

# Rarity, Commonness, and the Contribution of Individual Species to Species Richness Patterns

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Submitted July 31, 2008; Accepted February 10, 2009; Electronically published May 22, 2009

Online enhancements: appendixes.

**ABSTRACT:** Common species have a greater effect on observed geographical patterns of species richness than do rare ones. Here we present a theory of the relationship between individual species occurrence patterns and patterns in species richness, which allows purely geometrical and statistical causes to be distinguished from biological ones. Relationships between species occupancy and the correlation of species occurrence with overall species richness are driven by the frequency distribution of species richness among sites. Moreover, generally positive relationships are promoted by the fact that species occupancy distributions are mostly right skewed. However, biological processes can lead to deviations from the predicted pattern by changing the nestedness of a species' spatial distribution with regard to the distributions of other species in an assemblage. We have applied our theory to data for European birds at several spatial scales and have identified the species with significantly stronger or weaker correspondence with the overall richness pattern than that predicted by the null model. In sum, whereas the general macroecological pattern of a stronger influence of common species than of rare species on species richness is predicted by mathematical considerations, the theory can reveal biologically important deviations at the level of individual species.

*Keywords:* macroecology, diversity patterns, diversity distribution, occupancy distribution, nestedness, incidence matrix.

## Introduction

Large-scale spatial patterns in species richness are subject to unprecedented levels of research and debate (for reviews see Gaston 2000; Hawkins et al. 2003; Currie et al. 2004; Evans et al. 2005c). The vast majority of studies that have attempted to understand the determinants of spatial patterns in species richness have focused on the covariation

of those patterns with abiotic and biotic variables. These variables include area, topography, ambient energy (temperature), productive energy, water availability, habitat heterogeneity, elevation, land cover, and human population density (e.g., Currie 1991; Wright et al. 1993; Kerr and Packer 1997; Waide et al. 1999; Mittelbach et al. 2001; Davies et al. 2007). Analyses have principally sought to ascertain which variables and combinations of variables have the greatest explanatory power and how this varies with spatial resolution, between regions, and with the analytical approach employed (e.g., Rahbek 2005; Storch et al. 2006; Davies et al. 2007; Rahbek et al. 2007). While this work has provided valuable insights, explicit empirical tests of the secondary (and often more distinct) predictions made by many environmental hypotheses for patterns in species richness have been surprisingly scarce (Evans et al. 2005c).

An alternative approach to understanding the determinants of spatial patterns in species richness involves deconstructing these patterns into those for different component species groups and ascertaining how these give rise to the overall richness patterns (Marquet et al. 2004). Such an approach has been used in a number of studies, variously deconstructing an overall richness pattern into patterns for various taxonomic groups (Marquet et al. 2004), groups defined by phylogenetic age (Hawkins et al. 2007), functional groups (Keil et al. 2008), and classes of commonness/rarity (Jetz and Rahbek 2002; Lennon et al. 2004). Arguably, the results of distinguishing between common and rare species have proven particularly illuminating (Gaston 2008). Common species have repeatedly been found to be much better correlated with overall spatial patterns of species richness than are rare species (Jetz and Rahbek 2002; Lennon et al. 2004; Vásquez and Gaston 2004; Mora and Robertson 2005; Beck et al. 2006; Cabrero-Sanudo and Lobo 2006; Kreft et al. 2006; Rahbek et al.

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2007; Pearman and Weber 2007; Lozada et al. 2008; for a review, see Gaston 2008). This seems contrary to long-prevailing assumptions that overall richness patterns were foremost driven by the occurrences of the larger numbers of species with highly restricted distributions and low abundances rather than the smaller numbers of species that are more widespread and have high abundances (e.g., Berg and Tjernerberg 1996).

The reasons why common species contribute disproportionately to overall richness patterns remain poorly understood. There is evidence that the richness of common species is better correlated with environmental variables than is that of rare species (Jetz and Rahbek 2002; Evans et al. 2005a, 2005b; Cabrero-Sanudo and Lobo 2006; Fu et al. 2006; Kreft et al. 2006; Rahbek et al. 2007). However, this may constitute little more than a restatement of the observations that overall richness is correlated with environmental variables and with the richness of common species (Gaston 2008). Here we develop a theory for the relationship between the occurrence patterns of individual species and overall richness patterns, stressing the difference between common and rare species. Then we apply the theory to data for observed large-scale bird assemblages, demonstrating its ability to distinguish geometrical and statistical causes of the patterns from biologically relevant observations.

### Theory

Following our predecessors, we start with Pearson's correlation coefficient to assess the agreement between species occurrence and spatial species richness patterns. It is a reasonable choice, for the Pearson correlation coefficient  $r$  (hereafter "the correlation") always reflects the left-right asymmetry in an  $X$ - $Y$  plot and thus a tendency of  $Y$  to increase ( $r > 0$ ) or decrease ( $r < 0$ ) with  $X$ . Then we show in a step-by-step manner how systematic differences can arise in the contribution of species differing in relative occupancy to overall species richness patterns. First, we demonstrate that relative occupancy itself does not provide a direct clue to the greater contribution of common species to overall species richness patterns. Second, by analyzing the formula for calculating the correlation, we show that it is the sum of species richness values across all of the sites occupied by a focal species that is the major driver of this outcome. Third, we show that this parameter increases with the relative occupancy of the species and that this increase is affected by the skewness of the frequency distribution of species richness values at individual sites, which thus affects the overall richness pattern. Fourth, we show that the increase can be modified by biological processes leading to deviations from random patterns. Fifth, we argue that a positive relationship between occupancy

and the contribution to the overall richness pattern results if most species have relatively low occupancy (i.e., if the occupancy distribution is right skewed). Sixth, we extend the theory based on one species to the patterns occurring at the level of subassemblages comprising several species. Finally, we interpret these theoretical considerations in terms of the nestedness of species ranges.

### The Role of Relative Occupancy

Consider four sites with richnesses of 5, 4, 3, and 2 species. Imagine that there is a species that occupies just one site; alternatively, the first, second, third, or fourth site, respectively (hereafter we will use notation

$$\begin{pmatrix} 1 & 0 & 0 & 0 \\ 5 & 4 & 3 & 2 \end{pmatrix}, \begin{pmatrix} 0 & 1 & 0 & 0 \\ 5 & 4 & 3 & 2 \end{pmatrix}, \begin{pmatrix} 0 & 0 & 1 & 0 \\ 5 & 4 & 3 & 2 \end{pmatrix}, \text{ and } \begin{pmatrix} 0 & 0 & 0 & 1 \\ 5 & 4 & 3 & 2 \end{pmatrix},$$

respectively). This gives us four pairs of data points {5, 1}, {4, 0}, {3, 0}, and {2, 0} in the first case; {5, 0}, {4, 1}, {3, 0}, and {2, 0} in the second case, and so on; and we can calculate the correlation between the partial assemblage (an assemblage of one species in this case) and the full species richness pattern. Now imagine a more widespread species that occurs in all but one of the sites. It is possible that spatial distributions are then

$$\begin{pmatrix} 1 & 1 & 1 & 0 \\ 5 & 4 & 3 & 2 \end{pmatrix}, \begin{pmatrix} 1 & 1 & 0 & 1 \\ 5 & 4 & 3 & 2 \end{pmatrix}, \begin{pmatrix} 1 & 0 & 1 & 1 \\ 5 & 4 & 3 & 2 \end{pmatrix}, \text{ or } \begin{pmatrix} 0 & 1 & 1 & 1 \\ 5 & 4 & 3 & 2 \end{pmatrix}.$$

Since these various redistributions (alternatively various species) have correlations with the overall richness pattern of 0.775, 0.258,  $-0.258$ , and  $-0.775$ , respectively, for both cases (i.e., both species), it is obvious that the level of occupancy itself has little effect on the correlation between the spatial distribution of one species and the overall species richness pattern. Therefore, the driver of higher correlations between species incidence and this richness pattern for common species has to be found elsewhere. To this end, we need to investigate the formula for the correlation coefficient, assuming mutual spatial independence of species ranges (more generally "a random process").

### Drivers of the Correlation

Here we explore the correlation between the occupancy pattern of one species (hereafter focal species) and the species richness pattern of the whole assemblage. We express the form for calculating the correlation  $r$  (eq. [A1]

in the online edition of the *American Naturalist*) in terms of proportional occupancy  $p$ , the sum of species richnesses across the sites occupied by the focal species  $D_s$ , the sum of species richnesses across all the sites  $\sum D_j$ , and an assemblage-specific constant  $\kappa$  (for all definitions, see table 1). The correlation then follows as

$$r = \frac{\kappa}{\sum D_j} \frac{D_s - p \sum D_j}{\sqrt{p(1-p)}} \quad (1)$$

(“Thesis 1” [app. A]). The correlation calculated for a single species cannot be affected by the potential spatial dependency of species ranges (see the proof in “Thesis 1” [app. A]). Obviously, keeping occupancy constant, the correlation increases linearly with  $D_s$ . A high  $D_s$  indicates that a given species (with a given  $p$ ) occupies sites with high species richness. The effect of occupancy itself is not so simple. If occupancy is below 0.5 and  $D_s$  remains constant, then  $[p(1-p)]^{1/2}$  is increasing and  $D_s - p \sum D_j$  is decreasing

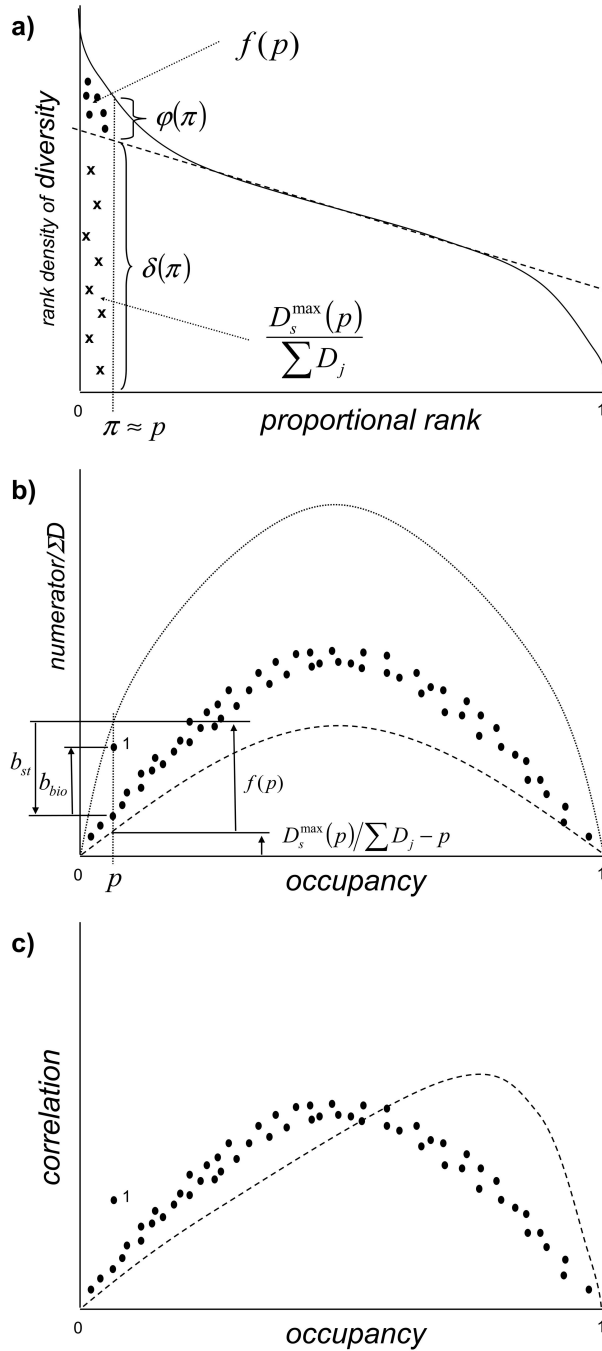
with  $p$ ; the correlation thus decreases with occupancy. Thus, the only way to make the correlation increase with occupancy is to make  $D_s$  increase with  $p$  so fast that this prevails over the effect of the other terms in equation (1) (i.e.,  $p \sum D_j$  and  $[p(1-p)]^{1/2}$ ).

The overall average correlation-occupancy relationship is a hump-shaped curve and thus does not increase for all possible occupancies. However, as we will show, under some conditions the relationship between the correlation and occupancy is left-right asymmetric (*dashed line*, fig. 1c), and thus, the more common species have generally higher correlations—the relationship is generally increasing. Here we define the correlation-occupancy relationship as generally increasing if (and only if) its regression line is increasing. The general increase of the correlation with occupancy depends on the relationship between the sum of richnesses across sites occupied by the focal species ( $D_s$ ) and occupancy, and hereafter we will investigate this relationship.

**Table 1:** Terms and definitions

Pattern of occurrence	A pattern of a species' presences and absences within a set of sites in a landscape
SSRD	Site species richness distribution; the frequency distribution of species richnesses among sites
$p$	Occupancy; the number of occupied sites divided by the total number of sites in question ( $L$ )
$r$	Pearson's correlation coefficient between pattern of occurrence and the pattern of total species richness, that is, between occurrence of a given species (either 0 or 1) and number of species within a site
$r$ -nestedness	Nestedness of species ranges; for a pair of species, the probability that the rarer species is found in the range of the more common species; for a species, mean $r$ -nestedness across all pairs of species that contain the species in question; for an assemblage, mean $r$ -nestedness across all the species of the assemblage
Generally increasing relationship	Relationship is generally increasing if (and only if) its regression line is increasing, regardless of the curvature of the relationship
Indexes $i, j$	Indexes that label summation across species or sites, respectively
$D_s, D_s^{\max}$	Sum of species richnesses across the sites occupied by the focal species and its maximum possible value, respectively
$D_j, \sum D_j$	Species richness of site $j$ and the sum of species richnesses across all the sites of an assemblage, respectively
$L$	Number of all sites of the assemblage
$\bar{D}$	$\bar{D} = \sum D_j / L$
$\sigma_D$	Variance of SSRD
$\kappa$	Assemblage specific constant; $\kappa = \sum D_j / (L - 1) \sigma_D$
$f(p)$	Cumulative residual of observed rank plot of SSRD from a rank plot of the regular model of SSRD with variance set as observed; rank plot is plotted as a rank density plot, that is, the area below the plot is normalized to 1; see figure 1
$b_{st}(p), b_{bio,i}(p)$	Statistical and biological bias from the null model; $i$ indexes the focal species with particular $D_s(p)$ , $b_{st}(p) - b_{bio,i}(p) = (D_s^{\max}(p) - D_s(p)) / \sum D_j$ ; see figure 1
$\pi$	Proportional rank; proportional number of sites with species richness equal or greater than the species richness of the site in question; $\pi \equiv \text{rank} / L$ ; see figure 1
$\varphi(\pi)$	Rank density of the cumulative residual $f(p)$ ; $f(p) \equiv \int_0^p \varphi(\pi) d\pi$ ; see figure 1
$\delta(\pi)$	Rank density of species richness modeled by regular distribution with variance $\sigma_D$ ; $D_s^{\max}(p) = \sum D_j \int_0^p \delta(\pi) d\pi$ ; see figure 1

## Null Model



**Figure 1:** Effect of the species richness distribution on the correlation-occupancy relationship (“Thesis 3” [app. A]). *a*, Rank plot of rank density of species richness ( $\delta$ ; the “rank density” means that the area below each rank plot is 1) is shown. Area ( $x$ ) between 0 and proportional rank ( $\pi$ , which corresponds to occupancy  $p$ ) under plot for a regular distribution (*dashed line*) is proportional to maximum sum of richnesses across occupied sites ( $D_s^{\max}$ ). The area (*circles*) between the rank plot for the regular distribution and the observed distribution (*solid line*) is proportional to cumulative residuals ( $f$ ; the residuals are  $\varphi$ ) from the regular distribution.

First, we argue that under an assumption of a random process, the whole numerator of equation (1) ( $D_s - p \sum D_j$ ) is positive and thus the correlation is positive, which means that all ranges are likely to match the full species richness pattern. It is apparent, given that the richer sites have a greater probability of being occupied (since ranges are assumed to be independent from each other, the species richness of a site increases with its probability of being occupied and vice versa), and thus,  $D_s$  is likely to be greater than  $p \sum D_j$  (for details, see “Thesis 2” [app. A]).

Now we show that the main driver of the relationship between the numerator and occupancy is the distribution of species richnesses among sites (the site species richness distribution [SSRD]). Let us start with a regular SSRD with variance  $\sigma_D$ , that is, the same as observed. We have taken it as the null model, because each SSRD can be investigated using deviations from the regular distribution and because a regular distribution is easy to treat with mathematical calculus. A rank plot of a regular distribution is a line with a slope corresponding to its variance (*dashed line*, fig. 1a; Nekola et al. 2008). The maximum possible values of the numerator follow a parabolic relationship in this case (i.e.,  $D_s^{\max} - p \sum D_j = 3^{1/2} \sigma_D [p - p^2] \sum D_j / L$ , where  $L$  is a number of sites; *dashed curve* in fig. 1b). The reason is entirely formal, and thus, we highlight only the important points of the proof (for details, see “Thesis 3,” “Note 4” [app. A]): (i) the rank corresponds to the occupancy if considering maximum estimation of the correlation, because in such a case the species occupies only sites with highest species richnesses; (ii)  $D_s^{\max}$  corresponds to the area below the rank plot; and (iii) the area under a steep line always changes with a power of 2 (integral from a steep line is always a parabola). Since both the numerator (i.e., the parabola) and the denominator of equation (1) are symmetric about the occupancy of 0.5, a regular distribution produces a symmetric correlation-occupancy relationship. In this case, both common and rare species explain the overall species richness pattern equally well. The maximum value is, however, seldom reached because species are unlikely to occupy only those

*b*, Numerator of equation (1) is proportional to maximum sum of species richnesses ( $D_s^{\max} / \sum D_j - p$ ; i.e., *dashed line* in subplot *a* [i.e.,  $x$  area in *a* lowered by occupancy]) plus cumulative residuals ( $f$ ; i.e., *dashed line* [i.e., *area with circles*] in *a*) minus statistical bias ( $b_s$ ; *dotted relationship*) plus biological bias ( $b_{bio}$ ; the biased point 1). *c*, Correlation-occupancy relationship. If distribution in *a* is symmetric about  $p = 0.5$ , then the numerator in *b* is symmetric and the correlation is symmetric as well (*dotted relationship*). Point 1 shows the biologically biased point in *b*. If the distribution is asymmetric, the correlation-occupancy relationship is also asymmetric (*dashed line*), which is observed as generally increasing.

sites with maximum species richness. If species are distributed independently, the maximum value is lowered by statistical random bias,  $b_{st}(p) \sum D_j$  (fig. 1*b*; “Note 5” [app. A]), and the numerator ( $D_s - p \sum D_j$ ) then follows  $[3^{1/2} \sigma_D (p - p^2)/L - b_{st}(p)] \sum D_j$  (“Thesis 3” [app. A]). This bias will be assessed using computer simulation of assemblages that follow a random process (see “Data Tests”). Nevertheless, this bias is assumed to be roughly symmetrical (“Note 6” [app. A]), and thus it does not affect the asymmetry imposed by the SSRD.

#### *Deviations from the Null Model*

Deviation from the null model is caused by (i) the deviation of the SSRD from the null expectation and/or (ii) the deviation from randomness in species’ spatial distribution caused by particular biological processes, that is, species-environment interactions (namely, habitat selection by individuals and natural selection). We will discuss each source of the deviations separately.

*Site species richness distribution.* The effect of any SSRD can be modeled by adding the cumulative residuals from the regular approach,  $f(p) \sum D_j$ , to the numerator, which then becomes  $[3^{1/2} \sigma_D (p - p^2)/L - b_{st}(p) + f(p)] \sum D_j$  (fig. 1*b*; “Thesis 3” [app. A]). Apparently, if the residual function  $f(p)$  is symmetric about an occupancy of 0.5, the whole numerator is symmetric as well, and no relationship occurs between the correlation and a species level of occupancy (fig. 1*b*, 1*c*). If, however, the residuals have smaller values at smaller occupancies (more precisely, if  $f(p) < f(1 - p)$ ,  $p < 0.5$ ), the relationship becomes asymmetric and thus generally increasing (*dashed curve*, fig. 1*c*). The asymmetry in residuals occurs only if the SSRD is asymmetric. A generally increasing correlation-occupancy relationship then corresponds to negative skewness of the SSRD, and vice versa (for details, see “Thesis 7,” “Note 8” [app. A]).

*Biological processes.* Statistical bias,  $b_{st}$ , in correlation-occupancy relationships has no biological drivers, but there may also be bias caused by species-environment interactions,  $b_{bio}$  (fig. 1*b*). This comprises tendencies to increase or decrease the sum of species richnesses across occupied sites and, thus, to increase or decrease the correlation in comparison with values produced at random. It can be modeled in the same way as the statistical bias by adding a term  $b_{bio,i}(p) \sum D_j$  to the numerator of equation (1) (“Thesis 3” [app. A]). Since the biological bias is species specific, it is indexed as species  $i$ . The numerator then follows  $[3^{1/2} \sigma_D (p - p^2)/L - b_{st}(p) + f(p) + b_{bio,i}(p)] \sum D_j$ .

The contributions of the abovementioned individual factors to the correlation (i.e., the null model assuming a regular SSRD, the deviation from the null model given by a particular SSRD, statistical bias, and biological bias) are

additive, and the correlation can thus be split into four separate terms. The correlation-occupancy relationship of the species  $i$  then follows

$$r_i(p) = \sqrt{3} \frac{\bar{D}}{L-1} \sqrt{p(1-p)} + \kappa \frac{f(p)}{\sqrt{p(1-p)}} - \kappa \frac{b_{st}(p)}{\sqrt{p(1-p)}} + \kappa \frac{b_{bio,i}(p)}{\sqrt{p(1-p)}}, \quad (2)$$

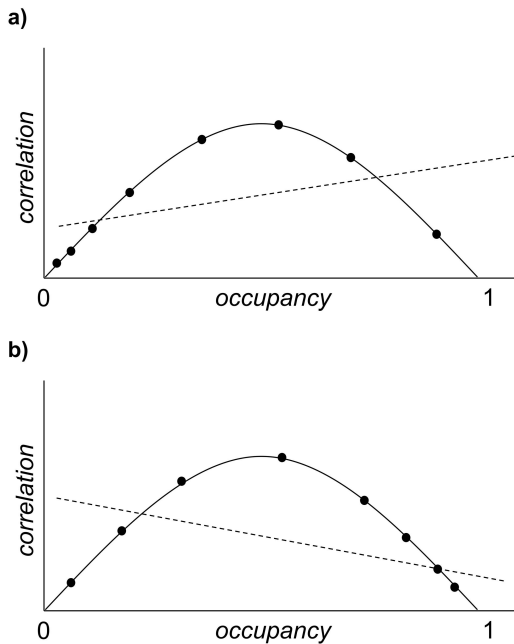
where  $\bar{D} = \sum D_j/L$ . The correlation-occupancy relationship thus has a hierarchical nature. Each additive term represents a different process, each affecting the sum of species richnesses across occupied sites,  $D_s$ , at a different hierarchical level (see above and “Note 9” [app. A]). The first additive term (the null assumption) depends only on mean species richness across all sites and the number of sites and does not produce a general increase in the correlation (due to its symmetry about  $p = 0.5$ ). The second additive term may produce increase or decrease in the correlation with occupancy because of the asymmetry of SSRD. Both the first and second terms represent strict geometrical constraints imposed on the correlation-occupancy relationship, which is not the case for the statistical and biological biases (the third and fourth terms).

#### *Undefined Points*

If all sites have equal species richness ( $\sigma_D = 0$ ) and/or if a species occupies all sites ( $p = 1$ ), the correlation is undefined, as both the numerator and denominator approach 0 (see definition of  $\kappa$  in “Thesis 1” [app. A]; eq. [1]). Therefore, we define  $r(\sigma_D = 0) \equiv 0$  and  $r(p = 1) \equiv 0$ , as there is no pattern to be explained, and there is no pattern to explain anything.

#### *The Role of the Species Occupancy Distribution*

So far we have developed the theory without accounting for the form of the frequency distribution of species occupancies. Clearly, this distribution is irrelevant when examining a single species pattern, that is, how a given species explains the whole species richness pattern. However, since the correlation-occupancy relationship is hump shaped (fig. 1), a large number of widespread species could change the observed relationship toward being generally decreasing, whereas a higher proportion of rare species makes the generally increasing relationship steeper (fig. 2). This necessarily affects the whole observed correlation-occupancy relationship, although it is not related to the power with which a species with a given level of occupancy can explain the overall pattern of species richness.



**Figure 2:** Effect of occupancy distribution on the observed general increase (dashed lines) of the correlation-occupancy relationship. Though the relationship given by the SSRD (full curve) does not change when changing the occupancy distribution, we can observe a general increase (a) or decrease (b) in the case of a prevalence of rare or widespread species, respectively.

#### Extension to a Partial Subassemblage of More Species

The correlation between the richness of a partial assemblage containing more species and the full assemblage richness pattern (e.g., Jetz and Rahbek 2002; Lennon et al. 2004) follows  $r_s = \sum_{k=1}^s w_k r_k$ , where  $s$  is the number of species in the partial assemblage,  $r_k$  is the correlation of the  $k$ th species (eq. [1]), and  $w_k$  (which equals  $[p_k(1-p_k)]^{1/2}/\sigma$ , where  $\sigma$  refers to the variation of occupancies) can be considered as a dominance of  $r_k$ . If ranges are mutually independent, then  $\sigma = [\sum_i p_i(1-p_i)]^{1/2}$ , and thus each dominance,  $w_k$ , is a real number between 0 and 1, and  $\sum_{k=1}^s w_k^2 = 1$ . The correlation for the partial assemblage is therefore an average value across the correlations of all species of the particular assemblage,  $r_k$ 's, weighted by their dominances,  $w_k$ 's. This follows from equation (A2). Generally, the higher the particular correlations of individual species are, the higher is the average correlation. However, the exact behavior of  $r_s$  is rather tricky, for  $r_s$  sometimes jumps down (because  $w_k$  depends on  $p_k$  and because of eventual spatial dependency of species ranges) even when adding a species with high  $r_k$ . This is reflected in oscillations of the “sequential correlation” curves, for example, in figure 1 in Lennon et al. (2004). In this case,

the frequency distribution of occupancies affects the exact behavior of the  $w_k$ 's and thus the exact behavior of the oscillations. The general increase of  $r_s$  with  $r_k$ 's, however, holds.

#### The Role of Species Range Nestedness and Its Relationship to $D_s$

The proper interpretation of  $D_s$  in terms of the properties of a species assemblage is not easy to determine. The best possibility seems, however, to associate it with a measure of how species ranges are nested within each other, which we call  $r$ -nestedness (for the concept and links to the nestedness of assemblages defined by Patterson and Atmar 1986, see Wright and Reeves 1992; Gotelli and Graves 1996; Almeida-Neto et al. 2008; Arita et al. 2008). A natural measure of mutual  $r$ -nestedness of a pair of species is the probability that the less widespread species occupies the range of the more widespread species. Such a measure is proportional to the amount of overlap between two ranges and takes values of 0 if neither range overlaps the other and 1 if the pair of ranges is entirely nested (i.e., the smaller range lies entirely within the larger). The probability is estimated as the ratio of the number of sites shared by both species and the number of sites occupied by the more restricted species (see also Almeida-Neto et al. 2008). The  $r$ -nestedness of a species with the whole assemblage is then a simple mean across all of the mutual  $r$ -nestedness values of the focal species with the other species of the assemblage. Consequently, the  $r$ -nestedness of the whole assemblage is a simple mean of the  $r$ -nestedness across all of the species in the assemblage. Defined in this way,  $r$ -nestedness is proportional to the sum of richnesses  $D_s$  (for details, see theses 10, 11, and 12 [app. A]; fig. C1 in the online edition of the *American Naturalist*).

In fact,  $r$ -nestedness (alternatively  $D_s$ ) is the proximate driver of the correlation between occupancy and overall species richness because the SSRD only imposes constraints on it. Indeed, if the SSRD comprises a small number of sites with high richness (i.e., it is positively skewed), rare species are forced to occupy the same sites, which increases their  $r$ -nestedness, and there is little room to decrease the  $r$ -nestedness by any biological process.

#### Data Tests

Using three data sets on European birds, we test (i) to what extent in practice the correlation-occupancy relationship driven by the SSRD follows a random process and (ii) which species contribute significantly to departure from such a random process.

### Data

1. We recorded spatial distribution of 146 bird species at each of 768 points along a linear east-west transect in south Bohemia and Moravia. Birds were mapped by the point count method (Bibby et al. 1992) within 150 m around each point during five early-morning visits in the breeding seasons (April–June) of 2004 and 2005. Points were separated by about 400 m. For the purpose of the analysis, we merged every three consecutive points into one, so that the final number of sites was 256.

2. We recorded spatial distribution of 216 bird species across all of the 624 mapping quadrats from the breeding bird atlas of the Czech Republic. Each quadrat spanned 6' latitude and 11' longitude (i.e., about 12 km × 11.1 km) and contained records of the presence of all species with confirmed or probable breeding during the period 1985–1989 (Štastný et al. 1996).

3. We used a square of 16 × 16 mapping quadrats within central Europe, taken from the European breeding bird atlas (Hagemeijer and Blair 1997). Each quadrat was about 50 km × 50 km and also contained presence/absence data for breeding species (see Storch and Šizling 2002).

### Tests

The data test was based on simulation of 100 assemblages of 144, 216, and 204 species and 256, 624, and 256 sites for the transect, the Czech Republic, and the central European data, respectively. We constructed randomized incidence matrices by simulation, which comprised three steps.

1. The underlying distribution of the probabilities of occupancy of each site was set up using the observed SSRD. We used a special algorithm that was not biased by spatial autocorrelation or the distribution of gaps in a species-incidence matrix and was robust against variation in number of species and sites (see app. B in the online edition of the *American Naturalist*).

2. For each species, a number of occupied sites was drawn from the observed species-occupancy distribution. This does not mean that only observed occupancies were drawn but that the final distribution followed the observed distribution (for details, see app. C; fig. C8).

3. Each species was distributed at random across sites such that no site could be occupied more than once by a given species. The first incidence was placed at a site according to the underlying distribution of probability of occupancy, and the other incidences (if any) were then placed following the same probabilities but under the condition that only free sites could be occupied (for exact procedures, see app. C). In consequence, the observed proportional richness in species-poor sites could be higher

than the respective underlying probability of being occupied, as common species spread out also into sites with a low probability of being occupied.

We performed 100 simulations for a whole species assemblage and calculated the correlation-occupancy relationships for the observed data sets and all of the simulated data sets. Species in the observed data sets departing from the random process were identified as those that lie out of the range delimited by 100 simulated relationships. This range contains 92% of all random values, with a confidence of 0.99 (the theory of the content-confidence limits was introduced by Wilks [1941]; for a detailed explanation, see “Wilks’s  $\beta$  Content- $\gamma$  Confidence Nonparametric Tolerance Limits” and fig. C7, which are according to Jílek [1988]). The effect of the shape of the SSRDs was tested by calculating their skewness.

Furthermore, we tested agreement between theory, data, and simulations for the  $r$ -nestedness- $D_s$  (“Thesis 10” [app. A]),  $r$ -nestedness-occupancy (“Thesis 11” [app. A]),  $D_s$ -occupancy (“Thesis 2” [app. A]),  $b_{st}$ -occupancy (a statistical bias), and correlation- $r$ -nestedness (“Thesis 12” [app. A]) relationships, as well as the agreement between the observed and simulated SSRDs (figs. C1–C6).

### Results

#### *Reliability of the Construction of Randomized Incidence Matrices*

All simulations presented here depend on the correct randomization of incidence matrices such that the row and column distributions are simultaneously retained. The first test thus focuses on the reliability of the random process used. Randomly distributing incidences and assuming that each species is distributed independently from others, constrained only by its occupancy and the underlying SSRD, resulted in surprisingly realistic SSRDs (fig. C6). Neither the mean, variance, skewness, nor kurtosis of the proportional diversity ( $D_i/\sum D_j$ ) distribution fell farther than 1.5% away from the values of observed distributions for all three data sets, and they all fell between the maximum and minimum of 100 simulations. This indicates that the randomization process is reliable and the null model can be used for further testing.

#### *Geometrical Constraints: The Correlation-Occupancy Relationship, Skewness of SSRD, and Occupancy Distribution*

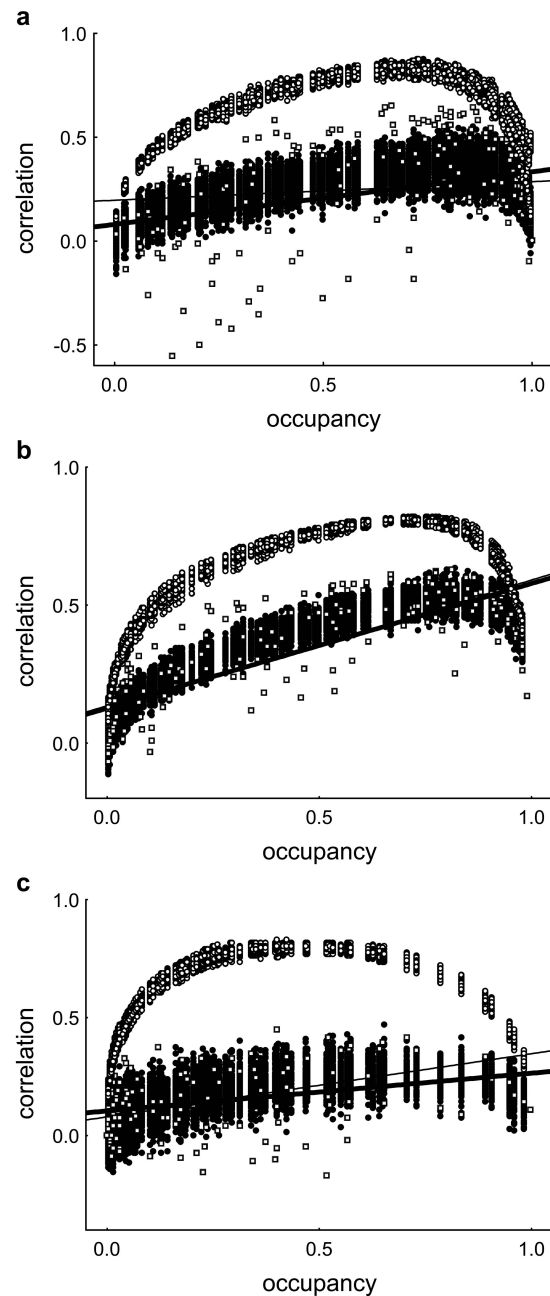
The skewnesses of the observed SSRDs were 0.23,  $-0.78$ , and  $-0.92$ , with standard errors of 0.15 ( $N = 256$ ), 0.1 ( $N = 624$ ), and 0.15 ( $N = 256$ ) for the transect, Czech Republic, and central European data, respectively. This

means that only in the case of the transect does the SSRD tend toward a shape for which a negative relationship between the correlation and occupancy would be expected, although zero skewness falls in the 95% confidence interval (assuming  $t$  distribution) in this case. The effect of the shape of SSRDs on the relationship is shown in figure 3 (*open circles*). As predicted by the skewness, the maximum estimations reveal asymmetry toward a generally increasing relationship in the observed central European and Czech data (fig. 3*a*, 3*b*) and toward a generally decreasing relationship in the transect data (fig. 3*c*). The transect data, however, reveal a prevalence of rare species (the skewness of the occupancy distribution is 1.2), which causes the observed general increase of the correlation-occupancy relationship. Conversely, the central European data reveal a slight prevalence of common species (the skewness of the occupancy distribution is  $-0.6$ ), and thus, the observed general increase of the correlation-occupancy relationship occurs rather in spite of the occupancy distribution; it is the SSRD that is responsible for the observed effect. The Czech Republic data reveal both negative skewness of the SSRD and positive skewness of the occupancy distribution (0.2), and thus, the general increase in relationship between the correlation and occupancy is supported by both distributions in this case (*solid lines*, fig. 3).

#### *Biological Drivers: Deviation of Individual Species from the Random Pattern*

In all three observed data sets, there are species that lie outside the 92% interval (with confidence = 0.99; fig. C7) of the associated simulations, and those species thus reveal nonrandom  $r$ -nestedness (squares that fell out of the range delimited by 100 simulations marked by solid circles in fig. 3). These species are listed in table 2. They cause a flatter observed regression line ( $r \cong 0.31$ ,  $P < .001$ ,  $N = 256$ ) in comparison with the simulation ( $r \cong 0.67$ ,  $P < .001$ ,  $N = 25,600$ ) in the case of the transect and a steeper regression line ( $r \cong 0.34$ ,  $P < .001$ ,  $N = 256$ ) than simulated ( $r \cong 0.25$ ,  $P < .001$ ,  $N = 25,600$ ) in the case of the central European data. The observation ( $r \cong 0.81$ ,  $P < .001$ ,  $N = 624$ ) does not deviate from the simulation ( $r \cong 0.89$ ,  $P < .001$ ,  $N = 62,400$ ) in the case of the Czech Republic data (bold and thin lines for observation and simulation, respectively, in fig. 3). The lists of species that deviate significantly in their  $r$ -nestedness from the random process (table 1) reveal that species that have higher  $r$ -nestedness than predicted occupy mostly lowlands and wetlands, whereas those with lower  $r$ -nestedness live mostly in mountains and coniferous forests.

Both simulations and data follow the relationships as predicted by these 1–3 and 10–12 (app. A) and figures C1–C5.



**Figure 3:** Correlation-occupancy relationship for maximum estimate (*open circles*; terms 1, 2 in eq. [2]), random process (*solid circles*; maximum estimate minus statistical bias of correlation; i.e., term 3 in eq. [2]), and observation (*squares*; random process plus biological bias of correlation; i.e., term 4 in eq. [2]) in the cases of central European (*a*), Czech Republic (*b*), and transect (*c*) data. Bold and thin lines are regression lines for observation and random approach, respectively. Those two regression lines overlap each other in *b*.



**Table 2:** List of species that reveal high or low  $r$ -nestedness (x) for their occupancy in comparison with a random process

High- $r$ -nestedness species	T	CR	EU	Low- $r$ -nestedness species	T	CR	EU
<i>Acrocephalus arundinaceus</i>		x	x	<i>Accipiter nisus</i>			x
<i>Acrocephalus schoenobaenus</i>		x	x	<i>Aegolius funereus</i>			x
<i>Acrocephalus scirpaceus</i>	x	x		<i>Anas platyrhynchos</i>		x	
<i>Alceda atthis</i>		x		<i>Anthus pratensis</i>		x	
<i>Anas clypeata</i>		x	x	<i>Anthus trivialis</i>	x		
<i>Anas crecca</i>		x	x	<i>Anthus spinoletta</i>			x
<i>Anas querquedula</i>		x	x	<i>Ardea purpurea</i>			x
<i>Anas strepera</i>		x	x	<i>Bonasa bonasia</i>		x	x
<i>Anser anser</i>			x	<i>Bubo bubo</i>		x	x
<i>Anthus pratensis</i>			x	<i>Carpodacus erythrinus</i>		x	
<i>Asio otus</i>		x		<i>Carduelis spinus</i>	x	x	
<i>Aythya ferina</i>			x	<i>Carduelis flammea</i>			x
<i>Botaurus stellaris</i>			x	<i>Ciconia ciconia</i>		x	
<i>Bucephala clangula</i>			x	<i>Ciconia nigra</i>		x	
<i>Certhia brachydactyla</i>		x		<i>Cinclus cinclus</i>		x	x
<i>Charadrius hiaticula</i>			x	<i>Coccothraustes coccothraustes</i>	x		
<i>Chlidonias niger</i>			x	<i>Corvus corax</i>		x	
<i>Ciconia ciconia</i>			x	<i>Dendrocopos leucotos</i>			x
<i>Ciconia nigra</i>			x	<i>Dendrocopos syriacus</i>			x
<i>Circus aeruginosus</i>			x	<i>Falco peregrinus</i>			x
<i>Dendrocopos minor</i>		x		<i>Falco vespertinus</i>			x
<i>Dendrocopos medius</i>			x	<i>Glauclidium passerinum</i>			x
<i>Emberiza schoeniclus</i>	x	x		<i>Lanius minor</i>			x
<i>Ficedula hypoleuca</i>			x	<i>Loxia curvirostra</i>	x	x	x
<i>Fulica atra</i>	x			<i>Merops apiaster</i>			x
<i>Gallinula chloropus</i>		x		<i>Motacilla cinerea</i>		x	x
<i>Gallinago gallinago</i>			x	<i>Nucifraga caryocatactes</i>		x	x
<i>Grus grus</i>			x	<i>Nycticorax nycticorax</i>			x
<i>Hippolais icterina</i>	x		x	<i>Otis tarda</i>			x
<i>Ixobrychus minutus</i>		x		<i>Periparus ater</i>	x		
<i>Lanius excubitor</i>			x	<i>Lophophanes cristatus</i>	x		
<i>Larus ridibundus</i>			x	<i>Pica pica</i>		x	
<i>Limosa limosa</i>		x	x	<i>Picoides tridactylus</i>			x
<i>Locustella fluviatilis</i>		x		<i>Picus canus</i>			x
<i>Locustella luscinioides</i>		x	x	<i>Prunella collaris</i>			x
<i>Locustella naevia</i>			x	<i>Pyrrhula pyrrhula</i>	x		
<i>Lullula arborea</i>			x	<i>Regulus ignicapillus</i>	x		x
<i>Luscinia luscinia</i>			x	<i>Regulus regulus</i>	x		
<i>Cyanistes caeruleus</i>	x			<i>Saxicola torquata</i>		x	x
<i>Perdix perdix</i>			x	<i>Tetrao tetrix</i>		x	x
<i>Podiceps nigricollis</i>		x	x	<i>Tetrao urogallus</i>			x
<i>Podiceps grisegena</i>			x	<i>Troglodytes troglodytes</i>	x		
<i>Porzana porzana</i>		x		<i>Turdus merula</i>		x	
<i>Rallus aquaticus</i>		x		<i>Turdus pilaris</i>		x	
<i>Riparia riparia</i>			x	<i>Turdus torquatus</i>		x	x
<i>Sylvia borin</i>	x						
<i>Sylvia communis</i>			x				
<i>Tringa totanus</i>		x	x				
<i>Tringa ochropus</i>			x				
<i>Tyto alba</i>			x				

Note: Results for the three data sets (T = transect, CR = Czech Republic, and EU = central Europe);  $P \leq .02$ ; see also squares that lie outside the area filled by circles in figure 3.

## Discussion

We have shown that the widely observed greater contribution of common species to overall patterns of species richness can be attributed to several factors, most of which are geometrical or statistical rather than biological. We found that the key characteristic that is responsible for the correspondence between the spatial pattern of species' occurrence and the species richness pattern of a whole assemblage is  $D_s$ , the sum of the richnesses across the sites that are occupied by the focal species. If this sum is high relative to the constraints imposed by the level of occupancy, the occurrence of a given species closely follows the overall richness pattern, as the species occurs on average at the most species-rich sites and does not occur at those that are species poor. Our theoretical considerations can be interpreted as follows. If the frequency distribution of species richness (the site species richness distribution) is symmetric (there is an equal proportion of species-poor and species-rich sites), the maximum correlation between species occurrence and species richness is attained by those species that occupy just one-half of all available sites. This is because those species have an equal chance of occupying the majority of sites with high overall richness and of not occupying the sites with low richness. However, if there are only a few sites with low species numbers (i.e., the SSRD is left skewed), the species that occupy just one-half of the sites cannot match the overall richness pattern well, simply because they can occupy only a small proportion of the species-rich sites. The relatively common species can match the overall richness pattern better in this case, as they can occupy nearly all of the species-rich sites and at the same time not occupy the species-poor sites. However, when a species is extremely common, it must occupy both species-rich and species-poor sites. The level of occupancy that allows the strongest correlation with the overall richness pattern thus depends on the proportion of species-rich and species-poor sites, that is, on the skewness of the SSRD.

We investigated the relationships between (i) the nestedness of ranges,  $r$ -nestedness; (ii) the sum of species richnesses of sites occupied by a focal species,  $D_s$ ; and (iii) the correlation between pattern of occurrence of the focal species and the whole species richness pattern. All the measures intuitively seem to be correlates of the same phenomenon, that is, the overlap in species occurrences. However, only  $r$ -nestedness and  $D_s$  are proportional to each other, while the correlation first increases and then decreases with the other two measures. Therefore, the correlation is not proportional to the other two measures and must be a measure of a different phenomenon. The difference consists of the fact that whereas  $r$ -nestedness and  $D_s$  measure only overlap in species occurrences, without

reflecting how such occurrences miss each other, the correlation reflects both the overlap and the nonoverlap (in other words, absences are as important as presences in the incidence matrix). This can be seen as an explanation of why the incidences of both the extremely common and extremely rare species correspond poorly to the overall species richness pattern.

This reasoning applies if we assume random distributions of species incidences within the strict geometrical constraints given by their occupancies and an SSRD. This effectively means an assumption of spatial independency of species ranges. As we have shown, these constraints are relatively broad, so that biological processes can both strengthen or weaken the correlation. The species whose spatial distribution follows the overall species richness pattern more closely than predicted have at the same time higher  $r$ -nestedness, as they preferentially occupy the sites with higher species richness and their ranges are thus spatially nested within those of other species. However, our data indicate that the deviations from the random patterns, though often prominent, do not substantially affect the overall pattern shaped only by the SSRD. The reason is that the biological deviations toward higher or lower  $r$ -nestedness are more or less symmetrical; that is, we find both species that preferentially occupy species-rich and species-poor sites. The overall pattern can thus be attributed to random processes inasmuch as there is no bias from randomness.

The SSRD has been proven as the main driver of the correlation-occupancy relationship. Though this distribution almost necessarily results from the way in which species ranges aggregate in space (Storch et al. 2008), there is a gap in theory on this topic. The SSRD is thus far a largely unexplored macroecological pattern that could potentially be used to discriminate between various models of species ranges (Kunin 1998; Harte et al. 2005; Šizling and Storch 2007; Hui and McGeoch 2008) and may illuminate processes responsible for the uneven distribution of biodiversity across Earth's surface.

The left-skewed SSRD, which we have shown to be the main driver of the observed patterns, may not be typical for the majority of data. Our analyses show such skewness in only two of three cases, and there is no reason why this pattern should necessarily be expected elsewhere. However, the disproportionate influence of common species on patterns of overall species richness has been reported quite universally (Gaston 2008). It is probable that the other contribution to the positive relationship between the correlation (i.e., between species occurrence and species richness pattern) and species occupancy is the right-skewed occupancy distribution, that is, the fact that most species occupy only a small portion of available sites. The positive relationship then arises from the increasing part

of the hump-shaped relationship between occupancy and the correlation (see fig. 2). Indeed, our data suggest that the influence of the right-skewed SSRD can be compensated by a right-skewed occupancy distribution (e.g., as in the case of the transect data), which is in fact the generally reported pattern (Gaston and Blackburn 2000; Gaston 2003). Whether the diversity and occupancy distributions are mutually interconnected to produce the positive relationship between correlation and species occupancy in all cases remains unexplored.

We have shown that the disproportionate influence of common species on spatial patterns of overall species richness is almost inevitable. This does not mean, however, that deeper examination of the pattern is not interesting. If we know what to look for, that is, how to disentangle the geometrical necessity from the biologically relevant signal, we can explore the deviation from the random pattern for each species. For the avian data sets considered here, the gradient from lowland wetlands to mountainous coniferous forests is particularly important (table 1). This is the most important habitat gradient distinguishing bird assemblages in central Europe (Reif et al. 2008), and it also represents a gradient of decreasing species richness. The species that deviate in their  $r$ -nestedness from the random process thus represent indicators of an environment that is either very suitable or generally unsuitable to most species within a given occupancy class.

#### Acknowledgments

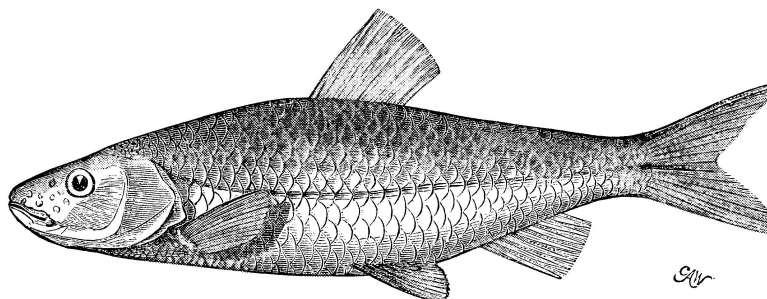
A.L.Š. was supported by the Marie Curie Fellowship 039576-RTBP-EIF. K.J.G. holds a Royal Society–Wolfson Research Merit Award. The study was supported by Czech Ministry of Education grants LC06073 and MSM0021620845 and the grant agency of the Academy of Sciences of the Czech Republic (IAA601970801 and KJB601110919).

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Chub (*Semotilus rhotheus*) from “Notes on Fresh-Water Fishes of New Jersey” by Charles C. Abbott (*American Naturalist*, 1870, 4:99–114).