influenced by the way individuals are spatially distributed. It is the non-random pattern of individuals in space that confounds a theoretical derivation of species accumulation as constructed in practice (Goodall, 1952; Wright, 1988). Consequently, one is left with invoking empirically based criteria in selecting among alternative model specifications (see Connor & McCoy, 1979).

The results presented here provide initial support for the use of accumulation curves to characterize species assemblages and indicate how accumulation rates may covary with land use intensity. Avian communities, however, are likely to be affected by attributes of landscape structure that are more complex than the simple proportion of intensive human land use activity. In addition, land use intensity is a function of inherent landscape heterogeneity. Consequently, cross-sectional data such as that used here makes it difficult to differentiate effects attributable to land use disturbance from the inherent physiographic character of each landscape. Addressing these issues will require land inventories that permit an analysis of the spatial arrangement of the land type mosaic and extending analyses in the temporal dimension. Holding physiography constant and letting land use intensity vary by studying landscapes and accumulation patterns over time is required to fully evaluate the utility of this approach to regional land use planning.

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APPENDIX A. Major land resource areas for the eastern United States that can support forest vegetation (U.S. Soil Conservation Service 1981).

MLRA Code	MLRA Name	Area (km²)	Average Annual Precipitation (mm)	Average Annual Temperature (C)	Average Freeze-Free Period (days)	Elevation (m)
57	Northern Minnesota Gray Drift	21,440	525-675	3-6	100-120	300-500
88	Northern Minnesota Glacial Lake Basins	31,010	500-675	3-5	95-105	300-400
90	Central Wisconsin and Minnesota Thin Loess and Till	55,750	625-750	4-7	120-140	300-500
91	Wisconsin and Minnesota Sandy Outwash	52,780	625-825	4-7	125-145	300
92	Superior Lake Plain	4,950	625-875	3-6	100-140	200-300
93	Superior Stony and Rocky Loamy Plains and Hills	56,080	750	2-6	80-140	200-600
94A	Northern Michigan and Wisconsin Sandy Drift	39,920	675-850	4-7	120-140	200-500
94B	Michigan Eastern Upper Peninsula Sandy Drift	15,170	725-850	4-6	90-155	200-300
95A	Northeastern Wisconsin Drift Plain	15,760	700-750	6-8	120-160	200-400
95B	Southern Wisconsin and Northern Illinois Drift Plain	28,530	750-825	7-9	140-170	200-300
96	Western Michigan and Northeastern Wisconsin Fruit Belt	10,650	675-750	6-8	135-170	200-300
97	Southwestern Michigan Fruit and Truck Belt	5,960	825-925	9-10	160-180	200-300
98	Southern Michigan and and Northern Indiana Drift Plain	60,050	750-925	8-9	140-150	200-300
99	Erie-Huron Lake Plain	35,780	700-875	7-11	140-160	200
100	Erie Fruit and Truck Area	4,260	750-900	10-11	160-180	220
101	Ontario Plain and Finger Lakes Region	32,790	900-1150	7-10	140-160	100-400

105	Northern Mississippi Valley Loess Hills	57,520	750-900	7-10	140-160	200-400
108	Illinois and Iowa Deep Loess and Drift	79,790	750-900	8-12	160-180	200-300
109	Iowa and Missouri Heavy Till Plain	37,110	825-1025	10-13	160-180	200-300
110	Northern Illinois and Indiana Heavy Till Plain	26,350	750-900	9-11	160-180	200
111	Indiana and Ohio Till Plain	84,980	900-1025	10-13	155-180	200-300
112	Cherokee Prairies	57,520	900-1050	13-17	190-235	100-400
113	Central Claypan Areas	28,570	1025	13	180-190	200-300
114	Southern Illinois and Indiana Thin Loess and Till Plain	34,880	900-1150	12-14	180-200	100-400
115	Central Mississippi Valley Wooded Slopes	60,860	900-1150	12-14	180-200	100-300
116A	Ozark Highland	69,810	1025-1225	13-16	180-200	200-500
116B	Ozark Border	35,470	975-1225	13-16	180-200	200-500
117	Boston Mountains	14,930	1150-1325	14-17	180-205	200-800
118	Arkansas Valley and Ridges	27,250	1125-1275	16-17	200-240	100-900
119	Ouachita Mountains	24,640	1225-1425	16-17	200-240	100-800
120	Kentucky and Indiana Sandstone and Shale Hills and Valleys	30,990	1175	14	185	100-200
121	Kentucky Bluegrass	29,490	1125	13	180	200-300
122	Highland Rim and Pennyroyal	52,640	1125-1375	13-16	180-205	100-400
123	Nashville Basin	15,680	1275	14-16	192	200-400
124	Western Allegheny Plateau	19,040	1025-1150	9-13	140-160	200-400
125	Cumberland Plateau and Mountains	63,840	1175	13	175	200-1200
126	Central Allegheny Plateau	50,770	900-1150	4-13	120-170	200-400
127	Eastern Allegheny Plateau and Mountains	43,680	1025-1425	7-11	110-160	300-1400
128	Southern Appalachian Ridges and Valleys	69,430	925-1400	13-16	170-210	200-1500
129	Sand Mountain	17,540	1300-1400	16-17	200-210	100-500
130	Blue Ridge	47,030	1025-2025	10-16	150-220	300-2000
131	Southern Mississippi Valley Alluvium	93,600	1150-1650	14-21	200-340	0-200
133A	Southern Coastal Plain	285,050	1025-1525	16-20	200-280	25-200

133B	Western Coastal Plain	140,640	1025-1350	16-20	200-270	25-200
134	Southern Mississippi Valley Silty Uplands	73,890	1150-1525	16-20	200-280	25-100
135	Alabama, Mississippi and Arkansas Blackland Prairie	21,550	1225-1425	16-18	220-260	25-100
136	Southern Piedmont	161,430	1150-1400	14-18	205-235	100-400
137	Carolina and Georgia Sand Hills	22,680	1150-1275	17-18	220-240	50-200
138	North-Central Florida Ridge	3,400	1300-1400	20-21	280-290	25-50
139	Eastern Ohio Till Plain	15,030	900-1025	10	160	200-300
140	Glaciated Allegheny Plateau and Catskill Mountains	70,540	750-1025	8-10	110-160	200-1100
141	Tughill Plateau	3,080	900-1025	4-7	110-135	300-600
142	St. Lawrence-Champlain Plain	14,260	900	4-7	120-140	25-300
143	Northeastern Mountains	101,760	875-1325	3-7	80-130	300-1500
144A	New England and Eastern New York Upland, Southern Part	52,040	825-1275	7-10	120-200	0-600
144B	New England and Eastern New York Upland, Northern Part	48,570	900-1225	4-7	110-160	0-900
145	Connecticut Valley	6,560	1025-1275	7-11	150-195	0-300
146	Aroostook Area	2,700	925-1025	3-6	100-120	200
147	Northern Appalachian Ridges and Valleys	48,210	900-1275	8-13	120-170	100-900
148	Northern Piedmont	29,870	900-1150	10-14	160-200	25-500
149A	Northern Coastal Plain	20,870	900-1275	10-13	170-210	0-100
149B	Long Island-Cape Cod Coastal Lowland	6,830	1025-1150	10-13	180-220	0-100
152A	Eastern Gulf Coast Flatwoods	34,120	1325-1625	19-21	270-290	0-25
152B	Western Gulf Coast Flatwoods	16,890	1175-1400	19-21	260-280	25-100
153A	Atlantic Coast Flatwoods	73,760	1025-1400	13-21	200-280	25-50
153B	Tidewater Area	31,020	1150-1275	13-24	200-300	0-25
153C	Mid-Atlantic Coastal Plain	15,510	1175	13-14	185-220	0-25
154	South-Central Florida Ridge	24,290	1275-1400	21-23	290-350	25-100
155	Southern Florida Flatwoods	54,570	1300-1525	21-23	290-365	0-25