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*Oikos*, Vol. 86, No. 1. (Jul., 1999), pp. 45-54.

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# Estimating species-area relationships from plot to landscape scale using species spatial-turnover data

**John Harte, Sarah McCarthy, Kevin Taylor, Ann Kinzig and Marc L. Fischer**

Harte, J., McCarthy, S., Taylor, K., Kinzig, A. and Fischer, M. L. 1999. Estimating species-area relationships from plot to landscape scale using species spatial-turnover data. – Oikos 86: 45–54.

Vegetation census data from montane meadow plots are used to test a predicted connection between the species-area relationship, $S = cA^z$, and the dependence of interpatch species turnover on patch area $A$, interpatch distance $D$, and the species-area exponent $z$. At small spatial scales, from $D \approx 1-10$ m, where species-area parameters can be independently estimated, the prediction is confirmed; at larger scales, from $D \approx 1-10^4$ m, the scale-dependence of $z$ is deduced. A predicted dependence of species richness on the shape of censused patches is also confirmed. Our results indicate that readily obtainable species-turnover data between distant small patches can be used to estimate species-area exponents at landscape scales where census data for nested areas are generally not available, thereby improving our ability to estimate landscape-scale species richness and rarity.

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Species-area relationships, such as the commonly cited power law

$$S = cA^z, \quad (1)$$

provide estimates of total species richness at large scales and predictions of the number of species likely to go extinct under habitat loss (May et al. 1995, Rosenzweig 1995). Direct estimation of the parameter $z$ requires species presence/absence data in a sequence of patches with area extending up to the scale of interest. Because $z$ is likely to be scale-dependent (Rosenzweig 1995), values of $z$ obtained from census data within small areas may not apply to larger areas. Unfortunately, direct estimation of $z$ at landscape or regional scales by the method of complete censusing of ever-larger areas is often impractical (although see Condit et al. 1996). Thus, other methods for estimating $z$ at large spatial scales are needed for accurate estimates and predictions. The basis for such a method is provided by a previous theoretical study (Harte and Kinzig 1997). Here we present results of an empirical test of the relevant theory.

## Background

In a previous paper, Harte and Kinzig (1997) derived from Eq. 1 a formula for the fraction of species in common to two patches of area $A_1$ and $A_2$ separated by an interpatch distance $D$ (defined here as the distance between the centers of the two patches). The derivation was based on the assumption that a species-area power law (Eq. 1) holds from the small scales defined by $A_1$

Accepted 14 October 1998

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ISSN 0030-1299
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and $A_2$ to the larger areal scale defined by $D^2$. Denoting this commonality fraction by $\chi$, the formula takes the form

$$\chi(A_1, A_2, D) = 2\eta[2 - 2^{-z}][A_1 A_2 / D^2]^{-z} \div [A_1^{-z} + A_2^{-z}]$$
$$= \eta[2 - 2^{-z}][A/D^2]^{-z} \quad \text{for } A_1 = A_2 = A \tag{2a}$$

The coefficient $\eta$ in this expression is a geometric correction factor that, for $D^2 \gg A$, ranges from 1 to 1.03 for $z$ in the range of 0.05 to 0.35. When $D^2 = A$, $\eta \equiv 1$ for all $z$. We note that $\chi$, defined as the number of species in common to the two patches divided by the average number in the two patches, is simply related to spatial turnover (Cody 1993) by $T = 1 - \chi$.

Eq. 2 can in principle be used to deduce a value for $z$ at large spatial scales simply by censusing patches of manageable size separated by the scale distance $D$. As written, however, Eq. 2a assumes that $z$ is constant over the characteristic scales of $A_1$, $A_2$ and $D^2$ – or $z(A_1) = z(A_2) = z(D^2) = z$. In practice, these equalities will often be violated (Rosenzweig 1995). If, for instance, two small patches are very far apart, $z$ would have to remain constant from patch to landscape scales for $z(A) = z(D^2)$; as mentioned above, this is often not the case. In addition, $z$ may take on different values at the same spatial scale (patch scale) but at widely separated locations within the larger biome. Thus a modified version of Eq. 2a that avoids this requirement of scale invariance must be used.

If we return to our original derivation of commonality (Harte and Kinzig 1997), and keep careful track of the relevant scales for $z$ as it appears in the derivation, then Eq. 2a becomes:

$$\chi(A_1, A_2, D) = 2\eta[2 - 2^{-z(D)}][A_0^{-z(D)} / D^{2z(D)}]$$
$$\times \frac{[(A_1/A_0)^{-z(A_1)}(A_2/A_0)^{-z(A_2)}]}{[(A_1/A_0)^{-z(A_1)} + (A_2/A_0)^{-z(A_2)}]} \tag{2b}$$

where $A_0$ is the area of the larger biome containing the censused patches and $z(X)$ gives the value for $z$ at spatial scale $X$.

It is generally possible to census pairs of patches of similar area, so that $A_1 = A_2 \equiv A$, in which case Eq. 2b simplifies to:

$$\chi(A, A, D) = \eta[2 - 2^{-z(D)}][A_0^{-z(D)} / D^{2z(D)}](A/A_0)^{-z(A)} \tag{2c}$$

To circumvent the need to know the larger biome area, and to simplify use of Eq. 2c, consider cases where $D$ is kept constant but pairs of patches of several different areas are censused. Assume that the censused patches are sufficiently similar, biologically, so that even though they may be distantly separated, $z(A)$ is the same within each of the two patches comprising a pair. Finally, assume that $z$ is constant within the range of variation of patch area $A_{\min} < A < A_{\max}$. Then from Eq. 2c we find that a plot of $\ln(\chi)$ versus $\ln(A)$ will yield a straight line with a slope of $z(A)$:

$$\ln \chi(A, A, D) = \text{constant} + z(A)\ln(A) \tag{3}$$

To validate our theoretical formula for commonality at the scale of small experimental plots, where $D$ in Eq. 3 will be of order $A^{1/2}$, the value of $z$ obtained from a regression of $\ln(\chi)$ against $\ln(A)$ can be compared to the value of $z$ obtained from Eq. 1, and here we present the results of such a test.

This, however, still leaves unanswered the question of how to determine $z$ at large spatial scales, $D^2 \gg A$, when $z(A) \neq z(D^2)$. To address this, consider Eq. 2c again, under the restricted circumstances in which the censused patches of area $A$ are held constant and $D$ is permitted to vary between $D_{\min} < D < D_{\max}$. If $z$ is constant across that range of values of $D$, then measurements of $\chi(A, A, D)$ over the range $D_{\min} < D < D_{\max}$ and for fixed patch areas permit calculation of $z$ in that larger scale range. In particular, a plot of $\ln(\chi)$ versus $\ln(D)$ will yield a straight line with a slope of $-2z$:

$$\ln \chi(A, A, D) = \text{constant} - 2z(D^2)\ln(D) \tag{4}$$

Note that in applications of Eq. 4, while the paired censused plots used to determine commonality can be separated by long distances, all of the patches of area $A$ must be chosen from regions that have a similar small-scale $z$, so that $z(A)$ remains constant over the landscape being studied.

The astute reader will note a possible problem: if Eq. 3 or 4 is used to determine $z$, how is one to know in advance whether $z$ is constant over the range $A_{\min} < A < A_{\max}$ (for Eq. 3) or the range $D_{\min} < D < D_{\max}$ (for Eq. 4)? The ln-ln plot, itself, will reveal scale variance or invariance – straight line-regions will correspond to ranges over which $z$ is relatively constant (and the value of $z$ can be determined from the slope) and regions of curvature will correspond to scales over which $z$ is changing. We note that even a small deviation from constancy in $z(D)$ can lead to large changes in the magnitude, and even the sign, of the slope of $\ln(\chi)$ versus $\ln(D)$ graphs (Fig. 1).

Because measurements of commonality or turnover at large spatial scales are readily carried out, Eq. 4 provides a means of determining the species-area exponent, $z$, at large spatial scales where census data to fit to Eq. 1 are not available. Here, we first test and apply our predictions for commonality (Eqs 2 and 3) at a range of values for $D$ and $A$ for which $z$ is independently known (from Eq. 1) and for which $z(D^2) \approx z(A)$. We then apply Eq. 4 to determine $z$ over a much wider range of values of $D$ for which $z(D^2) \neq z(A)$. We conclude with a discussion and test of a procedure for

using this approach to estimating $z$ at large spatial scales in order to estimate the total number of plant species over a landscape-scale area of habitat and the total number of locally endemic species in sub-areas within the entire landscape.

We emphasize that the purpose of this study is to test derived consequences of the power-law form of the species-area relationship; it is not to derive that relationship from underlying mechanisms. We also note that within each patch we census every individual plant, and thus the issue of within-plot sampling bias is moot. Our work differs from the many studies of scale dependence in plant species distributions in that we are testing explicit predictions (Eqs 2–4) that derive from an underlying theory relating the species-area relationship to species turnover.

Finally we turn to the issue of the dependence of species richness on the shape of censused patches. To our knowledge, all published models that have been invoked to explain or derive species-area relationships from underlying statistical assumptions such as species-abundance and/or species-range distributions (e.g., Preston 1962, Coleman 1981, Caswell and Cohen 1993, Leitner and Rosenzweig 1997) make no explicit prediction about how species richness depends upon patch shape. These models also do not predict how commonality depends upon interpatch separation. Yet, as we show next, our commonality formula indicates that shape does indeed matter in a testable manner.

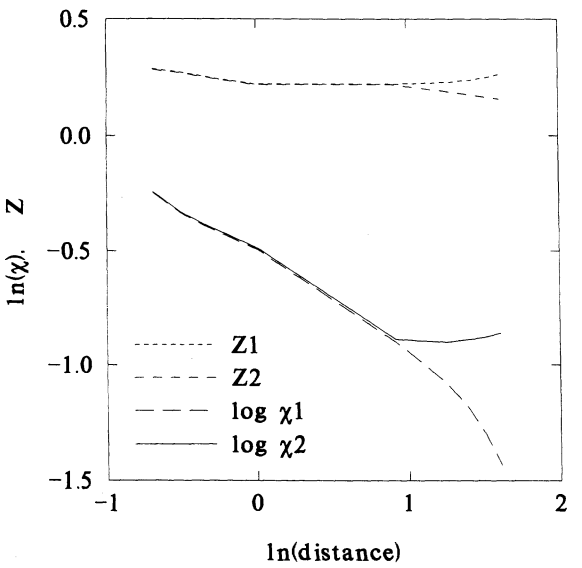


Fig. 1. Dependence of $z(D)$ and $\ln(\chi) = \ln[(2-2^{z(D)})(0.25/D^2)^{z(D)}]$ on $\ln(D)$ for two examples of $z(D)$ that exhibit curvature typical of that found from application of Eq. 1 to our census data for $0.5\ \mathrm{m} < D < 6$ m. Note that the slope of $\ln(\chi_i)$ versus $\ln(D)$ changes sign, even though $z$ remains positive, indicating that Eq. 4 can give a highly inaccurate estimate of $z$ if applied in a region where $z$ is scale-dependent. In the region where the $z_i$ are constant, the slopes of $\ln(\chi_i)$ versus $\ln(D)$ are identically equal to $z_i$.

To see this, consider two square patches, each of area $A$, and thus each with $S(A)$ species. If they share an edge, so that the combined patch is a $2 \times 1$ rectangle, then the interpatch distance is $D = A^{1/2}$ and so the fraction of species in common to the two patches is, by Eq. 2c, $\chi = 2 - 2^z$. Hence the total number of species in the two patches is $2S(A) - \chi S(A) = [2 - (2 - 2^z)]S(A) = 2^z S(A) = S(2A)$ from Eq. 1. But now place the two $1 \times 2$ rectangles together so that they share a short edge and form a $1 \times 4$ rectangle. Now $D = 2A^{1/2}$. Using Eq. 2c, it is straightforward to show that this patch, of area $4A$, contains $[2 - (2 - 2^z)/2^z]S(2A)$ species. For $0 < z < 1$, this expression is greater than the species richness expected from the species-area relationship for a square patch of area $4A$: $2^z S(2A)$.

More generally, consider a rectangular patch of width one unit and length $2^N$ units. Then repeated application of Eq. 2c yields an expression for the species richness of that patch:

$$S(1 \times 2^N) = S(1 \times 1) \prod_{i=0}^{N-1} [2 - (2 - 2^z)/2^{iz}] \qquad (5)$$

As $N \to \infty$, Eq. 5 predicts: $S(2^N) \to 2^N S(1)$.

An effective value of $z$ for long skinny patches can now be defined. For example, for the case $N = 3$ ($1 \times 8$ patches), the effective measured value of $z$ is given by $z_{\mathrm{eff,meas}} = \log_8[S(1 \times 8)/S(1 \times 1)]$. In comparison, the predicted effective value is given by:

$$z_{\mathrm{eff,pred}} = \log_8 \prod_{i=0}^{2} [2 - (2 - 2^z)/2^{iz}] \qquad (5a)$$

For $z = 0.25$, Eq. 5a predicts $z_{\mathrm{eff,pred}} = 0.39$; thus $S(\sqrt{8} \times \sqrt{8}) = 8^{0.25} S(1)$, whereas $S(1 \times 8) = 8^{0.39} S(1)$. Species richness is thus greater on long skinny patches than on square patches of the same area. Results of a direct test of Eq. 5a, as well as of Eq. 2, are presented here.

## Methods

Our approach consists of acquisition and analysis of vegetation census data from montane meadow plots, for patch areas, $A$, ranging from 0.25 m$^2$ to 16 m$^2$, and interpatch distances, $D$, ranging from 0.5 m to $10^4$ m. To test our commonality prediction, we evaluate $\chi$ at small interpatch distances ($D \approx 1$–6 m) and small areas (0.25 m$^2$ and 1 m$^2$) and then calculate $z$ from Eq. 3; we then compare these estimates of $z$ with those from independent estimation of $z$ using Eq. 1; the Eq. 1 estimate relies on direct measurement of species richness in an increasing sequence of patch areas rather than measurements of species turnover in space. At larger scales, up to $\sim 10$ km patch separation, we apply

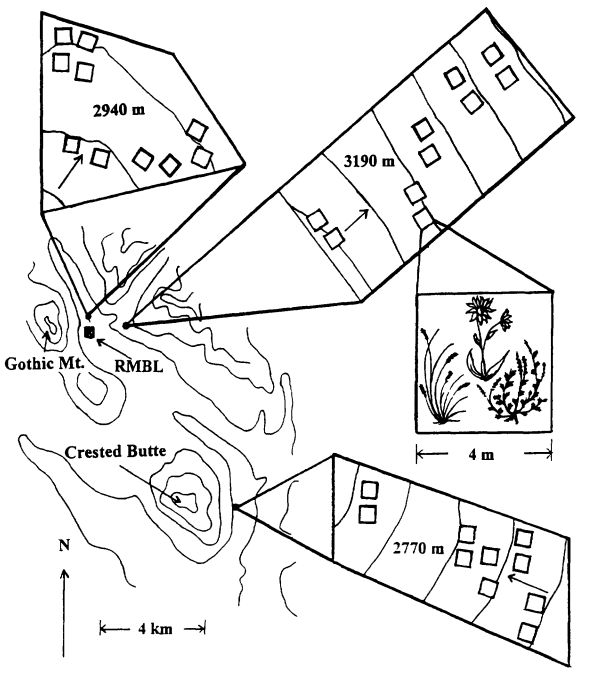


Fig. 2. Schematic map of the study area surrounding the Rocky Mountain Biological Laboratory, located in the East River Valley, Gothic, CO (latitude 38°53′ N; longitude 107°02′ W). The inset maps of the three study sites show the actual aspect; arrows on insets indicate increasing elevation. Contour intervals are 250 m and 5 m for the main map and the insets, respectively.

Eq. 4, with commonality data from a range of values of $A$ from 0.25 $m^2$ to 16 $m^2$ and $D$ from 6 m to $10^4$ m, to extract information about the value of $z$ at spatial scales of order $D^2 \gg A$. A total of $\sim 10^6$ pairwise comparisons of the species lists of patches comprise the commonality data set.

Our research sites are in Gunnison County, Colorado, USA, in the upper East River valley. The censused plots are located within three montane meadows at elevations of 3190, 2940, and 2770 m, respectively. The intersite distances are 2.0, 10.4, and 12.8 km, with the upper and mid-elevation sites closest together (Fig. 2). The three sites have similar parent material, and roughly similar slope and aspect. The habitat of each site consists of open subalpine meadow containing a diverse mixture of woody shrubs (primarily *Artemisia tridentata*), forbs, and graminoids. Species richness per unit area is comparable at the three sites (15–25 species/$m^2$). In the habitat classification scheme of Langenheim (1955, 1962), our meadow sites fall within the broad transzonal fescue grassland category that bridges upland herb and lower-elevation sagebrush communities. They lie within a landscape containing a mosaic of predominantly conifer and aspen forest and meadow. The three sites were selected because they each contain vegetation communities typical of their elevation (Langenheim 1955), all three are ungrazed, and they have been open meadow for at least the past century.

At each elevational site, we laid out ten 4 m × 4 m plots in open meadow in a stratified random pairwise design. (The plots were originally established as treatment pairs in the three meadows for an investigation of climate/ecosystem feedback interactions, but the absence of locational bias vis-à-vis species richness in the experimental design renders them suitable for this study.) Interplot distances within each site range from 6 m to 65 m, as measured from the centers of each plot. For each of the 64 0.5 m × 0.5 m quadrats within each of the ten 4 m × 4 m plots at each of the three elevations, we compiled a complete species list of vascular plants ($N = 1920$ 0.5 m × 0.5 m quadrats). We carried out all censuses during the period 15 June to 3 July, 1996. Snowmelt in 1996 was relatively early (between 5 May and 25 May at the three sites) and thus the vegetation was sufficiently advanced phenologically at the time of censusing to permit identification of most species present at any time during the growing season. Even the most early-blooming species such as *Mertensia fusiformis* and *Erythronium grandiflorum* were still clearly visible at the time of censusing. Because the meadow plants emerge and bloom later at higher elevation, we censused sites in order of increasing elevation to minimize the effect of this phenological trend on our estimates of species presence.

From the full data set, we extracted information about species commonality at three scales of patch separation: intraplot ($D$ in the range 1 m to 6 m), intrasite but interplot ($D$ in the range 6 m to 70 m), and intersite ($D$ in the range 2 km to 12.8 km).

At the intraplot scale, we calculated for each plot the average number of species in each square patch of area 0.25, 1, 4, and 16 $m^2$ and each rectangular patch of area 0.5, 2 and 8 $m^2$. For each area, we only used non-overlapping patches to avoid multiple contributions from interior regions of the plots. From these averages, we estimated $z$ at intraplot scale from Eq. 1 by determining the slope of the regression of $\ln(S)$ against $\ln(A)$.

Again at the intraplot scale, we also calculated from all the census data the value of $\chi$ for every pair of 0.25-$m^2$ patches ($64 \times 63/2 = 2016$ pairs) and of 1-$m^2$ patches ($16 \times 15/2 = 120$ pairs) within the plot. From these values, we computed the average value of $\chi$ at each interpatch distance and for each of the two patch areas ($D = 1$ m to 6 m, $A = 0.25$ $m^2$ and 1 $m^2$).

To test the commonality formula at the intraplot scale, where $z$ is known from application of Eq. 1, we derived a value of $z$ from the commonality data by two methods. First, for each plot we estimated $z$ by using Systat's nonlin estimation routine to fit Eq. 2 to values of $\chi$ for $A = 1$ $m^2$ and averaged over an intermediate and narrow range of values of $D$ from 2.7 m to 3 m. That range was selected because within the range of areas from 6.25 $m^2$ to 9 $m^2$ $z$ determined from Eq. 1 is most nearly constant. Then we used Eq. 3 to determine $z$ for each plot, with $D$ in the same range as above and

$A = 0.25$ m$^2$ and $A = 1$ m$^2$. We then compared the values of $z$ determined by these methods against the values determined directly from Eq. 1.

At the intrasite but interplot scale, we calculated from the census data the value of $\chi$ for all pairs of square patches with areas of 0.25 m$^2$ (184 320 pairs), of 1 m$^2$ (11 520 pairs), and of 16 m$^2$ (45 pairs). As above, we compute from these values the average value of $\chi$ for each interpatch distance (6 m to 65 m) for each of the three patch areas. Because our sampling units are not points, for purposes of plotting and statistical analysis we bin the intrasite data for each patch area into 5-m intervals spanning the range of interpatch distances.

At the intersite scale, we calculated for each pair of sites the value of $\chi$ between all pairs of patches of area 0.25 m$^2$ (409 600 pairs), 1 m$^2$ (25 600 pairs), and 16 m$^2$ (100 pairs). Because interplot distances within a site are very small compared to intersite distances at this scale, only three values of $D$, the three intersite distances, are used in our analysis. Thus, for each patch area, only three averaged estimates of $\chi$ are used in our analysis, each the average over a large number of pairwise measurements. We determined values for $z$ at this scale and at the intrasite but interplot scales by using Eq. 4; separate values were calculated for each of the three patch areas.

## Results

Plant species richness differed by a small but significant ($p < 0.05$, $t$ test) amount between the lower and the middle or upper sites; the means (and SEMs, $N = 10$) of plant species per 16-m$^2$ plot are 27.8 (0.8), 33.3 (1.4), and 34.7 (0.6) at the three sites, respectively.

### Species-area estimation of $z$ at the intraplot scale

For each of the 30 plots, we compiled the average species number for each square or $2 \times 1$ rectangular patch of area 1, 2, 4, 8, and 16 m$^2$. Regression of ln (species number) against ln (area) yields $R^2 > 0.98$ for 27 of the 30 plots and $R^2 > 0.99$ for 23 plots. The three plots for which $R^2 < 0.98$ are excluded from the subsequent analyses, leaving a total of 27 values of $z$ from the species-area relationships at plot scale ($z_{SAR}$). The mean values of $z_{SAR}$ differed significantly ($p < 0.05$, $t$ test) between the three sites (Table 1). Removal of the $2 \times 1$ rectangular patches (2 m$^2$ and 8 m$^2$) from the data set had no significant effect on the goodness of fit or on the values of $z_{SAR}$.

With the data at 0.25 m$^2$ and 0.5 m$^2$ included in the fits, $R^2 > 0.99$ for only three of the plots; for all plots, data points from these two smallest patches systematically fall below the linear regression line on the ln($S$) versus ln($A$) graphs. Thus $z$ is a decreasing function of $A$ at small $A$. At the largest values of $A$ (8 and 16 m$^2$), the data fall above the regression line in some of the plots and below in others, with the deviations from linearity typically in the range of 10–25%. These two deviations from linearity at the largest and smallest values of $A$ clearly indicate that $z$ deviates from constancy, even just within the intraplot scale from 0.25 m$^2$ to 16 m$^2$.

### Dependence of the species-area exponent on patch shape

Species richness for long, skinny rectangular patches was consistently higher than for square or $2 \times 1$ rectangular patches of the same area. As shown in Table 2, our census data confirm Eq. 5a.

Table 1. Values of the species-area exponent at various sites and scales as calculated by direct censusing of patches of increasing area ($z_{SAR}$) and from spatial turnover data ($z_\chi$). For explanations of the different methods of using spatial turnover data to estimate $z$, see text. Numbers in parentheses are standard errors of the mean.

| Scale for $z$ | $z_{SAR}$ (Eq. 1) | $z_{\chi,Eq.2}$ | $z_{\chi,\ Eq.3}$ | $z_{\chi,\ Eq.4}$ |
|---|---|---|---|---|
| Intraplot (1 m–6 m) | | | | |
| lower | 0.233 (0.010) | 0.233 (0.012) | 0.189 (0.007) | a. |
| middle | 0.286 (0.014) | 0.284 (0.011) | 0.234 (0.011) | a. |
| upper | 0.267 (0.010) | 0.259 (0.008) | 0.225 (0.007) | a. |
| Intrasite (6 m–70 m) | | | | |
| lower | b. | c. | c. | 0.003 (0.003) |
| middle | b. | c. | c. | 0.027 (0.014) |
| upper | b. | c. | c. | 0.053 (0.015) |
| Intersite (2 km–2.8 km) | b. | c. | c. | 0.076 (.013) |

a. Use of Eq. 4 to estimate $z$ at intraplot scale is not warranted because of the curvature in ln($S$) vs ln($A$) graphs (see text and caption to Fig. 4).
b. No estimate is possible because nested-area census data to use in Eq. 1 are not available at intrasite and intersite scales.
c. Use of Eq. 3 to estimate $z$ at intrasite and intersite scales is not warranted because the $z$ values estimated by Eq. 4 indicate that at values of $D$ characteristic of these scales and at values of $A$ for which we have census data, $z(D^2) \neq z(A)$.

Table 2. A comparison of the predicted and measured dependence of species richness on patch shape. The symbol $\langle\rangle$ refers to an average over plots within each site. $\langle z\rangle$ is the average value of $z$ for square patches; $\langle S(1\times1)\rangle$ and $\langle S(1\times8)\rangle$ are species richnesses for patches of dimension 0.5 m × 0.5 m and 0.5 m × 4 m, respectively, $z_{\text{eff,meas}}$ is $\log_8[\langle S(1\times8)\rangle/S(1\times1)]$ and $z_{\text{eff,pred}}$ is calculated from Eq. 5.

| | $\langle z\rangle$ | $\langle S(1\times1)\rangle$ | $\langle S(1\times8)\rangle$ | $z_{\text{eff,meas}}$ | $z_{\text{eff,pred}}$ |
|---|---|---|---|---|---|
| Upper site | 0.27 | 8.54 | 20.49 | 0.42 | 0.41 |
| Middle site | 0.29 | 7.37 | 17.35 | 0.41 | 0.43 |
| Lower site | 0.23 | 8.37 | 18.03 | 0.37 | 0.36 |

The data not only demonstrate shape-dependence of species richness, thus casting doubt on the assumptions that underlie many attempts to derive a species-area relationship from underlying statistical assumptions, but also confirm the detailed prediction of our theory. We note that data from tropical forest censuses also point to dependence of species richness on patch shape (Condit et al. 1996). See also Kunin (1997).

## Species commonality within plots

Site-averaged values of $z$ obtained by fitting Eq. 2 to each plot's commonality data, thus yielding $z_{\chi,\text{Eq.2}}$, and by fitting Eq. 3 to the values of commonality, thus yielding $z_{\chi,\text{Eq.3}}$, are given in Table 1. Linear regressions of $z_{\text{SAR}}$ against $z_{\chi\text{Eq.2}}$ and $z_{\chi\text{Eq.3}}$ across the plots at all three sites indicate that the commonality formula predicts the gross trends in the means and variance of $z_{\text{SAR}}$ across plots (Table 1, Fig. 3a, b).

## Estimation of $z$ at intrasite scale

Ln($\chi$) versus ln($D$) plots for the data at all three sites and all three scales are shown in Fig. 4a–c. Use of Eq. 4 to determine $z$ at intrasite (but interplot) scale revealed site differences in the estimated value of $z$ (Table 1, Fig. 4a–c, hatched data symbols). At the lower site (Fig. 4a), for $A = 0.25$, 1, and 16 m$^2$, $z_{\chi,\text{lower,Eq.4}}$ is indistinguishable from zero for $A = 0.25$ m$^2$ and 1 m$^2$, and equals 0.008 for $A = 16$ m$^2$, yielding a mean of $0.003 \pm 0.003$. At the middle site (Fig. 4b), for $A = 0.25$, 1, and 16 m$^2$, we obtain $z_{\chi,\text{middle,Eq.4}} = 0.055$, 0.019, and 0.008, yielding a mean of a mean of $0.027 \pm 0.014$. At the upper site (Fig. 4c), for $A = 0.25$, 1, and 16 m$^2$, we obtain $z_{\chi,\text{upper,Eq.4}} = 0.073$, 0.063, and 0.023, yielding a mean of $0.053 \pm 0.015$.

## Estimation of $z$ at intersite scale

The intersite data are repeated on each of Fig. 4a–c (open squares). Although there are effectively only two points determining the regression line because the middle and upper sites are almost the same log(distance) away from the lower site, the values of $z$ obtained by fitting to Eq. 4 are 0.098, 0.075, and 0.054, respectively, for a mean of $z_{\chi,\text{intersite,Eq.4}} = 0.076 \pm 0.013$ (Table 1).

## Discussion

We note that the values of $z$ at intersite scale and at intrasite scale at the middle and upper sites that were obtained with the use of Eq. 4 varied with patch area in a systematic fashion. In particular, the $z$-values decreased with increasing patch area. This is consistent with the general trend within each of the plots at the middle and upper sites for the ln($S$) versus ln($A$) plots to display decreasing slope as $A$ increases toward 16 m$^2$.

In our analysis of $z_{\chi,\text{intersite}}$, we assumed the appropriate measure of separation between any two sites was the straight-line distance between them. An alternative measure of biological separation in the steep terrain in which the sites are located is elevational difference between sites. Re-analyzing the intersite data by plotting log(commonality) against log(elevation), the data form an "L"-shape for each patch area, indicating that at intersite scale, within the elevational range we investigated, commonality decreases as predicted with geographic distance rather than with elevational difference. Were we to have extended the elevational range of our study sites, which were all in the subalpine, to include true alpine habitat (the lower extent of which is found approximately 300 m in elevation above our upper site), this situation would likely have reversed; elevational change and not geographic distance, would probably be the best predictor of species turnover.

The use of Eq. 4, with values of $D$ in the range of 0–6 m, to estimate $z$ at intraplot scale yields values of $z$ that under- or overestimate $z_{\text{SAR}}$ by as much as a factor of two, depending on the plot and the actual values of $D$ over which Eq. 4 is evaluated. The reason is that $z_{\text{SAR}}$, as discussed above, is generally not constant over the measured intraplot scale range from $A = 0.25$ to 16 m$^2$. Even though the deviation from constancy is generally not large on a percentage basis, as evidenced by the fits to Eq. 1 having $R^2$ close to 1, just a small deviation from constancy can lead to large changes in the magnitude, and even in the sign, of the slope of ln($\chi$) versus ln($D$) graphs (Fig. 1). When averaged over all plots within a site, graphs of ln($\chi$) versus ln($D$) exhibit approximate straight-line behavior

(Fig. 4a–c), but ln–ln graphs for individual plots exhibit behaviors that range between the two cases shown in Fig. 4, with some of the graphs curving downward and others curving upward. Thus estimation of $z$ with the use of Eq. 4 gives wildly different results depending upon the value of $D$ at which the derivative is evaluated.

Similarly, use of Eq. 3, with values of $D \gg A^{1/2}$, to estimate $z$ at intraplot scale gives misleading estimates, which are generally smaller than those obtained by Eq. 1. Here, again, the reason is scale dependence, but of a different type. Two plots a large distance away from each other are likely to have considerably different values of $z$ (Fig. 2a, b) and thus $\ln(\chi)$ versus $\ln(A)$ graphs of commonality data from patches of such distant plots are not likely to yield reliable estimates of $z$ at plot scale.

The values of $z$ obtained at intrasite and intersite scales with Eq. 4 are smaller than those obtained at intraplot scale using the species-area relationship (Eq. 1) or the commonality relationship (Eqs 2 or 3), indicating the existence of large scale dependence in $z$. As discussed in the introduction, such scale dependence implies that the use of Eqs 2 or 3 to estimate $z$ at intrasite or intersite scales will give misleading results. The values of $z$ so obtained are always larger than those obtained from Eq. 4, as expected given that $z$ at intraplot scale is greater than $z$ at intrasite or intersite scale. Because of this scale-dependence the actual values of $z$ at intrasite and intersite scales are most reliably determined by fitting the commonality data to Eq. 4.

## Applications

### Estimation of total number of species on landscape scale

Knowledge of $z$ across the three scales we explored allows estimation of the total number of plant species within the entire meadow habitat spanned by our three sites. To illustrate the procedure for carrying out such an estimation, consider, first, the following fictitious case in which $z$ is known at two discrete scales. At plot scale, $z$ is known from direct censusing within nested areas and it equals 0.25. At landscape scale, $z$ is known from the same type of analysis of commonality data that we developed above, and it equals 0.1. Suppose that the entire habitat area is 100 km$^2$ and that the boundary between plot and landscape scale is 100 m$^2$. In reality, there is unlikely to be a sharp boundary between the two scales, but redoing the calculation below with a gradual transition rather than a discrete one makes little difference to our final result. Further assume that the average number of species as measured in plots of area 36 m$^2$ (the largest areas directly censused in their entirety) equals 80.

Using Eq. 1 at plot scale, we first calculate the number of species at the transition area between the two scales: $S(100\ \text{m}^2) = S(36\ \text{m}^2)\ (100/36)^{0.25} = 103.3$. To proceed, we use the fact that for areas, $A$, equal to or larger than this transition area, $S(A) = S(100\ \text{m}^2)\ (A/100\ \text{m}^2)^{0.1}$. Hence, the total number of species in the entire habitat is given by $S(100\ \text{km}^2) = 80\ (10^8/100)^{0.1}\ (100/36)^{0.25} = 411.2$.

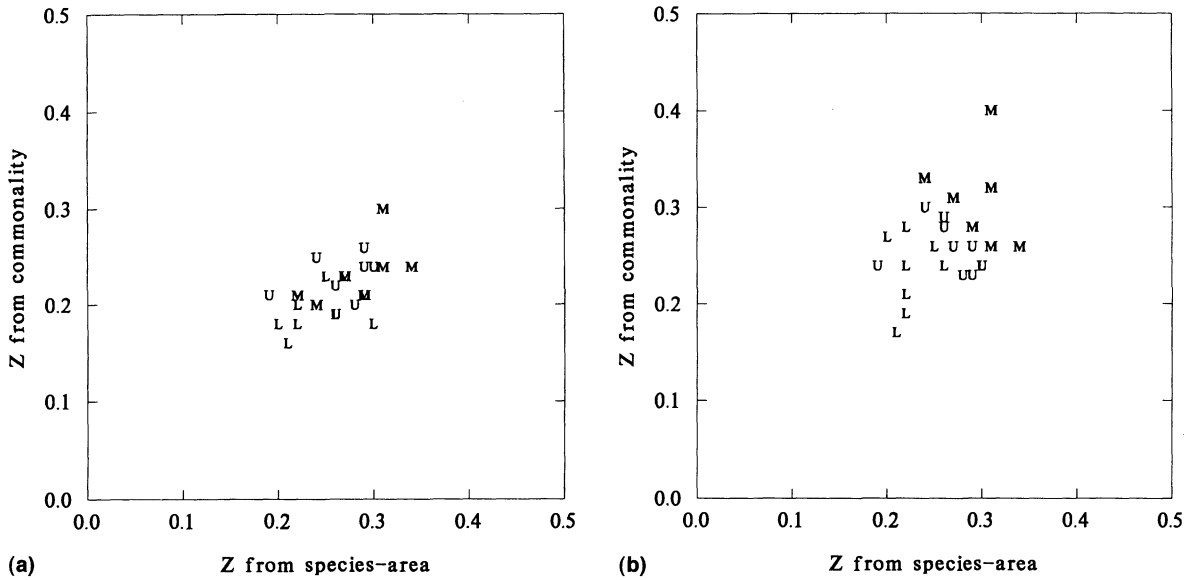


Fig. 3. Values of $z_\chi$ as estimated from Eq. 3 (Fig. 3a) and from Eq. 2 (Fig. 3b) vs $z_{SAR}$, as calculated from the species area relationship (Eq. 1). Data are shown for the 27 plots out of the 30 censused for which the linear regression of $\log(S)$ vs $\log(A)$ has $R^2 > 0.98$. Linear regressions constrained to pass through the origin give $z_{SAR} = 0.978\ z_{\chi,Eq.2}$ ($R^2 = 0.967$, $p < 0.001$) and $z_{SAR} = 1.23\ z_{\chi,Eq.3}$ ($R^2 = 0.984$, $p < 0.001$).

Application of this technique to our landscape, where we have prior knowledge of the plant species list, provides a further test of the commonality formula (Eqs 2–4). Consider first the case in which the entire landscape consists of meadow habitat. After examining that case, we will show how the "missing species" from forested patches can be accommodated in the analysis. At intraplot scale, up to an area of 36 $m^2$ (the minimum $D$ at interplot scale is 6 m), we take the average value of $z$ to be 0.23, 0.29, and 0.27 at the lower, middle, and upper sites (Table 1). From the average species count for the 16 $m^2$ plots at each site (27.8, 33.3, and 34.7) and using Eq. 1, we then estimate the number of species at the scale transition area of 36 $m^2$ to be $27.8(36/16)^{0.23} = 33.5$; $33.3(36/16)^{0.29} = 42.1$; and $34.7(36/16)^{0.27} = 43.2$ at the lower, middle, and upper sites, respectively.

At intrasite scale, up to areas of order $10^4$ $m^2$, we take $z = 0.003$, 0.027, and 0.053 at the lower, middle, and upper sites, respectively (Table 1). At this next transition area, we then get total species richnesses of $33.5(10^4/36)^{0.003} = 34.1$; $42.1(10^4/36)^{0.027} = 49.0$; and $43.2(10^4/36)^{0.053} = 58.2$ at the three sites. The predicted number of species for an average area of $10^4$ $m^2$ across the landscape is then 47.1.

To proceed, we use our result that at intersite scale, $z = 0.076$ (Table 1). Within the East River Valley, the total area between the elevation of our upper and lower

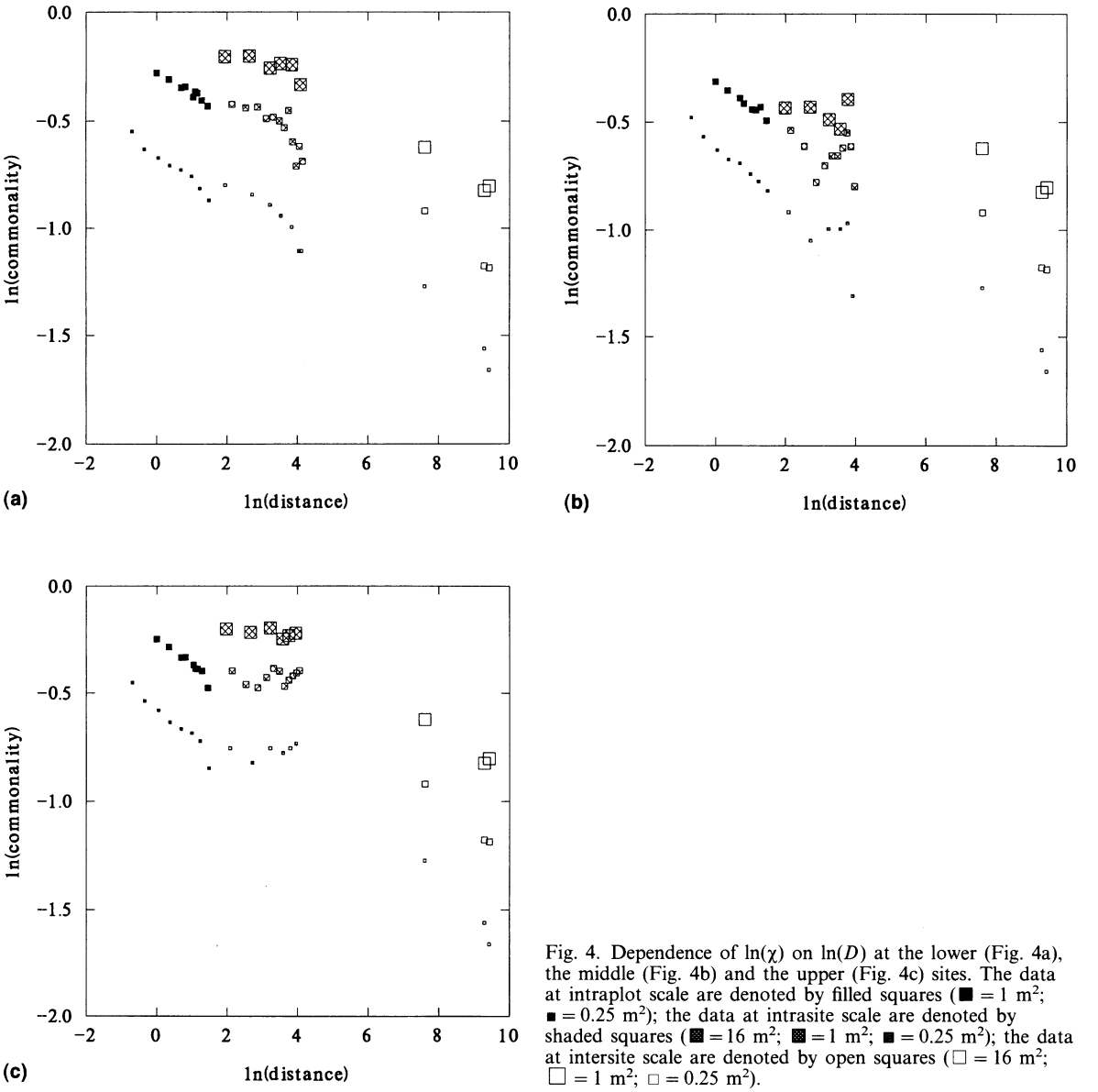


Fig. 4. Dependence of $\ln(\chi)$ on $\ln(D)$ at the lower (Fig. 4a), the middle (Fig. 4b) and the upper (Fig. 4c) sites. The data at intraplot scale are denoted by filled squares (■ = 1 $m^2$; ▪ = 0.25 $m^2$); the data at intrasite scale are denoted by shaded squares (▩ = 16 $m^2$; ▩ = 1 $m^2$; ▪ = 0.25 $m^2$); the data at intersite scale are denoted by open squares (□ = 16 $m^2$; □ = 1 $m^2$; □ = 0.25 $m^2$).

sites is approximately 100 km$^2$. If all of this area were occupied by our dry meadow habitat, then the total number of plant species would, according to our estimation strategy, be $S(100\ \text{km}^2) = 47.1(10^8/10^4)^{0.076} = 94.8$.

Aerial photos indicate, however, that roughly half the total area is dry meadow like the habitats we studied, with the other half being either conifer or aspen forest or wetland habitat. If the dry meadow habitat were a contiguous patch of 50 km$^2$, then we would simply have used an area of 50 km$^2$ instead of 100 km$^2$ as above. But instead, the three habitats form a mosaic, with meadow patches ranging from a few hundred square meters to a few square kilometers.

The number of species "missing" from our landscape-scale dry meadow because of the forested and wetlands areas is just the number of meadow species that are not in the existing dry meadow but would have existed within the 100-km$^2$ landscape had the non-meadow patches been meadow. We can estimate this number from an "endemics-area" law previously derived from the species-area law (Harte and Kinzig 1997). This derived relationship states that the number of species $E(A)$, in an area $A$, that are found only in that area and not in a larger surrounding area, $B$, is given by:

$$E(A) = S(B)(A/B)^{z'} \tag{6}$$

where $z' = -\ln(1-2^{-z})/\ln(2)$. A derivation of Eq. 5 and empirical evidence supporting it are given in Harte and Kinzig (1997). For $z = 0.076$ and 0.25, $z' = 4.28$ and 2.65 respectively. Using this relation, it can be shown that the number of "missing" species in the dry meadow habitat is a negligible fraction of the total. In particular, the total number of missing species, $S_{\text{missing}}$ is approximately:

$$S_{\text{missing}} = \sum_{\text{patches}} S(100\ \text{km}^2)(\text{patch area}/100\ \text{km}^2)^{z'} \tag{7}$$

where the sum is over non-dry-meadow patches of habitat and $S(100)$ is estimated above to be $\sim 95$ species. The actual number of plant species in the 50 km$^2$ of dry meadow habitat is then given by $S(100\ \text{km}^2) - S_{\text{missing}}$.

Because $z'_{\text{intersite}} \sim 4.3$, and the patches are all relatively small in comparison to the total habitat area of 100 km$^2$, the sum above is very nearly zero. For example, for the largest patches of non-meadow habitat ($\sim 10$ km$^2$) the fraction of missing species is $0.1^{4.3} = 0.00005$. Hence, we predict that in the dry meadow habitat, there ought to exist roughly 95 vascular plant species. This is in reasonable agreement with results from our census of all 1920 quadrats, on which a total of exactly 90 species were observed. In fact, at least one species (*Arnica cordifolia*) is known to exist within the 50 km$^2$ of dry meadow but was not found on the 30 16-m$^2$ experimental plots. Moreover, while all graminoids within the study plots were keyed to species level, several graminoids within the meadow habitat but outside the plots may have been inadequately distinguished in existing surveys.

We note that if we over- or underestimated the total area of dry-meadow habitat, or the transition area between intersite and intrasite, by as much as a factor of 2, the error induced in our estimate of total species richness would be only about 5% because $2^{0.076} = 1.054$. If we overestimated the area of the transition between the intraplot and intrasite scales, so that the transition occurred at, say, 24 m$^2$ rather than 36 m$^2$, then our final estimate for the total species richness of the entire landscape would have come out to be 86.3 instead of 94.8 species.

### Estimation of number of species unique to a site within a region

Using Eq. 6, we can also predict the number of species that will be found at one site, say the lower, but are not found at the other two. Because each site occupies approximately 1/3 of the total area of the region, the number of species unique to each site is predicted to be $(1/3)^{z'}(95) = 0.8$. Thus on average no more than 1 species should be unique to each site.

Complete census data for all the dry meadow subalpine habitat of the East River Valley are not available, so no direct test of this prediction is available. But from our surveys of the distribution of plant species throughout the East River Valley and from previous botanical surveys (Langenheim 1955, 1962), we know of only one species found in the dry meadow habitat of one third of the valley and not elsewhere (*Penstemon strictus*, found in the lower third of the valley and at our lower-site plots but not in the habitat characteristic of the middle or upper sites).

## Conclusion

Using vegetation species presence/absence data from montane meadow plots spread over a landscape, we have tested a method for determining the species-area exponent at spatial scales so large that direct evaluation by censusing ever larger areas would be impossible. Our approach requires only measurement of the degree to which the species lists in separated, small, censused patches overlap as a function of the distance between patches and the area of the patches. Values of the species-area exponents in the censused plots predicted from these measured commonalities agree well with values of the same exponents measured directly by censusing a sequences of patches of increasing area

within the plots (Table 1, Fig. 3). At larger scales, the values of the species-area exponent determined from this theory are smaller than at plot scale. Moreover, these values lead to two predictions that agree with available data: the total plant species richness of the entire meadow habitat at landscape scale and the number of plant species regionally endemic to portions of the landscape.

The predicted dependence of the species richness on patch shape was also tested; in particular, a theoretical expression for the effective species-area exponent for long, skinny patches was in good agreement with measured values at the three meadow sites (Table 2).

The strategy presented here for deriving a species-area exponent at landscape scale and using it to estimate total species richness at that scale can be used in biomes with areas so large that they cannot be censused directly. For example, with commonality data on tropical insects derived from fumigation studies, $z$ could be estimated on the scale of the distances between fumigated canopies. Then, following the calculation procedure presented here, the total number of insect species within a large area of tropical forest, and possibly within a large regional biome such as all of Amazonia, could be estimated with greater reliability than has been previously possible.

*Acknowledgements* – We gratefully acknowledge the Winslow Foundation, the Mellon Foundation, the Class of 1935 Endowed Chair at UC Berkeley, the NERC Centre for Population Biology, and the National Science Foundation's Research Experience for Undergraduates program for financial support, and Ian Billick, Jennifer Dunne, and Neo Martinez for helpful conversations.

## References

Caswell, H. and Cohen, J. E. 1993. Local and regional regulation of species-area relations: a patch-occupancy model. – In: Ricklefs, R. and Schluter, D. (eds), Species diversity in ecological communities. Univ. of Chicago Press, Chicago, pp. 99–107.

Cody, M. L. 1993. Bird diversity components within and between habitats in Australia. – In: Ricklefs, R. and Schluter, D. (eds), Species diversity in ecological communities. Univ. of Chicago Press, Chicago, pp. 147–158.

Coleman, B. 1981. On random placement and species-area relations. – J. Math. Biosci. 54: 191–215.

Condit, R., Hubbell, S. P., LaFrankie, J. V., Sukumar, R., Manokaran, N., Foster, R. and Ashton, P. S. 1996. Species-area and species-individual relationships for tropical trees: a comparison of three 50-ha plots. – J. Ecol. 84: 549–562.

Harte, J. and Kinzig, A. 1997. On the implications of species-area relationships for endemism, spatial turnover and food web patterns. – Oikos 80: 417–427.

Kunin, W. E. 1997. Sample shape, spatial scale and species counts: implications for reserve design. – Biol. Conserv. 82: 369–377.

Langenheim, J. H. 1955. Flora of the Crested Butte quadrangle Colorado. – Madrono 13: 64–78.

Langenheim, J. H. 1962. Vegetation and environmental patterns in the Crested Butte area, Gunnison County, Colorado. – Ecol. Monogr. 32: 249–285.

Leitner, W. A. and Rosenzweig, M. L. 1997. Nested species area curves and stochastic sampling: a new theory. – Oikos 79: 503–512.

May, R. M., Lawton, J. H. and Stork, N. E. 1995. Assessing extinction rates. – In: Lawton, J. H. and May, R. M. (eds), Extinction rates. Oxford Univ. Press, Oxford, pp. 1–24.

Preston, F. W. 1962. The canonical distribution of commonness and rarity: part I. – Ecology 43: 185–215.

Rosenzweig, M. L. 1995. Species diversity in space and time. – Cambridge Univ. Press, Cambridge.

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