Evolutionary Ecology Research, 2008, **10**: 987–1006

On the measurement of beta diversity: an analog of the species–area relationship for point sources

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ABSTRACT

Question: How can species–area relationships (SPARs) be studied in biotas where only data from isolated localities are available?

Data: The Breeding Bird Survey at a spatial scale of 10^2–10^3 km.

Analytic methods: I develop a method that involves numeric estimation of the shortest path connecting a set of localities and calculation of cumulative species richness (corrected for sample size) and distance along that path. The slope of the resulting species–distance relationship (SDR) is used as a measure of beta diversity.

Results: The slope of the SDR is insensitive to locality area and to inter-locality distance at the scales considered. It is, however, sensitive to the number of specimens per locality; in particular, the slope of the SDR declines as more specimens are included and is lowest when incidence data are used (i.e. all the specimens are included). The slope of the SDR is strongly correlated with and numerically similar to that of a corresponding SPAR. The slope of the relation between distance and similarity (measured as the Jaccard or Sørensen index) is also positively, but less strongly, correlated with the slope of the SPAR for these data.

Conclusions: The SDR is an analog for point sources of the SPAR. It estimates the SPAR slope more accurately than similarity metrics and sometimes just as precisely.

Keywords: Breeding Bird Survey, distance, fossil record, macroecology, paleoecology, sample size, similarity.

INTRODUCTION

Understanding the varying relationship between species diversity and geographic area is important in paleontology, not only because the fossil record provides a diachronic data set with which to test competing ecological hypotheses, but also for practical reasons. Early work on global biodiversity in the fossil record ran foul of sampling problems: broad-scale taxonomic diversity patterns covary with the area and volume of the sedimentary rock in which fossils are preserved (Raup, 1972), a point that has again been brought to prominence (e.g. Peters and Foote, 2001, 2002; Smith, 2001; Barnosky *et al.*, 2005; McGowan and Smith, 2008). This problem of

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covariation may be stated as follows: fluctuating amounts of preservational area amount to running up and down a species–area curve (or several such curves simultaneously) through time (Rosenzweig, 1997). Separating geographic (horizontal) from temporal (vertical) signals in the fossil record requires an understanding of how diversity scaled with space in different areas in the past. Normalizing past biodiversity by the available rock outcrop (Smith and McGowan, 2007) provides one potential way around the problem, but it would be useful also to examine directly the geographic scaling of diversity in individual time-planes. The most appropriate method is unclear.

The botanist Arrhenius (1921) first gave mathematical form to a modern species–area relationship (SPAR; also abbreviated SAR) in his work on islands in Stockholm's *skärgård*, or archipelago. SPARs have been subject to considerable scrutiny, which has aimed to clarify their biological basis (e.g. Preston, 1962a, 1962b; Coleman, 1981; Leitner and Rosenzweig, 1997; Hubbell, 2001), their consequences for macroecological pattern (Rosenzweig, 1995) and conservation (e.g. Brooks *et al.*, 1996; Kinzig and Harte, 2000), and their relationship to patterns in time (e.g. Rosenzweig, 1998; Hadly and Maurer, 2001; White *et al.*, 2006). Nested SPARs (e.g. Rosenzweig, 1995), in which samples of species are tabulated from increasingly larger contiguous areas, can often be expressed as power laws of the form $S = cA^z$, where S is species richness, A is area, and c and z are empirical constants. The exponent z describes not the absolute rate of species increase with area (Lomolino, 1989; Lyons and Willig, 2002), but rather how species richness scales with space. This scaling factor may be considered a measure of beta diversity (MacArthur, 1965; Connor and McCoy, 1979; Rosenzweig, 1995; Scheiner, 2004).[1]

The categorical distinction between these different aspects of diversity – species richness and its derivative with respect to space – is emphasized by the terms *inventory diversity* and *differential diversity*, respectively (Whittaker, 1972). Yet most measures that have been used for beta diversity do not explicitly address its spatial nature. Indeed, even Whittaker's (1960) original treatment is vague on this point. He defined beta diversity as $\beta = \gamma/\alpha$, where alpha diversity, α, is local or community diversity and gamma diversity, γ, is the species richness of the total landscape or entire environmental gradient. If the size of the landscape or the length of the gradient is kept constant, then beta diversity is spatially implicit, even if it is technically dimensionless. Most other measures of beta diversity are purely comparative metrics (see review in Koleff *et al.*, 2003) and do not refer to space at all (Vellend, 2001). A common one, Jaccard's (1912) index, may be expressed as $J = S_{A\cap B}/S_{A\cup B}$, where S is species richness and A and B are the sets of species found in (samples of) two communities. The similarity (J) of any two communities clearly depends in part upon their spatial proximity, so merely stating that they show a particular value of J is not especially meaningful. A more recent development is 'additive partitioning' (Lande, 1996), in which beta diversity is considered to constitute an additive rather than multiplicative link between α and γ, and to have the same units (Lande, 1996; Veech *et al.*, 2002; Olszewski, 2004; Veech, 2005). As Olszewski (2004, p. 385) recognized with respect to additive partitioning, without consideration of space, 'beta diversity should not be treated as a constant characterizing a region'.

Comparative measures, however, have the advantage that they may be applied to locality-based data, where nested SPARs may be difficult to estimate (Gray *et al.*, 2004). That is, they are useful in places like the fossil record where more complete biotic inventories are wanting.

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[1] MacArthur (1965, p. 528) related a steeper slope of the species–area curve to increased between-habitat diversity (i.e. beta diversity; ibid., p. 517).

Only one spatially explicit measure of beta diversity exists that makes use of locality-based data: the similarity–distance relationship, in which similarity (measured as the Jaccard index, for instance) tends to decline with distance as increasingly disparate habitats with different species compositions are sampled (e.g. Nekola and White, 1999; Green *et al.*, 2004; Horner-Devine *et al.*, 2004; Qian *et al.*, 2005). The relationship between similarity and distance may itself predict the scaling exponent z of the nested SPAR (Harte and Kinzig, 1997; Harte *et al.*, 1999), but this has not yet been examined at broad geographic scales.

In this paper, I explore a new spatially explicit metric for differential (beta) diversity in a large modern data set. The method makes use of locality-based data and so is applicable to both modern and fossil biotas. I test its sensitivity to potentially confounding factors, including locality size (area) and inter-locality distance. I examine its empirical relationships with species-accumulation curves and with distance–similarity metrics and SPARs and discuss its conceptual kinship with the latter. Finally, I discuss potential applications to the fossil record and the unique difficulties and opportunities that it may offer.

METHODS

Data sources

The data were culled from the North American Breeding Bird Survey (hereafter, BBS), available by anonymous ftp at ftp://ftpext.usgs.gov/pub/er/md/laurel/BBS/DataFiles/. The database includes abundance data for birds encountered annually on the thousands of permanent survey routes (Peterjohn and Sauer, 1993). On each survey route (hereafter, 'locality'), observations are recorded at each of 50 regularly spaced stops. For this study, abundance data were taken for the year 2004 from represented localities in four comparably sized geographic regions: the area south of Lakes Michigan and Erie, the Gulf Coastal states, the northern Texas/Oklahoma Panhandle, and the northern Great Plains (Fig. 1). Each of these areas falls within a single division (hereafter, 'region') in Bailey's classification of ecoregions (Bailey *et al.*, 1994): the hot humid continental, humid subtropical, subtropical steppe, and temperate steppe regions, respectively. The only localities excluded were those judged unacceptable by the BBS management and, for the temperate steppe region, localities in the Black Hills, as these present too significant an elevational range in comparison with the other regions. The total number of localities included per region was 104, 85, 46, and 28, respectively.

The BBS data reflect stringently controlled sampling effort: the duration of observation, time of observation, and season of observation are all controlled for, and should any of these factors, or the weather, deviate too strongly from established norms, the data are considered unacceptable. The number of observed individuals (sample size), of course, still varies among localities. Sample size per locality in the four regions averages 1019 ± 34 (1 standard error), 700 ± 26, 714 ± 73, and 934 ± 134 individuals (order as in previous paragraph). The data were not culled taxonomically.

A species–distance relationship: estimation and form

The new method explored here involves estimation of the path of minimum length connecting a set of (contemporaneous) localities and then calculation of (expected) cumulative species richness and distance along the path. The relationship between species

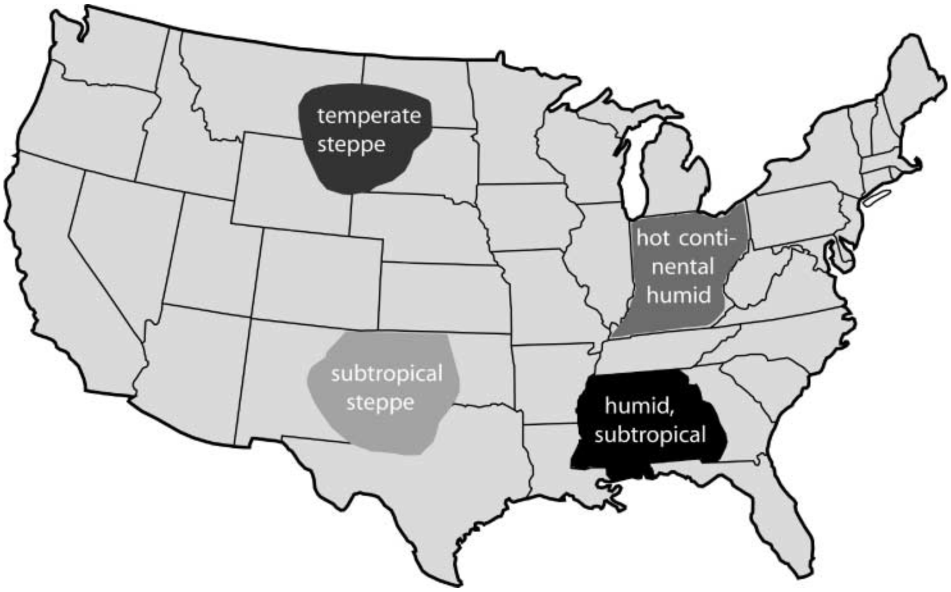

Fig. 1. Four regions in the United States in which Breeding Bird Survey routes (= localities) were examined. Each region falls within a single ecoregion division in Bailey and colleagues' (1994) classification.

richness and distance is what I will call the species–distance relationship (SDR) in the remainder of this contribution. All data analysis and graphics production were done in *R*, v2.3.1 (R Core Development Team, 2005). The basic *R* script is available from the author upon request. A compiled *C* version and code will also be available.

There are $m!/2$ possible paths (direction unimportant) connecting a set of localities, and finding the shortest of these is the 'travelling salesman problem'. A numerical solution is provided by simulated annealing (Metropolis *et al.*, 1953; Kirkpatrick *et al.*, 1983; Press *et al.*, 2001). Once the shortest path has been found, diversity is computed from a matrix of species abundance or incidence data (*sensu* Colwell *et al.*, 2004). An $n \times m$ matrix, A, is constructed, where n is the total number of species known from all selected localities, and m is the number of localities. The order of localities in the matrix reflects their order on the minimum path, and each element A_{ij}, $i = 1 \ldots n, j = 1 \ldots m$, indicates the number of individuals of species i in locality j.

Because species richness depends in part on sample size, abundance data may be adjusted as follows. The total number of individuals per locality, N_j, is given by $N_j = \Sigma_i A_{ij}$. The locality with the lowest number (x) of individuals is chosen as a 'baseline'. In the framework of individual rarefaction, the expected contribution to species richness of species i at locality j is $1 \cdot (1 - q_{ij}) + 0 \cdot q_{ij}$, where q_{ij} is the probability of finding no individual of species i at locality j given x (i.e. each species' contribution to richness is 1 times the probability it is found). q_{ij} is governed by the hypergeometric distribution:

$$q_{ij} = \binom{N_j - A_{ij}}{x}\binom{N_j}{x}^{-1},$$

where $N_j - A_{ij} \geq x$; else, $q_{ij} = 0$ (one cannot fail to observe the species). The procedure thus far is like rarefaction (Hurlbert, 1971; Simberloff, 1972; Heck *et al.*, 1975). The probability that any particular species i has been sampled in at least one locality up to j along the path is then given by:

$$C_{ij} = 1 - \prod_{k=1}^{j} q_{ik}.$$

This approach is formally similar to those of Cam *et al.* (2002) and Colwell *et al.* (2004). However, I have assumed homogeneous detection probabilities at the level of the individual organism only; that is, differences in local species abundance remain. Noting again that a species' contribution to richness is 1 times the probability that it is found in the subsample, expected cumulative species richness at locality j is given by $S_j = \Sigma_i C_{ij}$. This statistical correction was checked by randomization experiments.

For the BBS data, a number of localities was selected at random from a region. Distances between localities were computed using associated latitude/longitude data assuming a spherical Earth with a radius of 6371 km. The minimum path was estimated, and cumulative distance and richness were calculated, then log-transformed. Least-squares regression was used to find the best-fit linear relationship (excluding the first locality, where distance is assumed to be 0 km and ln(0) is not defined). It is the slope of this line, z_{SDR}, that I call beta diversity in the remainder of this paper. For a given sampling regime (see below), this procedure was repeated 100 times in each region to generate a sample of beta diversity.

Residuals about the SDR were examined to test the linearity of the relationship and therefore the appropriateness of the regression model. I calculated residuals on every data point for every path in a region (under a particular sampling regime) and then binned them on the basis of the associated cumulative distance: (0 km, 100 km], (100 km, 200 km], etc. If the SDR is systematically non-linear, these mean residuals should deviate from 0 as a function of distance.

Species accumulation curves

Species accumulation curves were also calculated for comparison with the SDR. For each set of localities for which the minimum path was estimated above, calculated inter-locality distances along the path were retained, but species composition was randomized by shuffling the full species abundance vectors among localities. Linear regression was again performed for each path, and residuals calculated and binned, as described above. If inter-locality distances were precisely equal along the path, then these randomized data should be mathematically equivalent to species accumulation curves, which are thought not to follow a power law (Ugland *et al.*, 2003; Colwell *et al.*, 2004; Gray *et al.*, 2004). As with species–area curves calculated from non-nested small areas (Rosenzweig, 1995; Scheiner, 2003), it is expected that diversity will rise more quickly when the species of distant localities are encountered prematurely. Because diversity rises more quickly at first than on the minimum path, then rises more slowly thereafter, the relationship between cumulative diversity and distance may be convex-up in log-log space.

Sensitivity analyses

Analyses were conducted to establish how sensitive the slope of the SDR is to potentially confounding factors. One factor that might affect the slope of the SDR is inter-locality distance along a path, or, equivalently, point density in two-dimensional space (Harte and Kinzig, 1997). As distance between localities increases, it is expected that species with more restricted distributions are increasingly likely to be missed. Maximum species richness will drop, and the slope of the SDR may be depressed. The number of localities per path was therefore varied from 5 to 20 in increments of 5, resulting in a two-fold variation in inter-locality distance.

The size of individual localities might also affect the slope of the SDR (cf. Harte and Kinzig, 1997). As Cam *et al.* (2002) noted, each individual stop along a particular route of the BBS may be considered as a small area, a circle with a radius of 0.4 km (i.e. ~0.5 km^2). The number of stops per locality from which observational data were accumulated was varied from 10 to 50 (covering an area of 5–25 km^2) in increments of 10 to examine whether a five-fold difference in locality size had an effect on the slope of the SDR. The number of individuals assumed to be observed per locality (x) was held constant regardless of the number of stops in order to avoid conflating increased area with larger sample size (see also Cam *et al.*, 2002). Thus, x is necessarily very small because when data from only 10 localities are compiled, only about one-fifth of the observations are included.

Finally, the number of individuals (or specimens) per locality might have an effect on the slope of the SDR. In this final set of sensitivity analyses, data from all 50 stops for a locality were combined, but sample-size corrections were made under the assumption that only x individuals were observed, where x was varied in increments of 50, beginning with about 50 individuals and increasing to the maximum possible value in a region, which is given by $\min(N_j)$: 345, 288, 272, and 312 for the hot continental humid, subtropical humid, subtropical steppe, and temperate steppe regions, respectively. Additionally, the SDR was estimated using incidence data only (i.e. assuming all individuals were observed, making no correction for sample size).

Other spatially explicit metrics of beta diversity

For each set of localities chosen, pairwise comparisons were used to generate a sample of similarity values based on two commonly used indices, the Jaccard index (defined above) and Sørensen's (1948) index, which may be written $2S_{A\cap B}/(S_A + S_B)$. Least-squares regression of the natural logarithm of similarity on both distance (in km) and the natural logarithm of distance was used to estimate the decay of similarity with distance. The slope ($\times -1$) was then recorded as an alternative measure of beta diversity. Sensitivity of these metrics to changing locality density and to a combination of locality size and individual sample size was examined (but because similarity indices are calculated using raw data, it is not possible to distinguish the effects of the last two).

Finally, the density of localities within each region suggested that reasonable species–area curves might be constructed. These were generated by dividing each region into a $c \times c$ grid of cells, randomly selecting a starting cell, then expanding that cell as an ever larger sampling quadrangle until the whole grid was included. Area was calculated as $\int_{\phi_1}^{\phi_2}\int_{\theta_1}^{\theta_2} r^2 \cos(\theta) d\theta d\phi$ assuming a spherical Earth, where values of θ (latitude) and ϕ (longitude) bound each sampling quadrangle and r is Earth's radius, as given above. This procedure was repeated 100 times for each region to generate a sample of SPARs. To examine the potential effect of grain size (e.g. Palmer and White, 1994) in these data, c was varied from four to eight, resulting in 16 to 64 cells. Three possible effects might invite caution in the interpretation of these SPARs. First, there may be an edge effect, because the regions examined are not particularly square; this effect should be reduced because the computer was instructed to record a new data point only when new localities actually were encountered. Second, 64 significantly exceeds the number of localities in the the temperate steppe; thus, the 8×8-cell grid for this region might not produce reasonable results. Finally, no attempt was made to correct for the number of individuals per cell (cf. Cam *et al.*, 2002).

RESULTS

Form of the SDR

The relationship between expected cumulative species richness and cumulative distance along the path of minimum length is close to linear in logarithmic space, as seen in three typical sets of 20 localities in the hot humid continental region (Fig. 2A, B). Small sigmoids or steps are often present in individual SDR graphs, as they also are in SPARs (Scheiner, 2003, and herein). Mean residuals are plotted as a function of distance in Fig. 3A. Residuals appear to average close to 0 irrespective of distance, suggesting that a linear model is appropriate for the data. The strongest deviations appear at the beginning, where sample size is lower (relatively few of the second localities are located <100 km from the first). Pearson's correlation coefficient r may be used as a simple goodness-of-fit metric. Mean r for all paths was 0.97–0.98.

The slope of the SDR varies among the different regions. Values in the subtropical humid and hot humid continental regions are closely comparable, with means close to 0.20 and relatively small standard deviations (Fig. 4, solid lines; Table 1). The subtropical and temperate steppe regions show different distributions, which have higher means (around 0.30) and standard deviations. Both sets of values, however, are within the range of variation seen for z-values in modern SPARs (e.g. Rosenzweig, 1995; see also below).

Species accumulation curves are clearly different from the SDR. The fit of a linear model to the data is poorer; although mean r is still high (greater than 0.9), as expected of a cumulative function, it is always less than that of the corresponding SDR. The steep early rise and subsequent flattening of diversity is seen in plots of residuals, which are predominantly positive in the early middle of the paths and predominantly negative near the beginning and end (Fig. 3B; recall that regression was performed on log-transformed data).

Sensitivity of the slope of the SDR

A four-fold variation in point density resulted in a two-fold variation in mean inter-locality distance, from roughly 100 km to 200 km (Table 1). For comparison, a 1° latitudinal separation of two points on the same meridian amounts to ~111 km. The general character of the distributions is unchanged (Fig. 4): the tighter distributions of the humid regions remain tighter than those of the steppe regions, and the steppe regions retain higher means and standard deviations (Table 1). The standard deviation of beta diversity increases with decreasing point density in each region, but at the scale considered, mean beta diversity does not decrease (Fig. 5A), as might be expected. It is noteworthy, however, that the difference between the mean and median of beta diversity increases slightly with decreasing

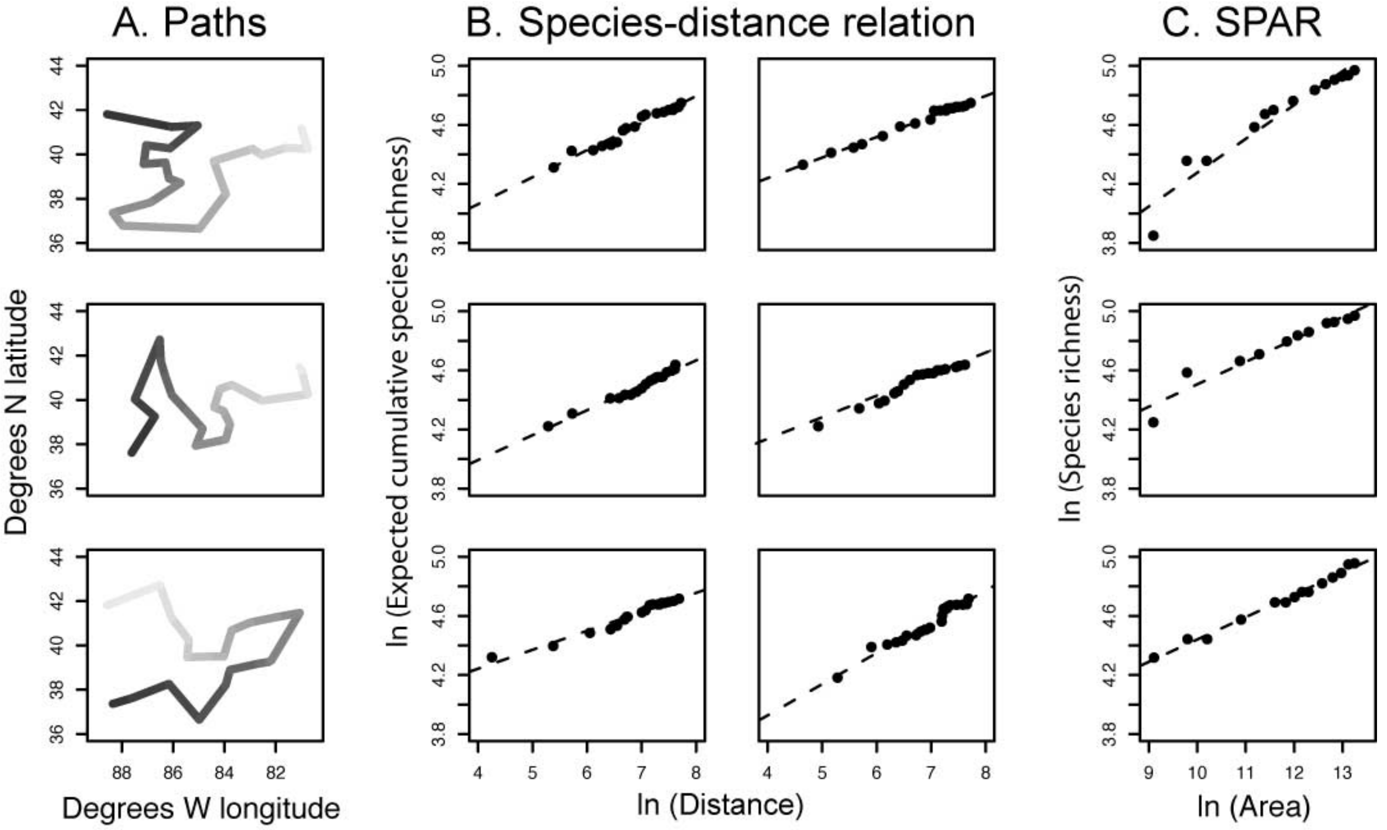

Fig. 2. (A) Three sample minimum paths, calculated for 20 localities each, in the hot continental humid region; ‘forward’ is defined as light to dark. (B) Cumulative diversity (rarefied for each locality to the minimum sample size for localities on the path) and distance (km) as measured in forward (left) and reverse (right) directions; distance in km. (C) Three species–area curves calculated by expanding sampling area in an 8 × 8-cell grid; area in km^2. The least-squares regression lines (dashed) are shown.

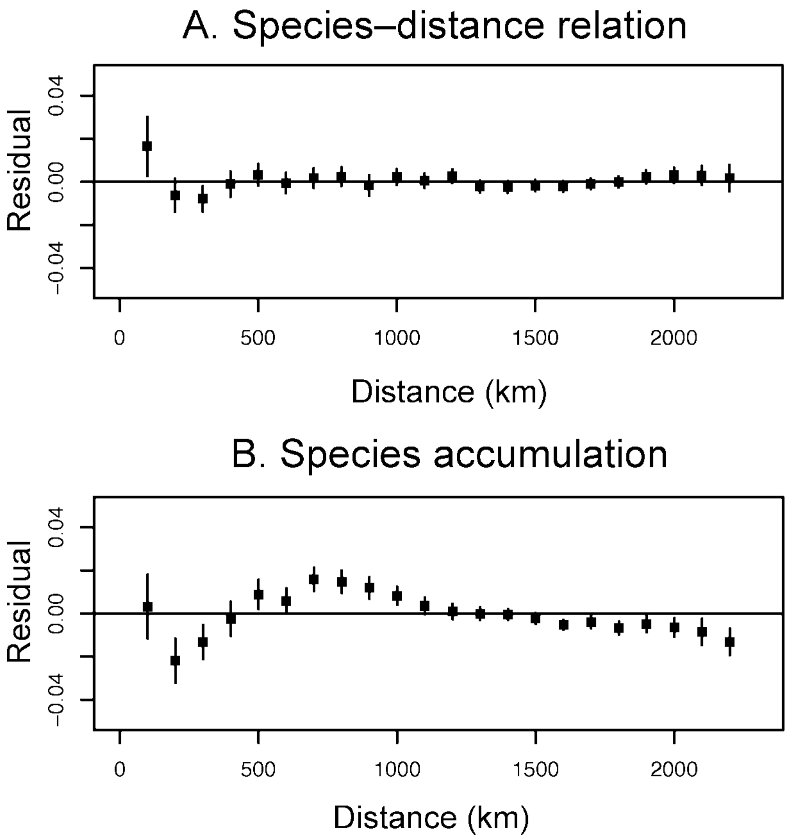

Fig. 3. (A) Residuals about the SDR least-squares regression lines as a function of distance. (B) Residuals about the least-squares regression lines in the same region as calculated from localities with shuffled species composition (see text). Data come from the same 100 sets of 20 localities in the hot humid continental region (with all 50 stops per locality). Residuals from all paths under this sampling regime were combined and binned into 22 distance classes: (0 km, 100 km], (100 km, 200 km], etc. Shown are the mean residuals for each class, with lines ± 2 standard errors.

point density (Table 1), reflecting a tendency towards right-skewness (Fig. 4). This is possibly an indication that slopes are declining.

A five-fold difference in individual locality size results in only a slight decline in mean beta diversity (Fig. 5B). Indeed, in most regions examined, beta diversity calculated from the largest localities (all 50 stops included) still lies within two standard errors of mean beta diversity calculated from the smallest (only 10 stops included). Nevertheless, the consistency of the small decrease in mean beta diversity seen in all four regions and from one locality size to the next suggests that the decrease is real. That the effect is small is particularly noteworthy given that BBS routes resemble the elongate sampling areas theorized by Harte *et al.* (1999) and documented by Condit *et al.* (1996) to have more species than square areas of the same size. That is, if locality area were increased more equidimensionally, it is expected that the effect on beta diversity would be diminished. (Beta diversity is higher here because low sample sizes were necessarily assumed: see Methods and below.)

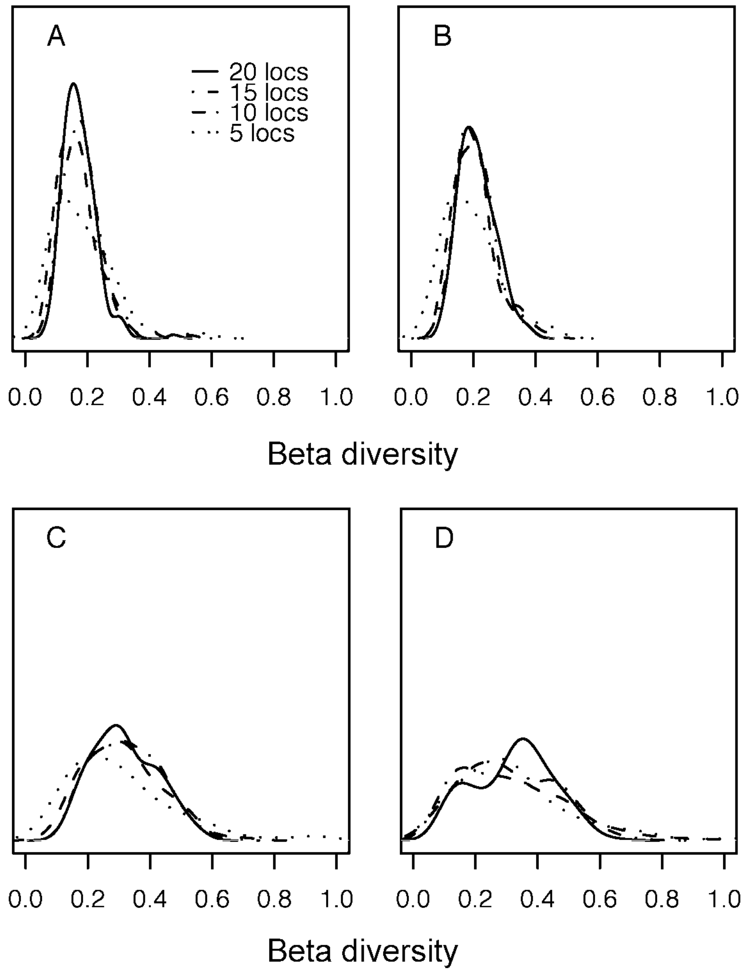

Fig. 4. Distributions of beta diversity estimates, based on the slope of the SDR, for four geographic regions, smoothed using a Gaussian kernel. (A) Hot humid continental; (B) subtropical humid; (C) subtropical steppe; (D) temperate steppe. The distributions are each based on 100 randomly selected sets of localities, where set size was varied from 5 to 20 localities.

In all four regions, beta diversity is markedly elevated in all cases when the minimal x is assumed and decreases as x is increased (Fig. 5C). At first, beta diversity decreases fairly rapidly, but after a sample size of 150 to 200 individuals per locality is reached, it decreases more slowly. It is possible that beta diversity approaches an asymptote, but this is not demonstrated. The similarity between the humid regions and between the steppe ones is still present in these analyses. Beta diversity is lowest when all individuals are assumed to have been observed (that is, when incidence data are used); for 10-locality paths, mean beta diversities of 0.152, 0.186, 0.300, and 0.294, respectively, were calculated for the hot humid continental, subtropical humid, subtropical steppe, and temperate steppe regions (cf. Table 1). However, sample size also differs among localities when incidence data are used, and the effects of varying intra-path sample size were not otherwise explored. Using incidence data,

Table 1. Statistical summary of the slope of the species–distance relationship (SDR) for Breeding Bird Survey routes in four regions (see text), with varying point density: hot continental humid, subtropical humid, subtropical steppe, and temperate steppe

	No. routes	Mean (D)	Mean (β)	Median (β)	S.D. (β)	Observed range (β)
Hot continental humid	20	107.4	0.174	0.166	0.052	0.071–0.479
	15	120.5	0.179	0.175	0.056	0.058–0.339
	10	143.1	0.169	0.160	0.068	0.057–0.533
	5	200.1	0.183	0.165	0.098	0.020–0.592
Subtropical humid	20	95.8	0.212	0.208	0.058	0.103–0.394
	15	108.2	0.205	0.197	0.058	0.068–0.386
	10	128.1	0.204	0.196	0.069	0.087–0.458
	5	176.2	0.192	0.179	0.089	0.022–0.486
Subtropical steppe	20	99.2	0.318	0.308	0.102	0.120–0.567
	15	117.8	0.326	0.320	0.109	0.137–0.630
	10	137.2	0.312	0.303	0.119	0.084–0.705
	5	199.9	0.308	0.272	0.174	0.048–0.966
Temperate steppe	20	100.3	0.322	0.336	0.126	0.092–0.652
	15	117.7	0.307	0.293	0.148	0.082–0.711
	10	144.3	0.318	0.290	0.167	0.057–0.949
	5	196.8	0.322	0.291	0.185	0.035–1.088

Note: The slope of the SDR is considered a measure of beta diversity, β. Mean distance (D) in kilometres is given for path comparison.

the same similarity between the steppe regions was recovered; similarly, both humid regions showed lower beta diversity, with values being slightly higher for the subtropical humid region.

The effect of individual sample size on the slope of the SDR is readily comprehended. When large numbers of individuals are assumed to have been observed in a locality (when x/N_j is high), most species' contributions to richness ($1 \cdot C_{ij}$) rise to >0.9 within two localities of their first appearance (results not shown). As x decreases to arbitrary and artificially low values, individual species – especially less common ones – make smaller contributions to richness when they first appear. Thus, richness is depressed near the beginning of a path, and the path must pass through many localities before individual species' contributions rise to 1. The slope, in consequence, is higher.

Comparison of SDR with other metrics

The slope of the relationship between the similarity and distance varies somewhat differently from that of the SDR, whether the slope is calculated from semi-log or log-log data, i.e. ln(similarity)–D or ln(similarity)–ln(D) (Table 2; Fig. 6A). This is true regardless of whether the Jaccard or Sørensen index is used as a measure of similarity. Most saliently, the quantitative similarity of beta diversity estimates in the steppe is not clearly seen in the similarity–distance approach. The subtropical steppe stands out as having distinctly higher beta diversity than the other regions. In all cases, beta diversity so measured is equal to or

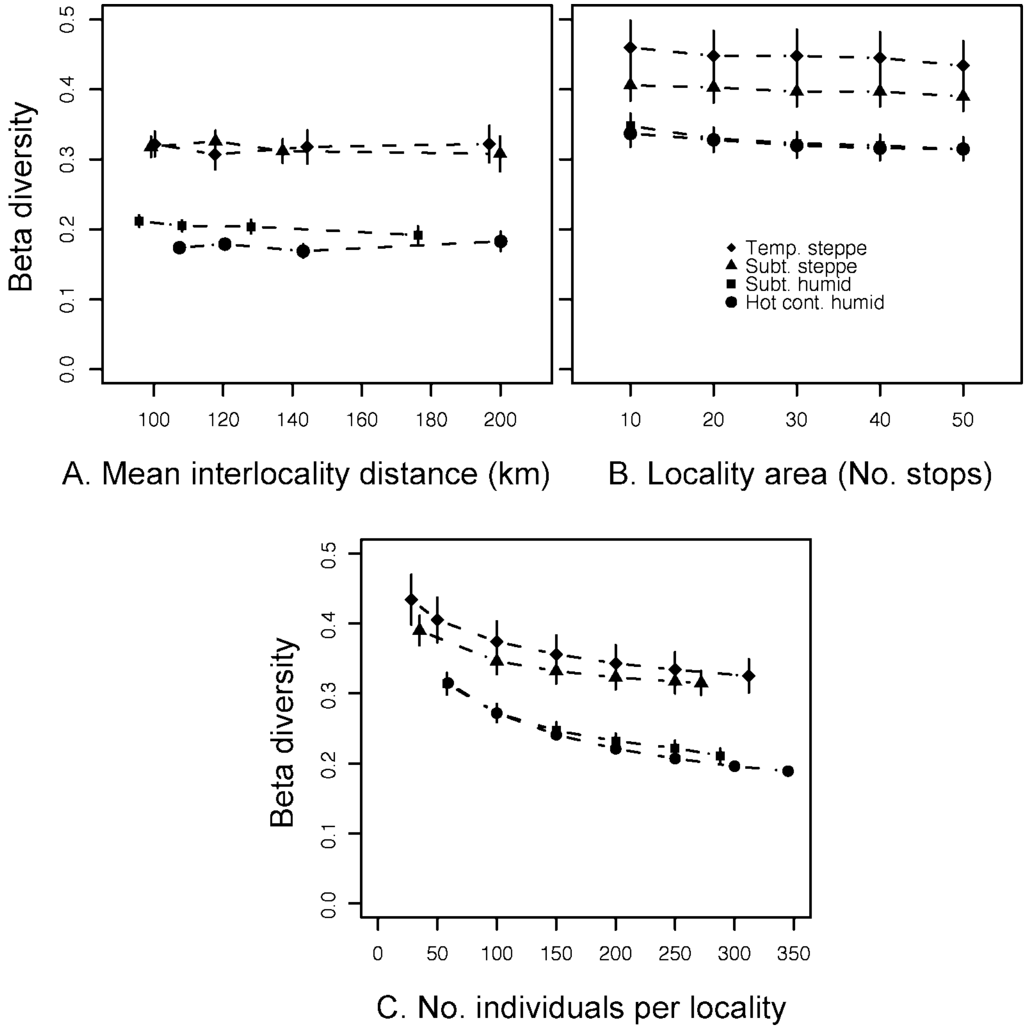

Fig. 5. (A) Relationship between point density (inter-locality spacing) and mean beta diversity (slope of the SDR) for all four regions. Data from all 50 stops per locality (route) were used; correction for locality sample size (rarefaction) was made only within a path. (B) Relationship between locality area (number of stops included) and mean beta diversity for all four regions. The number of individuals per locality was rarefied down to the largest possible value for use with localities of any size. (C) Relationship between locality sample size and mean beta diversity for all four regions. Data from all 50 stops per locality (route) were considered here, only the assumed number of individuals per locality (x) was varied. In all three graphs, the vertical bars are ± 2 standard errors.

lower than the slope of the respective SDR. The standard deviation of beta diversity is much lower than for the SDR when 20 localities are sampled (cf. Tables 1, 2).

Mean beta diversity, measured using similarity metrics, is not obviously sensitive to point density, although in two cases the 5-locality samples had somewhat higher (hot continental humid) or lower (temperate steppe) beta diversity (Table 2). As with the SDR, a decrease in point density produces an increase in standard deviation of beta diversity, but that increase

Table 2. Statistical summary of beta diversity calculated as the slope of the similarity–distance relationship (log-log) for Breeding Bird Survey routes in four regions (see text), with varying point density: hot continental humid, subtropical humid, subtropical steppe, and temperate steppe

	No. routes	Mean (β)	Median (β)	S.D. (β)	Observed range (β)
Hot continental humid	20	0.107	0.106	0.024	0.050 to 0.181
	15	0.109	0.107	0.037	0.028 to 0.216
	10	0.107	0.100	0.044	0.014 to 0.227
	5	0.131	0.121	0.103	−0.142 to 0.417
Subtropical humid	20	0.085	0.082	0.026	0.033 to 0.160
	15	0.087	0.083	0.034	−0.009 to 0.163
	10	0.086	0.082	0.046	0.005 to 0.269
	5	0.079	0.083	0.097	−0.301 to 0.371
Subtropical steppe	20	0.319	0.316	0.048	0.209 to 0.441
	15	0.321	0.327	0.064	0.152 to 0.464
	10	0.307	0.310	0.082	0.075 to 0.476
	5	0.316	0.310	0.168	−0.034 to 0.775
Temperate steppe	20	0.226	0.228	0.033	0.110 to 0.303
	15	0.230	0.229	0.049	0.126 to 0.341
	10	0.229	0.231	0.084	−0.028 to 0.403
	5	0.194	0.197	0.137	−0.222 to 0.556

Note: Similarity was calculated as the Jaccard index, *J*; similar results were obtained using the Sørensen index. All β values are the slope of the similarity–distance relationship × −1.

is much greater than for the SDR (cf. Tables 1, 2). The standard deviation for 5-locality samples is four times that of 20-locality samples, and the difference in standard deviation between the SDR and similarity metrics mostly disappears (Table 2). This strong response of standard deviation is expected, because similarity metrics are not cumulative and their effective sample size is related to the square of locality number: the number of unique pairs given m localities is equal to $(m^2 - m)/2$. There is little or no tendency towards right-skewness (Fig. 6A; Table 2), as seen in the SDR.

The data also suggest that sample size and/or locality area has a fairly strong effect on beta diversity as measured using similarity metrics. In the hot humid continental region, with 10 localities per sample, estimated beta diversity decreases regularly from 0.15 to 0.11 as locality size increases from 10 to 50 stops and average sample size increases from 183 to 1019 individuals. In the subtropical steppe, the decrease is from 0.38 to 0.31 over the same locality size interval; in the temperate steppe, it goes from from 0.28 to 0.23. Beta diversity in the subtropical humid region, however, showed almost no change. For further studies of the effects of sample size on the Sørensen index, see Wolda (1981).

Species–area relationships (SPARs) calculated from the same data are also nearly linear in logarithmic space, although small-scale sigmoids and steps are sometimes apparent (Fig. 2C). Beta diversity, measured as the slope of the SPAR, is similar in the humid regions and in the steppe (Fig. 6B). The humid regions tend to have tighter distributions with smaller means (between 0.15 and 0.20) than the steppe regions, which have higher standard deviations and means between 0.30 and 0.35 (Table 3). The fineness or coarseness of the

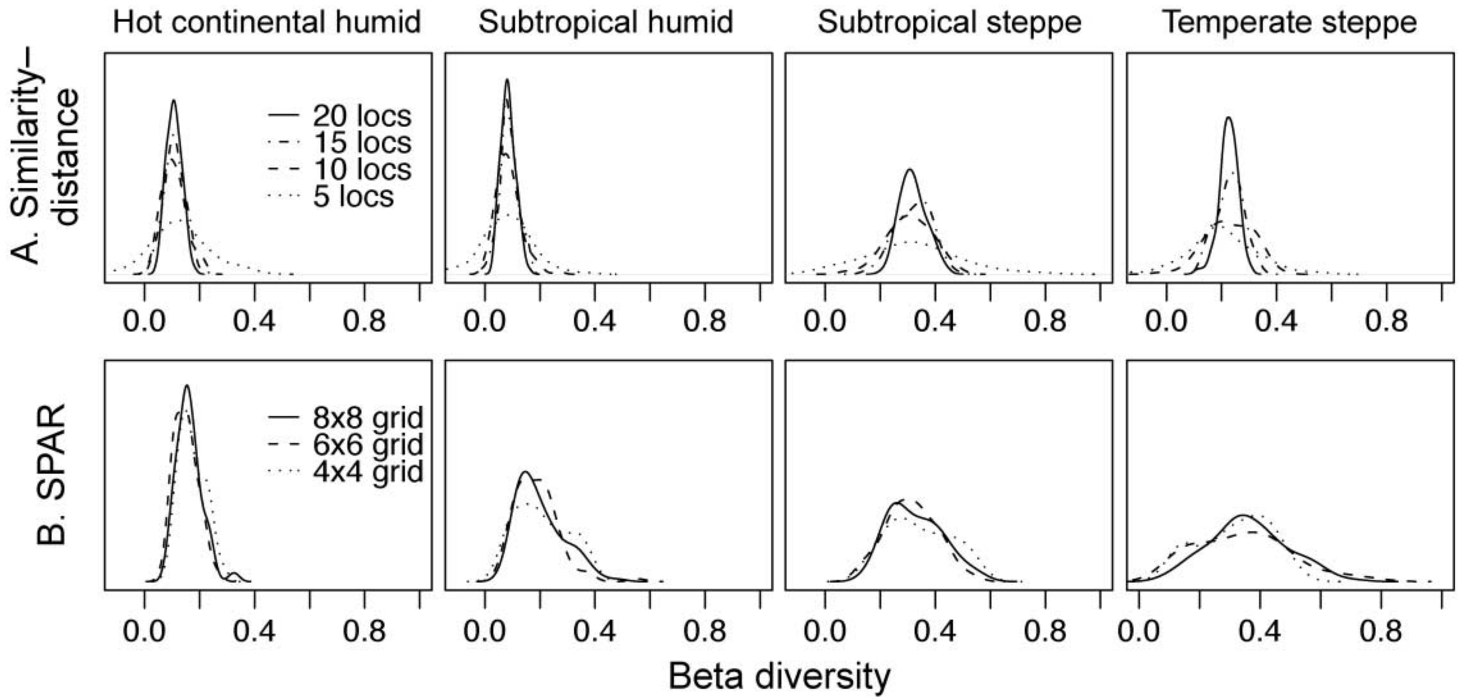

Fig. 6. (A) Distributions of beta diversity estimates calculated from the decay of similarity (measured by the Jaccard index) with distance in log-log space, smoothed using a Gaussian kernel. The sets of localities used for each estimate are the same as those used for the SDR estimates. For statistical summary, see Table 2. Results based on the Sørensen index are comparable. (B) Distribution of beta diversity estimates calculated as the slope of the SPAR, smoothed using a Gaussian kernel. For statistical summary, see Table 3.

Table 3. Statistical summary of the slope of the species–area relationship (SPAR) for Breeding Bird Survey routes in four regions (see text), with varying grain size: hot continental humid, subtropical humid, subtropical steppe, and temperate steppe

	No. cells (c)	Mean (β)	Median (β)	S.D. (β)	Observed range (β)
Hot continental humid	4	0.173	0.163	0.047	0.087–0.286
	6	0.150	0.150	0.043	0.061–0.273
	8	0.162	0.154	0.046	0.078–0.334
Subtropical humid	4	0.207	0.186	0.094	0.058–0.382
	6	0.187	0.180	0.078	0.064–0.555
	8	0.201	0.178	0.085	0.079–0.481
Subtropical steppe	4	0.343	0.331	0.114	0.155–0.568
	6	0.313	0.319	0.092	0.136–0.534
	8	0.328	0.322	0.098	0.151–0.571
Temperate steppe	4	0.318	0.332	0.115	0.110–0.517
	6	0.344	0.344	0.155	0.106–0.766
	8	0.362	0.350	0.128	0.095–0.709

Note: The slope here is considered a measure of beta diversity, β. Number of cells indicates how finely the grid ($c \times c$) was drawn over the study area. In the temperate steppe, the total number of localities is considerably smaller (28) than the number of cells in the 8×8 grid, making that estimate less reliable.

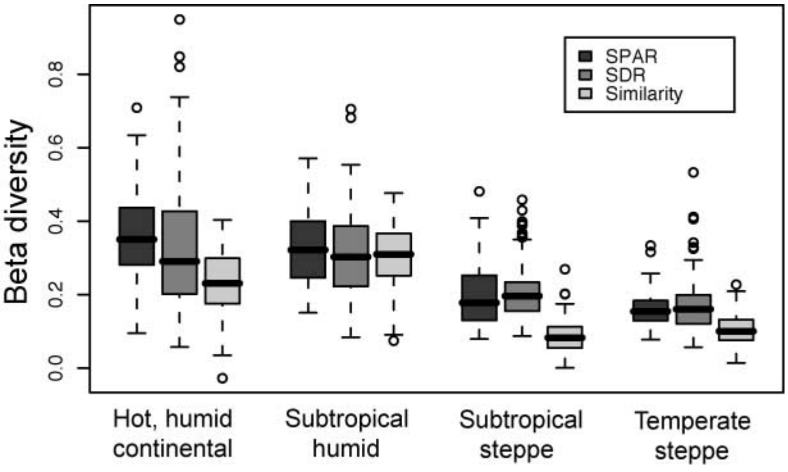

Fig. 7. Comparisons of beta diversity estimates based on three methods in four regions. The SPAR estimates are taken from the 8×8-cell grids (Table 3); the SDR estimates are taken from the 10-locality paths (Table 1), as are the log-log Jaccard estimates (Table 2).

grid used to estimate the SPARs has no strong or consistent effect on the mean or standard deviation of beta diversity estimates (cf. Palmer and White, 1994), except perhaps in the temperate steppe, where the 8×8 grid is probably overly fine, given the number of localities available.

The SPAR distributions are closely approached by those of corresponding SDRs (Fig. 7). Under both methods, the humid regions have means between 0.30 and 0.35, with higher standard deviations, and the steppe regions have means between 0.16 and 0.20, with lower standard deviations. Under both, the subtropical humid region always shows slightly higher beta diversity than the hot continental humid region. Mean SDR and SPAR estimates of beta diversity are also highly correlated. Using a linear regression model $\beta_{\mathbf{SPAR}(c)} \sim \beta_{\mathbf{SDR}(m)}$, where c is the fineness of the $c \times c$ grid and m the number of localities subsampled, the model slope takes on values of 1.10–1.29 for any c and m, regardless of whether incidence or abundance data are used; all combinations are significant, with $P < 0.01$ for all but two combinations, despite the low sample size (only four regions are being compared). The lowest slopes, all ~1.1, are found for $\beta_{\mathbf{SPAR(8)}} \sim \beta_{\mathbf{SDR}(m)}$.

The slope of the similarity–distance relation (β_J or β_S, using the Jaccard or Sørensen index, respectively) is also positively correlated with that of the SPAR, but the correlation is weaker. P-values for the linear regression model $\beta_{\mathbf{SPAR}(c)} \sim \beta_{J(m)}$ are not less than 0.1 and average ~0.15. Similar results obtain using β_S. The SDR slope, then, more closely approximates the SPAR slope than similarity–distance metrics (Fig. 7): the latter are less accurate than the SDR, and although they are more precise when many localities are included, this precision is matched by the SDR when fewer localities are included.

DISCUSSION

Differential (beta) diversity is one of the fundamental properties of species richness. It is of theoretical interest in its own right and of practical consequence in the fossil record (e.g. Rosenzweig, 1997; Whittaker *et al.*, 2001; Lyons and Willig, 2002; Willis and Whittaker, 2002; Barnosky *et al.*, 2005). Yet, existing metrics for beta diversity that treat it as a spatial rate or other derivative are few. Moreover, many data sets – most notably in the fossil record, but also in less well-known modern biotas like the deep-sea (Gray *et al.*, 2004) and tropical rainforests (Condit *et al.*, 2002) – consist of counts from geographically restricted areas (i.e. localities). While in well-known biotas a species–area relationship (SPAR) could be a useful way to understand the spatial scaling of diversity, comprehensive biotic surveys of the sort required to produce nested SPARs are often impractical (Harte *et al.*, 1999). Only one metric, the slope of the similarity–distance relationship, has been applied with much success to locality-based data (Nekola and White, 1999; Condit *et al.*, 2002; Poulin, 2003; Green *et al.*, 2004).

The additive partitioning of diversity (Lande, 1996; Veech *et al.*, 2002; Olszewski, 2004) shows much promise in permitting diversity comparisons among sample classes. However, 'beta' diversity in the additive framework does not explictly describe change in space (nor was it intended to). Diversity itself has multifarious aspects, but they deserve different names to avoid confusion, and since beta (differential) diversity was originally conceived to be a bridge between alpha and gamma (inventory) diversities that describes change in space, it makes sense to retain the term *beta diversity* for that differential metric. I would prefer to refer to the various levels of diversity in the additive framework simply as (first, second, etc.) *diversity partitions*.

The species–distance relationship (SDR) explored here may provide an alternative. The SDR and SPAR have quantitatively similar and highly correlated slopes, when examined in the Breeding Bird Survey data on a scale of 10^2–10^3 km, suggesting that these slopes are measuring the same property, which has previously been equated with beta diversity in the SPAR framework (e.g. MacArthur, 1965; Rosenzweig, 1995). Significant (100%) increases in inter-locality distance have no evident effect on the mean slope of the SDR, a fact that may be important in the fossil record, where the spacing of samples is largely controlled by geological factors extrinsic to study design. Yet, it is expected that much larger increases in locality spacing may well depress beta diversity, possibly by 'hopping over' habitats and species in between localities (Harte and Kinzig, 1997). Thus, very large differences in inter-locality spacing should be avoided until this effect is better characterized. Also important *vis-à-vis* the fossil record is the apparent resilience of the SDR slope to differences in locality size, for the exact geographic area represented by any given fossil assemblage will probably always be inaccessible. As with inter-locality distance, however, locality size is expected to have an effect (Harte and Kinzig, 1997), and in this study a small influence was observed. It remains to be determined at exactly what scale it begins to exert a significant influence. There may exist an optimal locality size for a given mean inter-locality distance and organism size.

The SDR can be considered an analog for point sources of the mainland, nested SPAR. Both seem to take the form of a power law. Both sample space and diversity cumulatively, and in a non-random fashion [unlike species accumulation curves (Gray *et al.*, 2004)]. Species accumulation curves (with randomized order) along a path are analogous in the SDR framework to accumulating small areas at random within a larger region; in both instances, convex-up curves in log-log space, which intersect the corresponding SDR or SPAR only at the beginning and end, are expected (cf. Wilson and Shmida, 1984; Rosenzweig, 1995; Scheiner, 2003). With SDRs, a curve is the spatial sampling universe, while for SPARs a plane is; both simplify the landscape by ignoring topography. Further application of the SDR may well result in additional similarities with SPARs, such as higher slopes or other mathematical relationships at smaller geographic scales, although such fine-scale patterns may seldom be accessible in the fossil record. A theoretical rather than intuitive explanation for their similarity, however, remains to be worked out. In other words, what is the expected relationship between $z_{\mathbf{SPAR}}$ and $z_{\mathbf{SDR}}$?

The BBS data were selected in part because they probably correspond closely to the kind of data obtainable in the vertebrate fossil record and therefore could be used to vet the SDR prior to paleontological application. In most cases, taphonomic processes – those responsible for the incorporation of an organism into the fossil record – tend to produce assemblages that are spatially averaged at the habitat scale (e.g. Hadly, 1999; Kidwell and Holland, 2002). Thus, small-scale variation in species distributions is generally not preserved. As the BBS data for each locality are a sum of observations encountered on the survey route [50 stops over ~40 km (Peterjohn and Sauer, 1993)], data for a particular locality are also spatially averaged.

Geographic and taxonomic variation in the SDR remains to be explored. The similarity of beta diversity distributions in the humid regions and the steppe ones, for instance, is noteworthy, and ongoing studies at a broader geographic scale should clarify the significance of this observation. Furthermore, the analysis of beta diversity in the fossil record by any means may entail additional problems that have yet to be addressed. For instance, precisely how close in age must localities be for their inclusion in a single time-plane to be meaningful? In other words, how might time-averaging (e.g. Badgley, 1982; Behrensmeyer and Hook, 1992) affect the interpretation of beta diversity? The dynamism or stability of species' geographic distributions, in the presence or absence of significant climate change, will be crucial (Holt, 2003; DiMichele *et al.*, 2004), especially in the pre-Quaternary fossil record, as the precision of age-estimates declines. It may also be that theoretical work on the distribution of organisms in space and time will show the problems of spatial and temporal averaging to be one and the same. However those studies may develop, the SDR shows promise in the estimation of beta diversity in less well-inventoried biotas (fossil or Recent) and a new way to measure differential diversity in the present and the geological past.

ACKNOWLEDGEMENTS

I am indebted to the managers of the BBS and to birders throughout the United States who have amassed the data examined in this study. I thank R. Benson, F. Bibi, R. Butler, R.K. Colwell, E.B. Davis, W.A. Green, M. Hernández Fernández, E.S. Vrba, and anonymous reviewers for helpful discussions and/or comments on the manuscript, and W.A. Green and E.S. Vrba for inspiration. T. Olszewski and two anonymous reviewers provided especially useful critiques of earlier drafts of this paper. Financial support during initial development of these ideas came from an NSF Graduate Research Fellowship and a Yale University Fellowship. Further support was provided by the Texas Memorial Museum at the University of Texas at Austin.

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