Abundance, diversity and body size: patterns from a grassland arthropod community

EVAN SIEMANN*, DAVID TILMAN and JOHN HAARSTAD
Department of Ecology, 1987 Upper Buford Circle, University of Minnesota, St. Paul, MN 55108 USA

Summary

1. The empirical relationships among body size, species richness and number of individuals may give insight into the factors controlling species diversity and the relative abundances of species. To determine these relationships, we sampled the arthropods of grasslands and savannahs at Cedar Creek, MN using sweep nets (90,525 individuals of 1225 species) and pitfall traps (12,721 individuals of 92 species). Specimens were identified, enumerated and measured to determine body size.

2. Both overall and within abundant taxonomic orders, species richness and numbers of individuals peaked at body sizes intermediate for each group. Evolution could create unimodal diversity patterns by random diversification around an ancestral body size or from size-dependent fitness differences. Local processes such as competition or predation could also create unimodal diversity distributions.

3. The average body size of a species depended significantly on its taxonomic order, but on contemporary trophic role only within the context of taxonomic order.

4. Species richness ($S_i$) within size classes was related to the number of individuals ($I_j$) as $S_i = I_j^{.3}$. This relationship held across a 100,000-fold range of body sizes. Within size classes, abundance distributions of size classes were all similar power functions. A general rule of resource division, together with similar minimum population sizes, is sufficient to generate the relationship between species richness and number of individuals.

5. Smaller bodied species had slightly shallower abundance distributions and may, in general, persist at lower densities than larger species.

6. Our results suggest there may be fewer undescribed small arthropod species than previously thought and that most undescribed species will be smaller than arthropods.

Key-words: abundance distributions, allometry, conservation, insects, minimum viable population sizes


Introduction

Two fundamental ecological problems are understanding what determines the number of species in a community and the relative abundances of these species (e.g. Preston 1948; MacArthur 1957; Hutchinson 1959; Whittaker 1970; Sugihara 1980; May 1986; Brown 1995; Rosenzweig 1995). Body size is correlated with an animal’s metabolic rate, assimilation efficiency, generation time, reproductive rate, diet, predators, perception of heterogeneity and other characteristics (Townsend & Calow 1981; Peters 1983; Morse, Stork & Lawton 1988; Brown 1995; West, Brown & Enquist 1997). Therefore, determining how species are distributed among body size classes and abundance classes and how these relationships depend on trophic role and taxonomic order may give insights into the determinants of diversity and abundance patterns.

Available data suggest that species richness is highest at intermediate body sizes within local communities, regions and globally (Stanley 1973; May 1986; Brown, Marquet & Taper 1993; Blackburn & Gaston 1994a, b; Brown 1995; Siemann, Tilman & Haarstad 1996; Navarrete & Menge 1997) and perhaps so is the number of individuals (e.g. Janzen 1973; Morse et al. 1985; Morse et al. 1988; Bassett & Kitching 1991; Siemann et al. 1996; Navarrete & Menge 1997; but
Materials and methods
Arthropods were sampled in 48 grasslands and oak savannahs at Cedar Creek, Minnesota in 1992 using both sweep nets (48 fields and savannahs) and pitfall traps (37 fields and savannahs). These grasslands and savannahs are dominated by herbaceous vegetation, especially native perennial prairie plants (Inouye et al. 1987). Sweep net sampling was undertaken at midday when the vegetation was dry. A sample represents the arthropods captured by 100 swings of a 38-cm diameter muslin net that was swung with each pace while walking a 50-m transect located near the middle of the field. Sampling was carried out semi-monthly from mid-May to mid-September for most of the fields, giving nine sweep samples per field, although some fields were sampled fewer times. Pitfall traps were 950 cm³ plastic containers with drainage pinholes in the bottom and lids with 2.5 cm holes. In May, four traps were buried in each field, with lids flush to the ground and lid holes covered. They were open from 10 July until 10 October and all dead or living arthropods were emptied every 10 days (100 days total).

Specimens were manually sorted and identified to species when possible, or otherwise to morphospecies within known genera or families, and enumerated. Eleven morphospecies of small-bodied arthropods that we were confident represented more than one species were considered two species of equal abundance because we could not reliably classify them more precisely.

Five individuals of the oldest life stage caught of each species (90% of the species in our samples were represented by only one life stage), unless fewer were caught, were measured for length, width and thickness using an optical micrometer. Length was the distance from forehead to tip of the abdomen. Width and thickness were measured at the widest and thickest parts, respectively, of the abdomen, thorax or head. We did not include antennae, legs, wings, ovipositors, mouthparts or any other projection in our measurements. The product of these three measurements we called biovolume. For Orthoptera, a sex-weighted average was used to correct for sexual dimorphism in size.

We summed and log transformed the number of species and the number of individuals in log, biovolume classes. A class of size N included those species ranging in biovolume from $2^{N-1}$ mm³ up to and including $2^N$ mm³. We used a nonparametric smoothing procedure (see Maurer & Brown 1988) to fit regressions through these points because the arbitrarily chosen locations and width of classes could influence the patterns we observed. In brief, this method fits a curve to the relationship between the number of species or number of individuals and body size by summing them within an interval of fixed width (1 unit in log, scale) that is moved in small increments (0.01 in log, scale) through the entire range of body sizes.

We examined body size patterns within and among trophic groups. Field observations and a literature review (Siemann 1997) were used to assign each species to one of four trophic categories. The parasite
category included all species that were either parasitic in the adult stage or were parasitic as larvae regardless of adult diet (mainly nectar, pollen and/or host fluids; Sweetman 1936; Clausen 1940). Non-parasites were classified into three other categories: (i) herbivore; (ii) predator, or (iii) detritivore, based on whether the adults fed primarily on (a) plants (b) animals or (c) dead matter or fungi, respectively. We performed an unbalanced ANOVA using the GLM procedure in SAS (version 6.09) to determine how a species’ body size depended on evolutionary history (categorical variable for taxonomic order), trophic role (categorical variable for trophic category) and the interaction of these two factors, for sweep-sampled species.

For the entire sweep net and pitfall trap datasets, analysed separately, simple regressions tested the dependence of species richness on the number of individuals and on the total biovolume summed across all of the individuals in the size class. Because the classes were arbitrarily located, regressions were repeated using randomly chosen locations (2\(^r\) biovolume classes, where N was an integer and r was a random number between 0 and 1). Furthermore, because class width was arbitrary, regressions were repeated with \(c^{N+r}\) biovolume classes. Additionally, the eight most abundant and speciose taxonomic orders and the four trophic groups in sweep net samples were examined to determine how they differed.

A relationship between species richness and number of individuals could arise from size-dependent differences in sampling effort. In order to estimate the completeness of our survey, for each sampling method and for each size class, increasingly larger random subsamples of all the individuals of that size class, up to a maximum of 500 such subsamples per size class, were used to construct species accumulation curves. The average of 10 such curves was fitted with a saturating curve [\(\text{Species} - (\text{Species} - a) \times e^{-b\text{individuals}}\)] in order to estimate the asymptote, which approximates the number of species that would be caught with infinite sampling effort if this increased effort did not involve increased sampling area or sampling dates. In addition, examining relationships between abundance and diversity vs. body size in multiple, simultaneously sampled orders gives insight into the role of sampling biases in producing the patterns.

All regressions were ordinary least-squares regressions. The only species of size class 13, Anax junius (Drury), a large dragonfly that was often seen in transects but rarely caught because of its agility and visual acuity, was excluded from all regressions.

### Results

Sweep net sampling caught 90,525 individuals of 1225 species (Table 1). Pitfall trap sampling caught an additional 12,721 individuals of 92 species (Table 1). In total this represented 1281 species (of which 59 were noninsects and the remainder insects), 169 families and 17 orders. Species-level identifications were possible for 89.8% of the specimens. The remaining specimens were identified to morphospecies, with 76% within known genera and the remaining 24% within known families. Excluding parasites, 17.5% of the species in our samples changed trophic roles during development with 67% of these switches being between herbivore and detritivore categories.

With each species as a separate data point, the log of abundance was unrelated to the log of body size for either sampling method as fitted by any linear, polynomial, power, exponential or peak function (small dots in Fig. 1a, b; \(r^2 < 0.01\), for all cases \(N_{\text{sweep}} = 1225, N_{\text{pitfall}} = 92\)).

Log species richness and log biovolume had a unimodal relationship for the entire sweep net (Fig. 1c) and pitfall trap datasets (Fig. 1d) and within each abundant sweep-net-sampled taxonomic order (Fig. 2). In an ANOVA, the size of a species depended significantly on its taxonomic order and the interaction of trophic group and taxonomic order, but not on trophic role alone (Table 2). For pitfall and sweep net datasets, the log of total number of individuals summed across all the species in log biovolume size classes was a unimodal function of log biovolume, although there was a hint of bimodality (large circles and lines in Fig. 1a, b). For each of the eight most abundant taxonomic orders, the number of individuals was a unimodal function of log biovolume (large circles and lines in Fig. 3).

For both sweep-net-sampled and pitfall-sampled arthropods, abundance distributions for species within single size classes were all of the form:

\[ A_i = A_i m^m, \]

where \(A_i\) is the abundance of the \(r^{th}\) most abundant species in the \(i^{th}\) size class and \(m\) is a positive constant describing how much more abundant a species is compared to the next most abundant species. Plotted as log abundance vs. log rank, these distributions were roughly parallel decreasing lines, with \(m\), on average, equal to 1.9 (Fig. 4, Table 3). Broken-stick, geometric, log-series or log-normal distributions are less linear in log(rank) vs. log(abundance) space (Fig. 4c,d,e). For sweep-sampled arthropods, smaller than modal size classes had significantly shallower distributions than larger than modal size classes [Fig. 4, Table 3; \(m = 1.41 + 0.10 \log_2\) (biovolume), \(r^2 = 0.67, F_{1,13} = 26.01, P < 0.001;\) size class -3 omitted]. Omitting size class 12 which was not well sampled (Table 3) did not change this result [\(m = 1.43 + 0.09 \log_2\) (biovolume), \(r^2 = 0.59, F_{1,12} = 17.42, P < 0.01;\) size classes -3 and 12 omitted]. However, there was no such relationship in the pitfall-sampled data, where the slope of the rank abundance distributions was independent of body size (Fig. 4; Table 3; \(P = 0.84\)).

In sweep data, species richness (S) in size classes was related to the number of individuals (I) in size
Table 1. Species and individuals within taxonomic and trophic groups

<table>
<thead>
<tr>
<th>Group</th>
<th>Species</th>
<th>Individuals</th>
<th>Species</th>
<th>Individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Araneida</td>
<td>58</td>
<td>929</td>
<td>1</td>
<td>14</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>212</td>
<td>6405</td>
<td>52</td>
<td>11498</td>
</tr>
<tr>
<td>Diptera</td>
<td>252</td>
<td>6016</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Hemiptera</td>
<td>89</td>
<td>22660</td>
<td>8</td>
<td>73</td>
</tr>
<tr>
<td>Homoptera</td>
<td>109</td>
<td>39476</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Hymenoptera</td>
<td>335</td>
<td>1936</td>
<td>8</td>
<td>639</td>
</tr>
<tr>
<td>Lepidoptera</td>
<td>99</td>
<td>1493</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Orthoptera</td>
<td>50</td>
<td>11353</td>
<td>22</td>
<td>496</td>
</tr>
<tr>
<td>Miscellaneous</td>
<td>21</td>
<td>259</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>1225</td>
<td>90525</td>
<td>92</td>
<td>12721</td>
</tr>
</tbody>
</table>

For the trophic groups in sweep data, species richness was a unimodal function of body size although the peak sizes and numbers of species differed among the groups (Fig. 5a). The numbers of individuals were unimodal functions of body size for parasites and predators and bimodal for herbivores and detritivores (Fig. 5b). $S_i$ and $I_i$ were strongly related for parasites, herbivores and predators but less so for detritivores (parasite: exponent $= 0.67$, $r^2 = 0.81$; herbivore: $0.48$, $0.83$; predator: $0.54$, $0.93$; detritivore: $0.32$, $0.28$).

Species accumulation curves had estimable asymptotes for all but the smallest and largest size classes (Table 3). The relationship between number of individuals and asymptotic species richness ($S_{\text{asym}}$) was almost identical to the relationship between number of individuals and observed species richness (sweep: $S_{\text{asym}} = 1.37I_i^{0.50}$, $r^2 = 0.74$, $N = 15$, $P < 0.01$; pitfall: $S_{\text{asym}} = 0.46I_i^{0.50}$, $r^2 = 0.72$, $N = 9$, $P < 0.01$).

### Discussion

We found repeatable patterns in the distributions of diversity and abundance vs. body size. Species richness and numbers of individuals had unimodal relationships with body size within both the entire sweep net and pitfall data (Fig. 1a–d) and within trophic groups (Fig. 5). But perhaps more importantly, within each of the eight most abundant and speciose taxonomic orders, species richness and numbers of individuals had unimodal relationships with body size (Figs 2 and 3). Among orders, the sizes with peak diversity and abundance differed more than 100-fold. Overall, within trophic groups and within the eight most abundant taxonomic orders, species richness within size classes was related to the number of individuals as a power function (Fig. 1e, f).

The body size of an individual species depended on taxonomic order and its trophic role only in the context of taxonomic order, but not on trophic role alone.
Arthropod diversity, abundance and size

Fig. 1. Body size relationships for sweep net (left column) and pitfall trap (right column) samples. For each graph, the curves represent the distributions obtained from the smoothing procedure described in Methods. The large circles are the numbers of species or individuals in integral $N$ biovolume categories (from $2^{N-1}$ to $2^N$ mm$^3$). (a, b) Number of individuals summed across species in biovolume categories. Small dots are the size and abundance of each species. (c, d) Species richness in biovolume categories. (e, f) Relationship between species richness and number of individuals in integral biovolume categories. Numbers identify the $2^N$ mm$^3$ size classes (after Siemann et al. 1996).

This result, together with the unimodal distributions of species richness and individuals vs. body size for taxonomic orders (Fig. 2) and different modal sizes for orders, strongly suggests that the evolutionary history or organisms is a major factor constraining body sizes (see Ricklefs & Schluter 1993). This may be the result of simple, random diversification around some ancestral body size (e.g. Stanley 1973; Maurer, Brown & Rusler 1992). Alternatively, several models predict unimodal species richness patterns on regional or continental scales as the result of evolutionary divergence of body sizes of species away from an optimal size (Hutchinson & MacArthur 1959; Dial & Marzluff 1988; Maurer et al. 1992; Brown et al. 1993; Marquet et al. 1995). In these models, individuals of this optimal size are the best at simultaneously meeting a pair of constraints, such as metabolic efficiency vs. reproductive rate (Dial & Marzluff 1988, Brown et al. 1993).

It is possible that local patterns of species richness and body size are simply the result of random sampling of individuals or species from a regional pool. However, animals of different sizes differ in many ways, such as mobility, predation risk and metabolic requirements (Peters 1983; West et al. 1997), that may affect their likelihood of colonizing or persisting in a given local habitat. Therefore, local patterns may at least partly be the result of local interspecific interactions such as competition, predation and/or parasitism (Brown & Nicoletto 1991). Comparisons of species richness and body size distributions at regional and local scales (Burbidge & McKenzie 1989; Brown & Nicoletto 1991; Blackburn & Gaston 1994a) suggest that both regional and local processes are important.
Fig. 2. The relationship between species richness and body size for the eight most abundant orders in sweep net samples [the large circles are the numbers of species or individuals in integral $N$ biovolume categories (from $2^{N-1}$ to $2^N$ mm$^3$)] with mean and modal body size (mm$^3$) for species in the order.

Table 2. ANOVA to determine the dependence of species body size (Log of biovolume in mm$^3$) on taxonomic order (categorical variable ORDER), trophic group (categorical variable TROPH) and their interaction(ORDER*TROPH), for sweep-net-sampled arthropods. Overall model $F$-value = 29.88, $P$-value < 0.0001, $R^2 = 0.25$

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>SS</th>
<th>MS</th>
<th>F-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>ORDER</td>
<td>15</td>
<td>133.14</td>
<td>8.87</td>
<td>21.89</td>
<td>0.0001</td>
</tr>
<tr>
<td>TROPH</td>
<td>3</td>
<td>1.03</td>
<td>0.34</td>
<td>0.84</td>
<td>0.4704</td>
</tr>
<tr>
<td>ORDER*TROPH</td>
<td>8</td>
<td>26.52</td>
<td>3.32</td>
<td>8.18</td>
<td>0.0001</td>
</tr>
<tr>
<td>Error</td>
<td>1198</td>
<td>486.32</td>
<td>0.41</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

in shaping local species richness and body size distributions. Significantly smaller arthropod species in Cedar Creek grasslands with naturally (Siemann, Haarstad & Tilman, in press) and experimentally greater plant diversity (Evan Siemann, unpublished data) are further evidence suggesting some role of local processes.

There was a simple, robust relationship between species richness ($S_i$) and the number of individuals ($I$) in size classes, $S_i \sim I_i^{0.5}$ (Fig. 1c, d) with similar relations within taxonomic orders and trophic groups. Furthermore, independent of choice of category size (i.e. log$_2$ or ln) or location of category borders, species richness was more closely related to the number of individuals than to population biomass. This suggests
Fig. 3. The relationship between number of individuals and body size for the eight most abundant orders in sweep net samples. The large circles are the numbers of individuals in integral $N$ biovolume categories (from $2^{x\cdot 1}$ to $2^x$ mm$^3$). Small dots are the size and abundance of each species.
classes may determine the community-level relationships between species richness, numbers of individuals and body size.

For sweep-sampled arthropods only, smaller size classes had significantly more species from the same number of individuals (Fig. 1e) and they also had shallower abundance distribution (Fig. 4; Table 3). This suggests that smaller arthropods species may, in general, persist at lower densities than larger species. Literature surveys have typically found that largest animals are the rarest (Peters 1983; Damuth 1987; Blackburn et al. 1993; Greenwood et al. 1996; Cyr, Downing & Peters 1997; Fa & Purvis 1997), although it has been suggested that these studies systematically underestimate the number of small, rare species (Lawton 1990) and thereby overestimate the average population sizes of small animals. It has been hypothesized that smaller species can persist at lower densities even though they may potentially have more variable population sizes because they have higher intrinsic rates of increase, but the evidence for this in the literature is unclear (Pimm et al. 1988; Lawton 1990; Gaston 1994;
Table 3. Observed species richness, asymptotic species richness and slope and $r^2$ values for OLS fitted lines (functions of the form $[\text{abundance} = a/rank^{m}]$) are reported for each size class and for each sampling method. NA means that the asymptote was not estimable.

<table>
<thead>
<tr>
<th>Class</th>
<th>Biovolume (mm$^3$)</th>
<th>Sweep net Species richness Regression</th>
<th>Pitfall trap Species richness Regression</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
<td>Asymptotic</td>
<td>$m$</td>
</tr>
<tr>
<td>−3</td>
<td>0.125</td>
<td>3</td>
<td>NA</td>
</tr>
<tr>
<td>−2</td>
<td>0.25</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>−1</td>
<td>0.5</td>
<td>17</td>
<td>18</td>
</tr>
<tr>
<td>0</td>
<td>1</td>
<td>50</td>
<td>58</td>
</tr>
<tr>
<td>1</td>
<td>2</td>
<td>130</td>
<td>143</td>
</tr>
<tr>
<td>2</td>
<td>4</td>
<td>152</td>
<td>167</td>
</tr>
<tr>
<td>3</td>
<td>8</td>
<td>195</td>
<td>234</td>
</tr>
<tr>
<td>4</td>
<td>16</td>
<td>153</td>
<td>179</td>
</tr>
<tr>
<td>5</td>
<td>32</td>
<td>146</td>
<td>175</td>
</tr>
<tr>
<td>6</td>
<td>64</td>
<td>117</td>
<td>126</td>
</tr>
<tr>
<td>7</td>
<td>128</td>
<td>109</td>
<td>122</td>
</tr>
<tr>
<td>8</td>
<td>256</td>
<td>63</td>
<td>84</td>
</tr>
<tr>
<td>9</td>
<td>512</td>
<td>44</td>
<td>47</td>
</tr>
<tr>
<td>10</td>
<td>1024</td>
<td>24</td>
<td>24</td>
</tr>
<tr>
<td>11</td>
<td>2048</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>12</td>
<td>4096</td>
<td>5</td>
<td>15</td>
</tr>
<tr>
<td>13</td>
<td>8192</td>
<td>1</td>
<td>NA</td>
</tr>
</tbody>
</table>

Fig. 5. The relationships between species richness, number of individuals and body size for trophic groups in sweep net samples. Lines are connected through points and rounded (not a statistical fit): solid = parasite; dashed = herbivore; dotted = predator; dot-dashed = detritivore.

Cook & Hanski 1995; Lawton & May 1995; Johst & Brandl 1997). Because rarer species typically have smaller geographical ranges (Brown 1984; Gaston & Lawton 1988; Brown, Stevens & Kaufman 1996; Gaston, Blackburn & Lawton 1997), the lower densities of small-bodied species probably represent, if anything, a greater disparity between small and large species in total population sizes across their full range.

The relationship between species richness and number of individuals could result from size-dependent differences in sampling effort. Because simultaneously sampled taxonomic orders had 100-fold differences in the body size with the highest species richness and unimodal distributions of individuals and body size, the decrease in species richness at small sizes within orders is unlikely to be a result of size-biased sampling. In addition, the thoroughness of our sampling is shown by the close agreement, for all but the smallest and largest size categories, between the number of species within each size class that would be caught with infinite sampling effort as estimated by species accumulation curves, $S_{\text{asym}}$, and the number actually caught (Table 3). The relationship between $S_{\text{asym}}$ and $I_n$ was virtually identical to the relationship between $S$ and $L$. Together, these results suggest that the relationships between body size and either $S$ or $I_n$ and between $S$ and $L$ are unlikely to be caused by sampling artefacts related to the intensity of sampling effort.
If, as occurred in our work, global diversity also has a maximum at some intermediate size, there may be fewer undiscovered small species than previously hypothesized (Morse et al. 1985; May 1986). It has also been argued that the unimodal relationship between species richness and body size is real (e.g. May 1986; Dial & Marzluff 1988; Blackburn & Gaston 1994a; Brown 1995; Navarrete & Menge 1997). Our data, with unimodal distributions of species richness and body size of taxonomic orders differing 100-fold in peak body size and with saturating species accumulation curves, provide some of the strongest evidence of data that most species in a taxonomic unit (taxonomic order or phylum) are intermediate in body size. Studies of rainforest canopy beetles support the contention that most undiscovered insect species will not be of the smallest body sizes (Morse et al. 1988; Bassett & Kitching 1991). Global diversity is then perhaps at the lower end of the 10–50 million estimate (May 1988) if other groups show the same patterns as grassland arthropods.

However, if \( S \sim L^{-2.5} \) holds for other taxa, then highly abundant, small-bodied organisms, such as bacteria and viruses, may still represent a vast number of undiscovered species. In fact, \( S \sim L^{-2.5} \) seems to underestimate nematode diversity (Bloemers et al. 1997). The global pattern of species richness and body size is still probably unimodal and so has some small size beyond which species richness will decline, but the peak size may be smaller than for insects. Thus, most of the undiscovered species may be from taxa far smaller than insects. The total number of undescribed species could then be at the higher end of estimates.

Because our study was local, extrapolating these results to global patterns of diversity depends on geographical turnover of species (Gaston & Lawton 1988; Brown & Nicoletto 1991; Fenchel 1993; Finlay, Esteban & Fenchel 1996). These suggestions are also, of course, contingent on the patterns that we report holding for other groups. The discovery of these patterns in other communities and at other spatial scales would provide further insight into the diversity and functioning of communities.

Acknowledgements

We thank Susan Weller and John Luhman for assistance and David Andow, Dennis Cook, Anthony Joern, John Lawton, Clarence Lehman, Shahid Naeem, Robert Sterner and an anonymous reviewer for comments. This study was supported by National Science Foundation (NSF) grants 8811884 and 9411972, a NSF predoctoral fellowship, the Andrew Mellon Foundation, the Sevilleta LTER grant (DEB-9411976) and a University of Minnesota Doctoral Dissertation Fellowship.

References


body size and number in British birds and mammals. *Philosophical Transactions of the Royal Society of London B*, 351, 265–278.


**Appendix**

**Proof of why our rank-abundance relations lead to $S_r \sim r^m$**

Assume that the relationship between rank and abundance within two size classes of animals are both of the form:

$$A_{ij} = A_{i1}/r^m$$  \hspace{1cm} eqn A1

where $A_{ij}$ is the abundance of the $r^m$ most abundant species in the $i$th size class, $A_{i1}$ is the abundance of the most abundant species in the $i$th size class, $r$ is the rank of the species and $m$ is a positive constant describing how much more abundant a species is compared to the next most abundant species. The total number of individuals ($I_i$) in the first size class is:

$$I_i = \sum_{j=1}^S (A_{i1}/r^m)$$  \hspace{1cm} eqn A2

where $S_i$ is the total number of species in the size class. Assume two size classes have identical $m$-values and identical minimum population sizes for persistence but with $S_i$ species in one size class and $n$ times as
many species in the second ($S_2 = nS_1$). In a graph
with $\ln A_{1,2}$ on the y-axis and $\ln n$ on the x-axis, the
abundance distributions of the two size classes would
be parallel straight lines. The numbers of individuals
in the two assemblages are related as follows:

$$I_2 = \frac{\sum_{r=1}^{nS_1} (A_{1,2}/n^m)}{\sum_{r=1}^{S_1} (A_{1,1}/n^m)}, \quad \text{eqn A3}$$

Because $m$ and minimum population sizes are equal
for the two assemblages:

$$\ln A_{1,2} - m \ln n \cdot S_1 \approx \ln A_{1,1} - m \ln S_1, \quad \text{eqn A4}$$

$$\ln A_{1,2} \approx \ln A_{1,1} + m n \quad \text{eqn A5}$$

$$A_{1,2} \approx n^m A_{1,1} \quad \text{eqn A6}$$

Expanding the sums in equation A3 and substituting
in equation A6 leads to:

$$I_2 = \frac{[n^m A_{1,1} (1/1^n + 1/2^n + \cdots + 1/(n \cdot S_1)^m)]}{(A_{1,1} (1/1^n + 1/2^n + \cdots + 1/S_1^m))}, \quad \text{eqn A7}$$

For sufficiently large $S_1$ and/or $m$ the sum:

$$I_1 = \sum_{r=1}^{S_1} (1/r^m) \quad \text{eqn A8}$$

is roughly constant. For our data with average
$m = 1.94$, this sum varies less than 5% between $S = 13$
and $S = 200$ and over this range can be approximated
by a constant. For some number of species in the most
speciose class ($S_{\text{max}}$), values of the minimum number
of species in the least speciose size class ($S_{\text{min}}$) and
$m$ can be found so that the sum will vary less than 5%.
Fitted sigmoidal curves to these values for a range
of $S_{\text{max}}$ from 50 to 500 show that the approximate
requirement for less than 5% variation in the sum A8
is:

$$(S_{\text{min}}/S_{\text{max}}) \{1 + \frac{\exp[(m - 1.2)/0.2]}{2}\} > 94.5. \quad \text{eqn A9}$$

Substituting a constant for the series in equation A7
leads to the relation:

$$I_2/I_1 \approx n^m \approx n^{1.94} \quad \text{eqn A10}$$

Therefore:

$$S_1 \sim I_1^{m} = I_1^{0.94} \quad \text{eqn A11}$$