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RELATIVE SPECIES RICHNESS AND COMMUNITY COMPLETENESS: BIRDS AND URBANIZATION IN THE MID-ATLANTIC STATES

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Abstract. The idea that local factors govern local richness has been dominant for years, but recent theoretical and empirical studies have stressed the influence of regional factors on local richness. Fewer species at a site could reflect not only the influence of local factors, but also a smaller regional pool. The possible dependency of local richness on the regional pool should be taken into account when addressing the influence of local factors on local richness. It is possible to account for this potential dependency by comparing relative species richness among sites, rather than species richness per se. We consider estimation of a metric permitting assessment of relative species richness in a typical situation in which not all species are detected during sampling sessions. In this situation, estimates of absolute or relative species richness need to account for variation in species detection probability if they are to be unbiased. We present a method to estimate relative species richness based on capture–recapture models. This approach involves definition of a species list from regional data, and estimation of the number of species in that list that are present at a site–year of interest. We use this approach to address the influence of urbanization on relative richness of avian communities in the Mid-Atlantic region of the United States. There is a negative relationship between relative richness and landscape variables describing the level of urban development. We believe that this metric should prove very useful for conservation and management purposes because it is based on an estimator of species richness that both accounts for potential variation in species detection probability and allows flexibility in the specification of a “reference community.” This metric can be used to assess ecological integrity, the richness of the community of interest relative to that of the “original” community, or to assess change since some previous time in a community.

Key words: capture–recapture models; conservation; ecological communities; estimation; integrity; landscape; Mid-Atlantic states; North American Breeding Bird Survey; relative species richness; species pool; urbanization.

INTRODUCTION

Identifying the nature of anthropogenic alterations of natural habitats associated with variations in animal and plant diversity is of major interest for management and conservation purposes. More generally, one of the main questions in ecology concerns the mechanisms determining local species richness. This question can be addressed by investigating patterns of spatial or temporal variation in habitat characteristics and in the attributes of local plant or animal communities. Many studies have focused directly on species richness to investigate these relationships (Blake and Karr 1987, Soulé et al. 1992, Herkert 1994). However, the inference that can be drawn from observed relationships between local habitat characteristics and species richness strongly depends on the conception of the processes determining local richness (Ricklefs and Schluter 1993).

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The idea that local ecological processes determine local richness has been dominant for years, but there is increasing interest in the idea that processes taking place at larger spatial and temporal scales also play a role in determining local richness (Ricklefs 1987, Taylor et al. 1990, Cornell and Lawton 1992, Zobel 1992, Cornell 1993, Eriksson 1993, Haila et al. 1993, Ricklefs and Schluter 1993, Jokimäki and Huhta 1996, Huggen et al. 1997, Augermeier and Wiston 1998, Karlson and Cornell 1998). It has been suggested that the size of the regional species pool influences local richness, i.e., that communities would seldom be saturated, and would be open to colonization from the regional pool (Cornell and Lawton 1992). Several studies focusing on the relationship between species richness at different spatial scales have provided evidence supporting this hypothesis (Cornell 1993, Karlson and Cornell 1998). Under this hypothesis, spatial variations in species richness may not be exclusively linked to variation in local ecological conditions: differences in local richness may also reflect differences in the size of the regional pool. In conservation biology, the question of spatial variation in species richness is often

tackled in relation to human-induced modification of habitat characteristics, and fewer species in a site is often interpreted as evidence of impoverishment of the community of interest, associated with habitat alteration. However, if the pool of available species differs for areas being compared, fewer species in one area may simply indicate a smaller species pool. A community harboring fewer species should not necessarily be considered as "less complete." Similarly, temporal variations in local richness may partly reflect modifications of the regional species pool. Under this view, it is desirable to take the available species pool into account when comparing communities over space or time, and to focus on "relative" species richness rather than species richness per se, when addressing questions about local factors.

In this paper, we consider the estimation of a relative species richness metric. This metric can be viewed as reflecting the degree of "completeness" of animal communities, relative to a species pool. We consider this estimation in situations in which not all species are necessarily detected during sampling sessions, i.e., where species detection probabilities are < 1 . In such a sampling situation, naive estimates computed as the number of species detected in samples of the community of interest divided by the number of species in the reference community or the potential species pool will be biased, and will be a function of both sampling variation and the true quantity of interest. We propose an estimator designed to eliminate this bias and the confounding influence of detection probability. We use this estimator to address a question about the possible influence of urban development at the landscape scale on avian communities in the Mid-Atlantic states of Delaware, Maryland, New Jersey, Pennsylvania, Virginia, and West Virginia.

Most previous studies have established that higher levels of urbanization are associated with a lower number of breeding species (Batten 1972, Emlen 1974, Huhtalo and Järvinen 1977, Hohtola 1978, Beissinger and Osborne 1982, Bezzel 1984, Rapport et al. 1985, Jokimäki and Suhonen 1993, Zalewski 1994, Flather 1996, Mikusiński and Angelstam 1997, Clergeau et al. 1998). Some studies have found that richness peaks at intermediate levels of disturbance (Jokimäki and Suhonen 1993, Blair 1996). A major change in landscapes associated with human activities is the fragmentation of original habitats (Bezzel 1984, Soulé et al. 1992, Jokimäki and Suhonen 1993), which implies "habitat loss, reduced patch size, and an increased distance between patches, but also an increase of new habitat" (Andrén 1994). There is no consensus on the respective roles of various factors associated with fragmentation (Blake and Karr 1987, Martin 1988, Soulé et al. 1992, Paton 1994, Hartley and Hunter 1998), but the negative influence of fragmentation on species richness has been widely documented (Robbins et al. 1989, Herkert 1994,

Tilman et al. 1994, Kareiva and Wennergren 1995, Boulmier et al. 1998b, Huhta et al. 1998).

It has been suggested that the influence of urbanization on species richness depends on the relative importance of modification of original habitats and the increase in new habitats created by urban development (Jokimäki and Suhonen 1993, Blair 1996). Among the factors associated with fragmentation, only the potential increase in habitat diversity may have a positive influence on species richness (Andrén 1994). Lancaster and Rees (1979) suggested that lower levels of urbanization lead to habitat diversification, whereas higher levels lead to loss of habitat diversity. In highly urbanized areas, the other factors associated with fragmentation (i.e., reduction in patch size, increasing isolation of habitat patches, and increase in edges; reviewed in Andrén 1994) are likely to add to loss of habitat diversity. Under that hypothesis, one might expect that the relationship between urban development and species richness is not linear. The studies showing that species richness "peaks at moderately disturbed sites" (Jokimäki and Suhonen 1993, Blair 1996) support that hypothesis.

Several studies examined the composition of urban communities and established that these communities comprise mostly native species found in predevelopment habitats that have the ability to colonize and persist in urban habitat, plus a few "new" exotic species not recorded in less urbanized habitat (Batten 1972; Lancaster and Rees 1979, Germaine et al. 1998). Not all of the species from the "predevelopment" bird communities remain in urban areas, and relatively few exotic species not belonging to the predevelopment pool are likely to colonize urban habitat. Lower levels of urbanization would increase richness through a community characterized by the coexistence of species associated with original and new habitat (i.e., an initial increase in species richness), whereas higher levels would lead to lower species richness (Lancaster and Rees 1979, Jokimäki and Suhonen 1993, Zalewski 1994, Blair 1996).

Predictions about the influence of urbanization on relative species richness depend on the approach to characterization of the level of urban development on the one hand, and to specification of the species pool on the other hand. Concerning measures of urbanization, the level of disturbance can be described by the relative development of different types of structures (e.g., residential areas, parks, business areas): this may reflect the level of habitat diversity. In this case, one might expect that relative species richness peaks at intermediate levels of urban development (Blair 1996). In this study, "Urban land and built-up land consists of areas of intensive use with much of the land covered by structures" (see Anderson et al. 1976 for information on the landscape data used), which corresponds to a high level of disturbance. An increase in the level of urbanization at the landscape scale (e.g., an in-

creased proportion of urban land) corresponds to a larger amount of land in intensive use in a mosaic of predevelopment and urban land. In a juxtaposition of patches where urban land corresponds to the extreme, in terms of disturbance, increased levels of urbanization may create opportunities for only very few new species, and may not permit persistence of predevelopment species in urban areas.

Concerning the species pool, we used a list reflecting the regional pool, i.e., all of the species potentially available for the locations of interest. Our aim was to use a pool including the "original" community plus new species specifically associated with urban habitat. Consequently, our underlying hypothesis was that urbanization would lead to reduction in species richness relative to the species pool. Even if urbanization creates opportunities for a few new species, we expect that bird communities in areas experiencing more urban development exhibit lower relative richness than areas experiencing less development. Basically, with this approach for defining the pool, predictions about the impact of urbanization on relative species richness and on species richness per se are similar. However, in the framework of a comparative approach among various locations, use of relative species richness ensures that potential differences in local richness among sites does not exclusively reflect differences in the corresponding species pools.

Avian data used in this analysis were collected as part of the North American Breeding Bird Survey, (BBS Robbins et al. 1986, Peterjohn and Sauer 1993). Landscape-level data on urban development were obtained from the Land Use and Land Cover data summarized by the U.S. Geological Survey (Anderson et al. 1976, USDI Geological Survey 1987). Here we present the relative richness estimator, briefly discuss avian and land use data sets, describe statistical analysis methods, and present results.

RELATIVE SPECIES RICHNESS: ESTIMATION AND INTERPRETATIONS

We sought a metric that would permit assessment of the relative richness of animal communities and be useful in comparing communities in different locations. A parameter that corresponds to the concept of completeness is the expected proportion of species in a pool that are present in a specific area of interest. Alternatively, we can think of this parameter as the probability that a member of a species pool is present in a specific area of interest.

Species pool specification and interpretations

The first step in estimating the relative richness metric is to identify the species pool associated with a community of interest. The metric that we propose allows flexibility in the specification of the pool. This permits use of various groups as "reference" communities, defined on the basis of different criteria ac-

ording to the question of interest. Interpretations of relative richness depend on specification of these pools, and the notion of "completeness" depends on the question addressed and the pool used.

There are several possible sources of information for these lists of species. To specify a regional pool, or a pool corresponding to some defined area of space, one possible source is contemporary state "atlases" for specific taxonomic groups (e.g., birds, mammals). These atlases typically specify grid blocks or counties in a state in which each species has been observed to breed (Robbins 1996). One can also use lists compiled from publications (e.g., Karlson and Cornell 1998). If a monitoring program has been operating for some time in the area of interest, then it may be possible to develop an operational species pool using data from all sampling years other than the year of interest. It is important to note that the approach is different when one uses independent sources of data for the area of interest and the region than when one does not (i.e., if the data collected in the location of interest are also used to specify the pool). If the sources are not independent, the species detected only on the specific site of interest in the year of interest must be excluded to compute relative species richness. This exclusion is needed to insure statistical independence of the numerator and denominator of Eq. 1 (see *Estimation*). In addition, if we intended the metric to reflect change since some previous time, we could perhaps develop a species list from historical records.

Of particular interest is a pool corresponding to an "undisturbed" situation. This can be achieved using a reference community considered as the "original" community; for example, Zampella and Bunnell (1998) used a "reference-site" fish assemblage to evaluate communities found in degraded sites. It is also possible to use a list of species corresponding to the "predisturbance" community, if historical records are available for the site of interest, or a reference site. In these cases, relative species richness is relevant to assessing ecological integrity, a concept currently receiving much attention in conservation biology (Karr 1981, 1987, 1990, 1991, 1996, Karr and Dudley 1981).

Subsequent sampling

Given a list of species that can be viewed as the species pool (or a representative sample from that pool) for a particular community or area, the next task is to estimate how many of the species in that list are present in the community or area for the year of interest. Several possible approaches can be used to sample an area for the purpose of estimating species richness (Nichols and Conroy 1996, Nichols et al. 1998b). Quadrat sampling has been especially popular and involves the subdivision of the total area of interest into a number of quadrats or small sampling units. A random sample of quadrats is selected, and the investigator(s) identifies and enumerates species found on each selected quadrat

using virtually any set of sampling methods, e.g., direct observation of animals and their sign (tracks, scats, nests, etc.), auditory identification, and trapping and netting with different trap and net types. It is best to use the same sampling methods and to expend similar effort on each quadrat sampled. However, this is not necessary, as models permitting variation in species detection probabilities among the different quadrats are available (see Nichols and Conroy 1996, Boulinier et al. 1998a). Such sampling efforts produce a species list for each quadrat specifying species detected and, in some sampling situations, the number of individuals detected that belong to each species.

Estimation

Several estimators have been proposed for the estimation of species richness from such quadrat species list data (reviewed by Bunge and Fitzpatrick 1993). Additional estimators developed for capture–recapture data from closed animal populations (e.g., see Otis et al. 1978, White et al. 1982, Rexstad and Burnham 1991) can also be used for estimating richness from quadrat community sampling data (Burnham and Overton 1979, Nichols and Conroy 1996, Boulinier et al. 1998a, Nichols et al. 1998b). Estimates based on these capture–recapture models can be computed using the software program CAPTURE (Rexstad and Burnham 1991). The richness estimates used in the proposed relative richness estimator can be computed using any appropriate model. Following the suggestion of Boulinier et al. (1998a), our example analyses are based on model $M(h)$, permitting heterogeneity of detection probabilities among different species in the community (Otis et al. 1978, White et al. 1982). We use the jackknife estimator for this model proposed by Burnham and Overton (1978, 1979). The particular feature of this approach is the incorporation of species detection probability for estimating species richness (Burnham and Overton 1978, Nichols and Conroy 1996, Boulinier et al. 1998a, b, Nichols et al. 1998a, b). This method accounts for the fact that investigators miss some species during sampling sessions, and thus it permits obtaining unbiased estimates of richness in year j with sampling data from a single year.

Denote the proposed integrity metric as ϕ_j , the probability that a member of the specified species pool is present in the community or area of interest in year j . The number of species in the associated species pool is denoted as R . Using data from the quadrat sampling in the area of interest in year j , we must estimate the number of members of R that are present in j , denoted as M_j^R . The R superscript indicates that we restrict interest to members of R . M_j^R cannot be directly observed, as it is very unlikely that all species present in j will be detected in the sampling effort. However, this quantity can be estimated using sampling data for the m_j^R species that are observed at time j . The observation frequency data for the m_j^R at time j (i.e., the number of

these species detected on exactly 1, 2, . . . , K of the sampling quadrats) can be used in conjunction with model $M(h)$, for example, in order to estimate M_j^R . Our estimator for the relative richness indicator of ecological integrity (the probability that a member of the species pool R is present at time j) is thus:

$$\hat{\phi}_j = \frac{\hat{M}_j^R}{R}. \quad (1)$$

The estimator in Eq. 1 has the same form as estimators used to estimate the complement of extinction probability, the complement of turnover, and the probability that a species at one location is present in another (Nichols et al. 1998a, b). The sampling variance of $\hat{\phi}_j$ and associated confidence intervals can be estimated using a bootstrap approach (Nichols et al. 1998a), e.g., as implemented in program COMDYN (Hines et al. 1999).

URBAN DEVELOPMENT AND COMPLETENESS OF AVIAN COMMUNITIES IN THE MID-ATLANTIC

Avian data

The BBS.—The BBS is a continental survey carried out every spring on permanent survey routes randomly located along secondary roads throughout the United States and southern Canada. This long-term monitoring program started in 1966 and continues at present (Sauer et al. 1997); see the BBS web page for further information.⁵

There are ~3700 active routes, and 2900 routes are surveyed annually. Each route is 39.4 km long and consists of 50 stops spaced at 0.80-km intervals. An observer drives along the route and conducts a 3-min observation at each stop, recording all birds seen or heard within 0.40 km of the stop (Robbins et al. 1986, Peterjohn and Sauer 1993). The data required for estimation of species richness with the jackknife estimator for model $M(h)$ (Burnham and Overton 1978, 1979) are observed frequencies f_h , the number of species observed on exactly $h = 1, 2, 3, 4, \dots, K$ sampling quadrats (i.e., stops). See Boulinier et al. (1998a) and Nichols et al. (1998a) for detailed information on the approach to estimation of species richness using the BBS data. For estimation of relative species richness, only the observed frequencies for species in the pool are used.

Our analysis included all routes in the six states of the Mid-Atlantic region. We computed relative richness estimates for 1975, as the landscape-level data on urban development were from the mid-1970s. Although it would have been possible to define the species pool for a subset of species, we did not restrict the analysis to a subset of avian species, but used all species encountered in the BBS data.

Species pool.—We needed to develop a species pool for each BBS route in the Mid-Atlantic states. Our aim

⁵ URL: (www.mbr-pwrc.usgs.gov/bbs/bbs.html)

was to account for the regional pool in order to address the influence of urbanization on the degree of completeness of communities. First, we defined an area including the route of interest and then listed all of the species recorded on BBS routes located within that area. We restricted the area used to specify a pool to an ecologically relevant region: we used the species recorded on BBS routes located in areas nested within a physiographic stratum (or region). This stratification was developed specifically for the BBS by modifying existing vegetation and soil maps (Robbins et al. 1986; see Bystrak 1981 for additional information and Butcher 1990 for maps). These strata include various types of habitats that can be considered as "predevelopment habitats" as well as urban habitat, and consist of areas of relatively homogeneous natural communities that could be expected to have generally consistent bird communities.

We used two alternative pools specified using BBS routes situated in areas of different size, successively. The two ideas underlying these attempts are: (1) use of smaller areas nested within the stratum, which aimed at limiting the distance between the site of interest and the other sampling locations also used to specify the pool (as species recorded in distant locations are less likely to be potential colonists for the site considered; Peterjohn et al. 1995); and (2) limiting variation in sample size (i.e., in the number of routes used to specify the species pool corresponding to each BBS route). In the first step, we specified an area corresponding to the intersection between the state and the physiographic region (Bystrak 1981) to which the route of interest belonged (Peterjohn et al. 1995). We then listed all of the species recorded on BBS routes located within that area. Pools specified in this manner led to some difficulties. The number of routes used to specify pools was highly variable and we suspected that variation in sample size influenced the results of analyses. More precisely, there was a negative relationship between relative richness and the number of routes used to specify the pool for the route of interest. The routes whose pool was specified using the smaller number of BBS routes were located in two strata: this may have resulted in an artificial influence of stratum on relative species richness.

Here, we consider the basis for this suspicion and the mechanism underlying possible dependence of relative richness analyses on the manner in which the species pool is defined. The relative richness estimator (Eq. 1) should perform well as long as its denominator (R) is a *representative* sample of the species in the relevant pool, where representativeness is judged relative to the probability being estimated. Specifically, representativeness is judged relative to the probability that a member of the pool is present in the community represented by the place-time for which relative richness is to be estimated. If there is heterogeneity among species in their probabilities of being a member of a

community of interest, and if the average probability for members of R is smaller or larger than the average probability for the entire pool, then we expect a biased estimate of relative richness. Specifically, we worry about the possibility that R will tend to include virtually all common species with large ranges, but will not include some uncommon species with small ranges. The former well-represented group of species will probably be characterized by high probabilities of occurring in any specific community of interest for which relative richness is estimated, whereas species in the more poorly represented group will probably tend to have smaller probabilities of occurring in any specified community. Thus, although the estimator in (1) should provide a good estimate of relative richness for the pool species appearing in R , it may be positively biased with respect to the entire species pool (because the pool species omitted from R will also have a smaller probability of being present in any other community). Having described this problem, we note that similar issues arise when estimating community-dynamic parameters such as local extinction probability and turnover. However, results of a recent investigation of bias in these situations led to the conclusion that bias was small and that the original estimators performed reasonably well in the face of this problem with heterogeneity among species in the probability being estimated (R. Alpizar-Jara, J. D. Nichols, J. E. Hines, J. R. Sauer, K.P. Pollock, and C. Rosenberry, *unpublished manuscript*).

Because of this worry about the dependence of the relative richness estimator on the degree to which the sample R represents the entire community, we considered another approach to defining the species pool. For each route, we specified an area corresponding to the intersection between the stratum and a circular scene of radius 80 km centered on the route of interest. We listed all of the species recorded on BBS routes located in that area (i.e., a route-specific pool). This was done to insure that sample R was reasonably complete (represented a large fraction of all species in the pool) in order to leave less potential for a nonrepresentative R . In addition, we excluded data from routes located in areas including fewer than five routes.

Given an area specified to compute the pool, we developed species lists from all BBS routes in the region for all available years, with the exception that we did not include species detected only on the specific route of interest in the year of interest. This exclusion aims at insuring statistical independence of the numerator and denominator of Eq. 1.

Estimation of M_{75}^R , the number of members of the species pool (R) present in the area sampled by the BBS route in 1975, was based on the numbers of species encountered in 1975 on 1, 2, . . . , 50 of the stops on the BBS route. This approach essentially treats each stop along a survey route as a "quadrat" sampling the area covered by the route. All computations were con-

TABLE 1. Pearson correlation coefficients among variables describing urban development.

Variables	Log(average urban patch size + 0.5)	Number of urban patches
Arcsine(sqrt(proportion of urban land))	0.87	0.68
Log(average urban patch size + 0.5)		0.38

Notes: $n = 200$; $H_0: \rho = 0$; all P values < 0.001 . Sqrt = square root.

ducted using program COMDYN developed by Hines et al. (1999).

Urban development data: the Land Use and Land Cover survey

Land Use and Land Cover Classification (LULC) data from the U.S. Geological Survey were used to quantify urban development within a circular scene radius of 19.7 km centered on each BBS route (area 1200 km²). A radius of half the length of a BBS route was chosen to guarantee that each landscape scene would contain the whole route. High-altitude photographs, usually at scales smaller than 1:60 000, were used to digitize and transfer land use and land cover data to 1:250 000 base maps in grid format (Anderson et al. 1976, USDI Geological Survey 1987). In these data, much of the land has to be covered by human structures to be considered as urban land (i.e., only intensively used land is considered as urban land; Anderson et al. 1976). We focused on three main variables describing urban development: (1) the proportion of the area characterized as urban, (2) the average size of patches characterized as urban, and (3) the number of patches characterized as urban. These three variables are clearly not independent. They were computed at the landscape scale and incorporate both areas immediately surrounding the survey route and areas more distant, but still near the route centroid.

Analysis methods

We used a logit transformation of $\hat{\phi}_{75}$ (the estimated probability that a member of the species pool is present on the BBS route of interest in year 75), and modeled that response variable as a linear combination of explanatory variables. Analyses were performed using SAS (PROC GLM; SAS Institute 1990). To conform to the requirements of regression using logit-transformed response variables, each transformed $\hat{\phi}_{75}$ was weighted by the inverse of the variance of the logit (Draper and Smith 1998).

Because the three variables describing urban development were not independent (Table 1), we built three separate initial models, each including one of the landscape variables. These models included the following variables: (1) the stratum, (2) one of the landscape variables, (3) the landscape variable squared, and (4)

the pairwise interactions between the stratum and the two other variables (2 and 3). The stratum was included because the nature of the ecological community is a potential source of variation of relative richness, and strata are very likely to harbor distinct communities (Bystrak 1981). Two independent variables had to be transformed in order to better approximate the assumption of normality; we used the arcsine of the square root of the proportion of urban land and the log(average urban patch size + 0.5).

Introduction of a quadratic term permits us to address whether relative species richness varies as a nonlinear function of the landscape variables. This may be the case if relative richness peaks at some intermediate value of urban development (e.g., Blair 1996). Because the third variable is created from the second one, these models present a structural collinearity problem. This can lead to elimination of terms because of redundancy between explanatory variables. Consequently, we centered the landscape variables (Glantz and Slinker 1990). We used a backward variable selection procedure.

RESULTS

In total, 200 routes were used in each analysis. Variable selection procedures led to a set of models that included the landscape variable and stratum. In all cases, however, relative species richness was higher in the strata least represented in our sample, i.e., relative richness was higher on routes located in strata including a small total number of routes (number of BBS routes per stratum: Coastal Flatwoods, 2; Southern New England, 2; Cumberland Plateau, 3; Southern Piedmont, 9; Ohio Hills, 19; Northern Piedmont, 32; Ridge and Valley, 41; Upper Coastal Plain, 43; Allegheny Plateau, 49). These results are not presented here. The influence of stratum could be partly linked to variation in the number of BBS routes used to specify the species pool corresponding to each route. Only small portions of some strata are represented in the Mid-Atlantic region, and the intersections between the states and these strata include a small number of routes.

Consequently, we performed the same analyses using only data from routes located in strata represented by a minimum of five routes in intersections with Mid-Atlantic states. In total, 179 routes were used. Concerning the variable *proportion of urban land*, there was an additive effect of stratum and proportion of urban land on relative species richness (Table 2). The proportion of urban land and relative richness were negatively correlated (Table 2, Fig. 1). The variable selection procedure also led to a model with an additive effect of stratum and average patch size (Table 3). There was a negative relationship between relative species richness and the average urban patch size (Fig. 2). Last, there was an additive effect of stratum and number of urban patches, and the final model included only

TABLE 2. Test for an effect of proportion of urban land (arcsine square-root transformed) and stratum on relative species richness; final model.

Variable	df	F	P	Parameter label†	Estimate	SE‡
Proportion of urban land	1	6.18	0.0139		-0.49	0.20
Stratum	5	6.22	0.0001	4	0.23	0.09
				10	0.24	0.10
				11	0.60	0.12
				13	0.09	0.08
				22	0.41	0.12
				24	0.00	...
Intercept					-0.50	0.06

Notes: Initial model: $F = 2.42$, $df = 17$, $P = 0.0022$, $R^2 = 0.20$; model $ss = 64.04$, $df = 17$; error $ss = 250.74$, $df = 161$. Final model: $F = 5.66$, $df = 6$, $P = 0.0001$, $R^2 = 0.16$; model $ss = 51.88$, $df = 6$; error $ss = 262.91$, $df = 172$.

† Stratum label: 4, Upper Coastal Plain; 10, Northern Piedmont; 11, southern Piedmont; 13, Ridge and Valley; 22, Ohio Hills; 24, Allegheny Plateau.

‡ Estimated standard error. Ellipsis indicate a reference category for which SE was not estimated.

the quadratic term (Table 4). Relative richness peaked at an intermediate number of urban patches (Fig. 3).

In a second step, we used route-specific species pools (see *Species pool*); as in the previous set of analyses, this was an attempt to mitigate the possible influence of unequal sample size. In total, 152 routes were used in this set of analyses. There was some evidence of an influence of the proportion of urban land on relative species richness ($P = 0.0526$; Table 5), so we retained that variable. The final model was similar to the previous one, with an additive effect of stratum and the landscape variable. The proportion of urban land and relative richness were negatively correlated (Table 5, Fig. 4). Regarding the variable *average urban patch size*, the test of the hypothesis that all of the coefficients associated with explanatory variables are equal to 0 provided some evidence of relevant association ($F =$

1.64; $df = 17, 134$; $P = 0.0632$; Table 6), so we performed the variable selection procedure. This led to a model with an additive effect of stratum and the average patch size (Table 6). There was a negative relationship between relative species richness and the average urban patch size (Table 6, Fig. 5). Last, regarding the number of urban patches, the complete variable selection procedure led to a model including the variable stratum exclusively. However, the probability associated with the landscape variable squared provided some evidence of the relevance of this variable ($F = 3.36$; $df = 1, 145$; $P = 0.0691$; Table 7). The corresponding model included an additive effect of stratum and the landscape variable squared (Table 7). Estimates made under this model showed that relative richness peaks at an intermediate number of urban patches (Fig. 6).

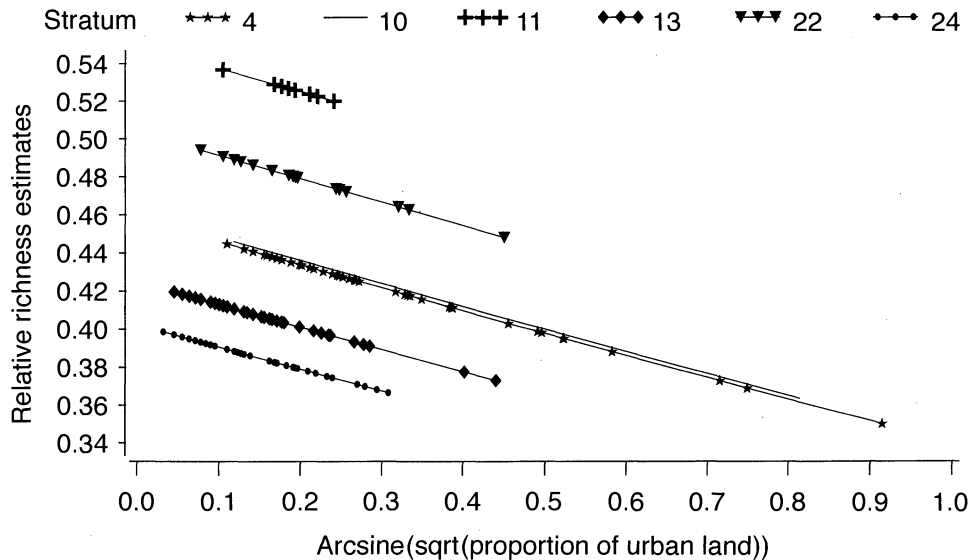


FIG. 1. Relationships among relative species richness, proportion of urban land (arcsine square-root transformed), and stratum. Estimates are made under the model with an additive effect of stratum and proportion of urban land. Stratum labels are: 4, Upper Coastal Plain; 10, Northern Piedmont; 11, Southern Piedmont; 13, Ridge and Valley; 22, Ohio Hills; 24, Allegheny Plateau.

TABLE 3. Test for an effect of log(average urban patch size + 0.5) and stratum on relative species richness; final model.

Variable	df	F	P	Parameter label†	Estimate	SE
Average patch size	1	4.81	0.0297		-0.10	0.05
Stratum	5	6.18	0.0001	4	0.20	0.09
				10	0.18	0.09
				11	0.61	0.13
				13	0.07	0.08
				22	0.39	0.12
				24	0.00	...
Intercept					-0.49	0.06

Notes: Initial model: $F = 2.05$, $df = 17$, $P = 0.0115$, $R^2 = 0.18$; model $ss = 55.93$, $df = 17$; error $ss = 258.86$, $df = 161$. Final model: $F = 5.39$, $df = 6$, $P = 0.0001$, $R^2 = 0.16$; model $ss = 49.83$, $df = 6$; error $ss = 264.95$, $df = 172$.
 † Stratum labels are as in Table 2.

DISCUSSION

Relative species richness and urbanization

Previous studies that have investigated the influence of urbanization on the number of breeding species have either provided evidence of a negative relationship between the level of urban development and richness (Batten 1972, Emlen 1974, Huhtalo and Järvinen 1977, Beissinger and Osborne 1982, Bezzel 1984, Rapport et al. 1985, Jokimäki and Suhonen 1993, Zalewski 1994, Flather 1996, Mikusiński and Angelstam 1997, Clergeau et al. 1998), or evidence that richness peaks at intermediate levels of urban development (Jokimäki and Suhonen 1993, Blair 1996). Our results indicate a monotonic negative relationship between relative species richness and two of the variables describing the level of urbanization: proportion of urban land and average urban patch size. The high positive correlation between these two variables may explain the consistency of the results of these two analyses. These results

indicate that the higher the amount of urban development surrounding BBS routes, the lower the proportion of species belonging to the regional pool also present on these routes. This supports our prediction.

In contrast, the relationship between relative richness and number of urban patches is not linear: relative richness peaks at an intermediate number of patches. Gustafson and Parker (1992) and Andrén (1994) investigated the relationship between land cover proportion and the number of patches using simulated landscapes, and the patterns obtained indicate that the relationship is not monotonic. This is true in our case, which could explain why the correlation coefficient between the number of urban patches and the two other landscape variables was low, and why results vary according to the landscape variable considered. Our results provide evidence that the level of urban development influences relative species richness, but the discrepancy between results obtained with the different landscape variables indicates that the shape of the relationship between

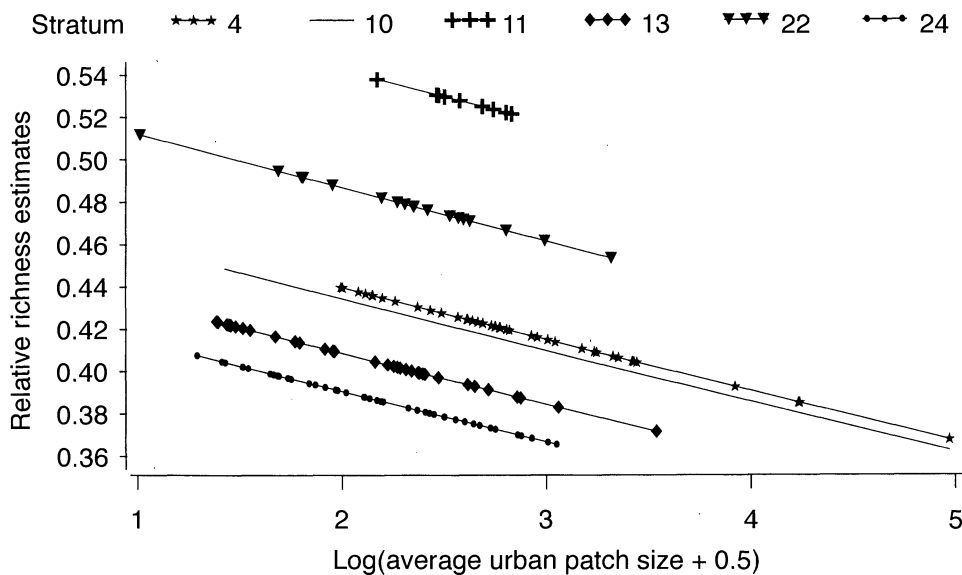


FIG. 2. Relationships among relative species richness, log(average urban patch size + 0.5), and stratum. Estimates are made under the model with an additive effect of stratum and average urban patch size. Stratum labels are as in Fig. 1.

TABLE 4. Test for an effect of number of urban patches and stratum on relative species richness (final model).

Variable	df	F	P	Parameter label†	Estimate	\widehat{SE}
(No. patches) ²	1	10.95	0.0011		-1.10×10^{-5}	3.34×10^{-6}
Stratum	5	5.26	0.0002	4	0.15	0.08
				10	0.21	0.09
				11	0.54	0.12
				13	0.07	0.08
				22	0.34	0.11
				24	0.00	...
Intercept					-0.40	0.06

Notes: Initial model: $F = 3.05$, $df = 17$, $P = 0.0001$, $R^2 = 0.24$; model $ss = 76.71$, $df = 17$; error $ss = 238.08$, $df = 161$. Final model: $F = 6.58$, $df = 6$, $P = 0.0001$, $R^2 = 0.19$; model $ss = 58.74$, $df = 6$; error $ss = 256.05$, $df = 172$.

† Stratum labels are as in Table 2.

urbanization and the degree of completeness of avian communities is unclear. Basically, very high levels of development are associated with decreased relative species richness, but the influence of lower levels of urbanization on avian communities is ambiguous.

One reason invoked to explain why most previous studies have not found evidence that species richness peaks in moderately disturbed areas is that the range of urban development taken into account was not wide enough (Blair 1996). We believe that, in the present study, a curvilinear relationship between relative richness and urbanization was unlikely because of the measures of urbanization we used. Indeed, the variables that we used to quantify urbanization only account for intensively used land, i.e., stages of urban development where species of the predevelopment community are less likely to persist, when curvilinear relationships are thought to result from an initial increase in species richness through coexistence of predevelopment and exotic species. More qualitative questions about the

proportion of native species that persists (or not) in urban areas could be addressed using our approach by specifying subgroups of species, but this is beyond the scope of this paper. More generally, the predictions about the shape of the relationship between (relative) species richness and urban development are very likely to depend on the approach to quantification of urbanization, and on whether or not the measures used integrate qualitative elements describing the level of habitat diversity and complexity (e.g., distinction between parks and business areas).

Definition of the species pool

One of the common points between the results of our various sets of analyses is that the strata exhibiting the highest relative species richness are systematically the same (strata 11 and 22). All of the BBS routes in these strata have species pools specified using data from a small number of routes (slightly more than five). The approach used in the second set of analyses aimed

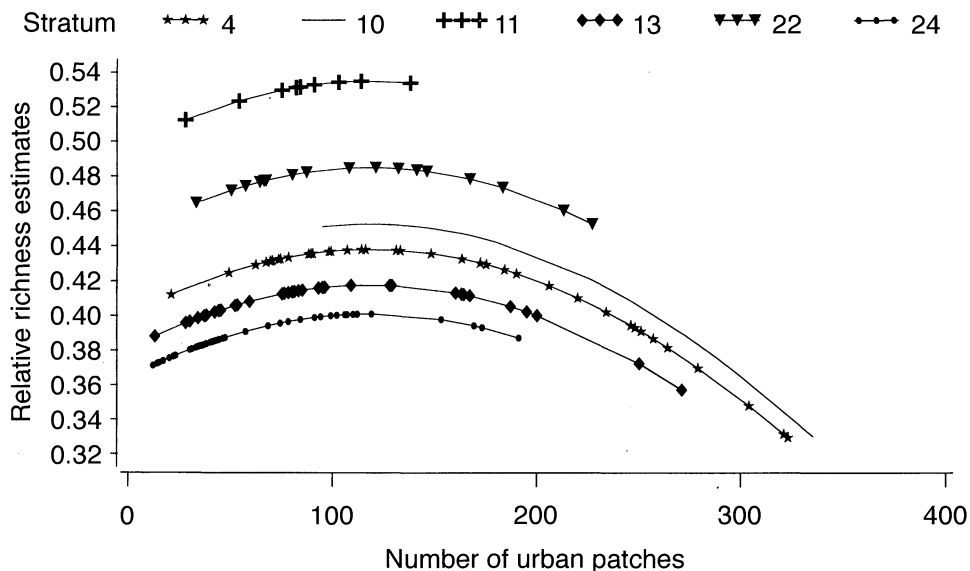


FIG. 3. Relationships among relative species richness, number of urban patches, and stratum. Estimates are made under the model with an additive effect of stratum and number of urban patches squared. Stratum labels are as in Fig. 1.

TABLE 5. Test for an effect of proportion of urban land (arcsine square-root transformed) and stratum on relative species richness (route-specific species pool; final model).

Variable	df	F	P	Parameter label†	Estimate	SE
Proportion of urban land	1	3.82	0.0526		-0.38	0.19
Stratum	5	4.38	0.0010	4	0.11	0.09
				10	0.01	0.10
				11	0.58	0.18
				13	-0.01	0.09
				22	0.52	0.16
				24	0.00	...
Intercept					-0.26	0.07

Notes: Initial model: $F = 1.81$, $df = 17$, $P = 0.0321$, $R^2 = 0.19$; model $ss = 43.10$, $df = 17$; error $ss = 187.22$, $df = 134$. Final model: $F = 4.16$, $df = 6$, $P = 0.0007$, $R^2 = 0.15$; model $ss = 33.82$, $df = 6$; error $ss = 196.49$, $df = 145$.
 † Stratum labels are as in Table 2.

at mitigating the potential influence of variation in sample size (in terms of number of sampling locations), but pools were still defined on the basis of very different numbers of routes. There is no systematic positive relationship between relative richness and the number of routes used to specify the pool, and the high relative richness in strata 11 and 22 could reflect an actual ecological phenomenon (e.g., lower habitat diversity within those strata). However, we have to consider the possibility that observed variations in relative species richness among strata could result partially from variations in the number of routes used to specify species pools. This illustrates one of the main difficulties encountered in all studies of relative species richness: the specification of the species pool.

Our main aim was to investigate the influence of urbanization on relative species richness, not the potential difference in relative richness among strata. Even if the various species pools used do not provide

equally reliable descriptions of reference communities, this should not mask factors influencing relative species richness within strata (such as urbanization). However, it is desirable to use an approach insuring that pools are equally representative of reference communities when one is interested in questions requiring comparisons of communities that do not share the same pool. In this case, data collection should probably be designed so that equal sampling effort is devoted to the specification of the various pools.

Inevitably, there will be debate about specification of a pool exactly relevant to the question that one intends to investigate. For example, identification of the “original” or “pre-disturbance” community is likely to raise both conceptual and practical difficulties. The metric that we presented here corresponds to the expected proportion of species in a pool present in a site in a point in time. Pools specified from the literature (e.g., Karlson and Cornell 1998), or based on all the

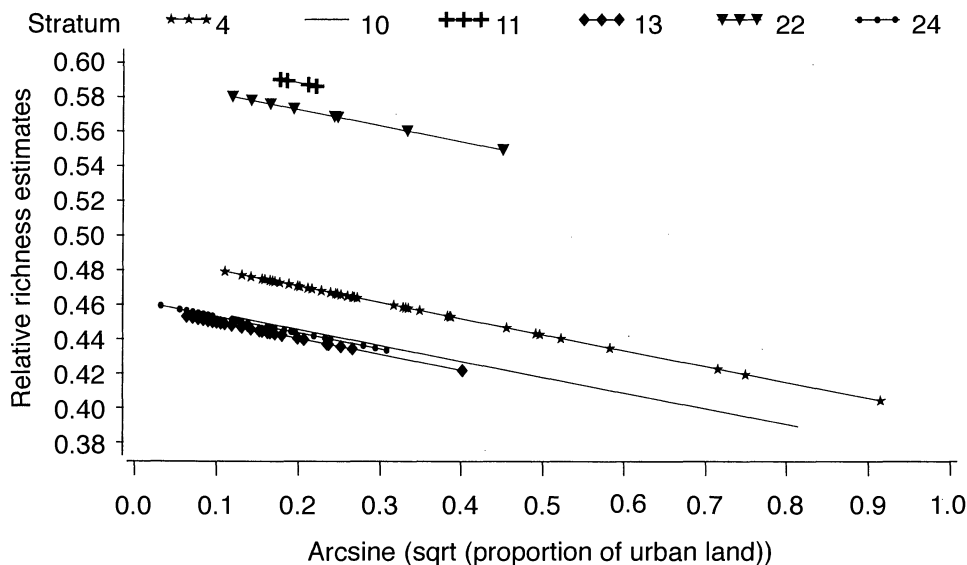


FIG. 4. Relationships among relative species richness (route-specific species pool), proportion of urban land (arcsine square-root transformed), and stratum. Estimates are made under the model with an additive effect of stratum and proportion of urban land. Stratum labels are as in Fig. 1.

TABLE 6. Test for an effect of log(average urban patch size + 0.5) and stratum on relative species richness (route-specific species pool; final model).

Variable	df	F	P	Parameter label†	Estimate	SE
Average urban patch size	1	5.26	0.0232		-0.10	0.04
Stratum	5	4.83	0.0004	4	0.11	0.09
				10	-0.02	0.09
				11	0.60	0.18
				13	-0.04	0.09
				22	0.52	0.16
				24	0.00	...
Intercept					-0.23	0.06

Notes: Initial model: $F = 1.64$, $df = 17$, $P = 0.0632$, $R^2 = 0.17$; model $ss = 39.60$, $df = 17$; error $ss = 190.72$, $df = 134$. Final model: $F = 4.43$, $df = 6$, $P = 0.0004$, $R^2 = 0.15$; model $ss = 35.71$, $df = 6$; error $ss = 230.32$, $df = 145$.
† Stratum labels are as in Table 2.

years of a monitoring program (e.g., this study) might not provide an exact description of the regional pool of species actually available for that location in that year. However, in situations involving sampling of natural communities or populations, we usually have to make assumptions in order to draw inference from samples. Specifically, one of the assumptions that we have to make here is that the species pool we used is representative of the entire pool (i.e., the probability that a species in the pool is in the community of interest is the same for members in the pool we used, R , and for the entire regional pool; see *Avian data*). Because we used data from all the years of the BBS, it is possible that some species went extinct in the region before the year of interest and that some others colonized the region after the year of interest. However, we suspect that such regional extinction and colonization will be relatively rare. We conclude that our approach to de-

veloping a species pool is reasonable, and that other approaches are possible.

Use of relative richness estimates

We believe that the metric presented here could prove useful not only for studies addressing conservation issues, but also for those focusing on community ecology in general. First, our metric is based on an estimator of species richness that accounts for the probability of detecting species, more precisely for heterogeneity in detectability among species (Otis et al. 1978, White et al. 1982, Nichols and Conroy 1996, Boulinier et al. 1998a). Although the problem of species missed during sampling sessions has long been recognized (Preston 1979), statistical inference procedures and associated software (Rexstad and Burnham 1991, Boulinier et al. 1998a, Nichols et al. 1998a,b, Hines et al. 1999) permitting correction for the probability of de-

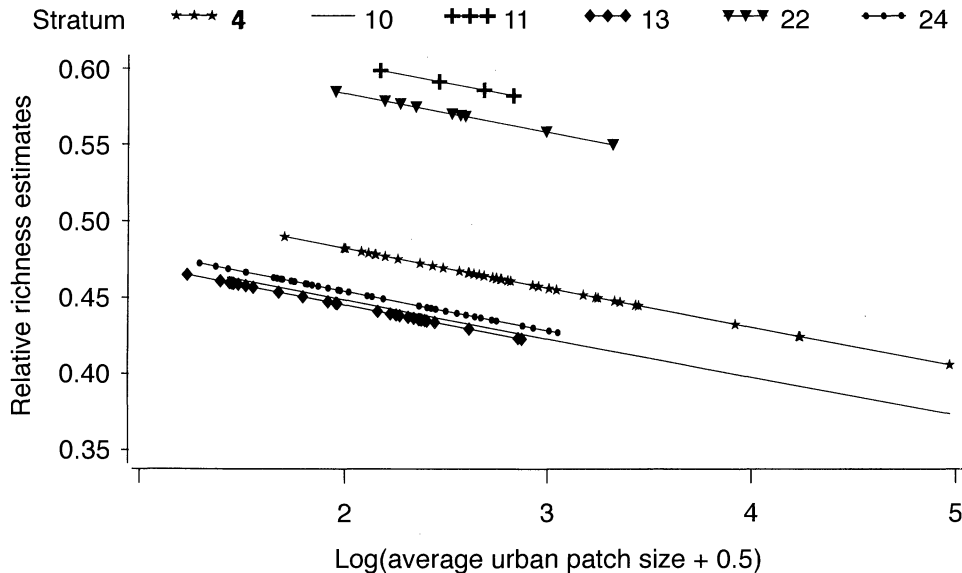


FIG. 5. Relationships among relative species richness (route-specific species pool), log(average urban patch size + 0.5), and stratum. Estimates are made under the model with an additive effect of stratum and average urban patch size. Stratum labels are as in Fig. 1.

TABLE 7. Test for an effect of number of urban patches and of the stratum on relative species richness (route-specific species pool; final model).

Variable	df	F	P	Parameter label†	Estimate	\widehat{SE}
(No. patches) ²	1	3.36	0.0691		-6.86×10^{-6}	3.74×10^{-6}
Stratum	5	3.62	0.0041	4	0.03	0.08
				10	-0.04	0.09
				11	0.51	0.19
				13	-0.04	0.09
				22	0.45	0.16
				24	0.00	...
Intercept					-0.16	0.07

Notes: Initial model: $F = 1.99$, $df = 17$, $P = 0.0159$, $R^2 = 0.20$; model $ss = 46.43$, $df = 17$; error $ss = 183.89$, $df = 134$. Final model: $F = 4.07$, $df = 6$, $P = 0.0008$, $R^2 = 0.14$; model $ss = 33.21$, $df = 6$; error $ss = 197.11$, $df = 145$.
 † Stratum labels are as in Table 2.

tecting species have rarely been used until now. The probabilistic approach presented here (see also Nichols and Conroy 1996, Boulinier et al. 1998a,b, Nichols et al. 1998a, b) permits obtaining unbiased estimates of richness in year j with data from a single year. This method is generally applicable and permits assessment the state of the community of interest in the year of interest. This approach does not require knowledge of the exhaustive list of species in the entire pool: if the pool specified is representative of the entire pool of interest (where representativeness is assessed relative to the probability that a member of the pool is present in the locality of interest), then our estimator provides a good estimate of relative species richness. Second, the species pool used to compute relative richness is actually “user defined,” which permits one to address a wide variety of questions.

When using appropriate species pools, interpretations of the relative richness metric can be relevant to

the concept of “integrity” of ecological communities (Karr 1981, 1987, 1990, 1991, 1996, Karr and Dudley 1981), a concept developed in response to increasing concern for human impact on ecological systems. It is widely suggested that one of the main consequences of increasing human populations and activities is rapid loss of biological diversity (Forester and Machlis 1996), which poses a dangerous threat to the persistence and integrity of ecological systems (Karr 1987). Appropriate tools to assess levels of anthropogenic disturbance of these systems seem to be lacking (Karr 1987). J. R. Karr has championed the need for operational definitions of biological integrity, methods for measuring and estimating biological integrity, and biomonitoring programs designed to collect data relevant to biological integrity and to variation in integrity over time and space (Karr 1981, 1987, 1990, 1991, 1996, Karr and Dudley 1981).

A popular definition of “biological integrity” is that

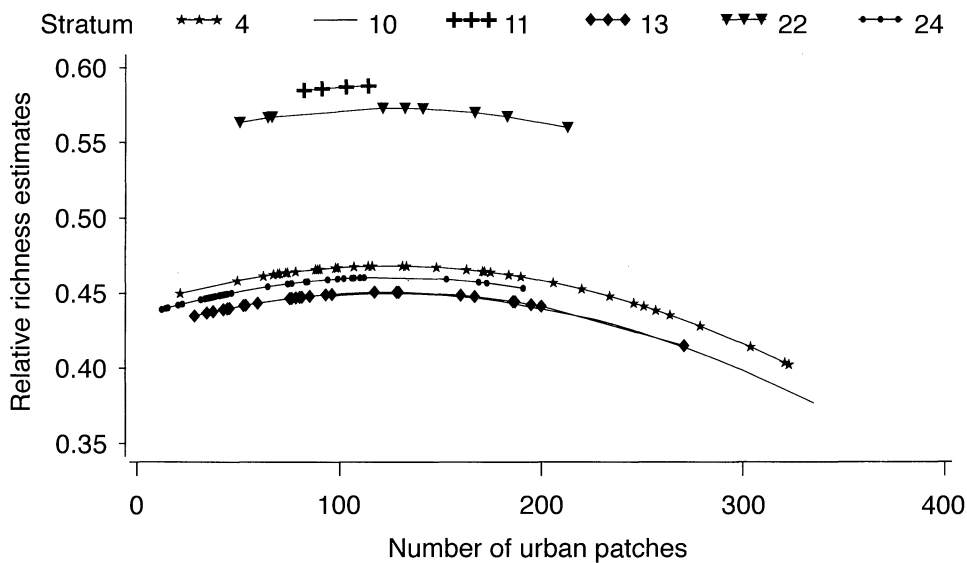


FIG. 6. Relationships among relative species richness (route-specific species pool), number of urban patches, and stratum. Estimates are made under the model with an additive effect of stratum and number of urban patches squared. Stratum labels are as in Fig. 1.

of Karr and Dudley (1981): "the capability of supporting and maintaining a balanced, integrated, adaptive community of organisms having a species composition, diversity, and functional organization comparable to that of natural habitat of the region." "Integrity implies an unimpaired condition or the quality or state of being complete or undivided; it implies correspondence with some original condition" (Karr 1996). We believe that this comparative nature of the integrity concept is important and that the relationship between attributes of a community of interest and attributes of "some least disturbed reference community" (Karr 1991) are quite relevant to assessing integrity. Species richness of local communities, considered for groups defined either taxonomically or ecologically, has been an important component in measures and indices of biological integrity (e.g., Karr, 1981, 1987, 1991, Kerans and Karr 1994, Harig and Bain 1998). Relative species richness (conditional on the original pool) is relevant to assessing integrity.

In addition to interpretations relevant to the concept of the "integrity" of ecological communities (Karr 1981, 1987, 1990, 1991, 1996, Karr and Dudley 1981), the relative richness metric is relevant to the question of community saturation. The question of a dependency of local species richness on regional richness has implications from theoretical and conservation viewpoints. This question has often been addressed by investigating the relationship between local and regional richness (Cornell 1993). However, Cresswell and Vidal-Martinez (1995) pointed out that regressions of local richness on regional richness contain an element of autocorrelation corresponding to the set of common species, which probably biases these analyses. They recommended using independent measures of local and regional richness (Cornell and Lawton 1992), which is a feature of the approach used here to estimate relative species richness.

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