

Insect species diversity, abundance and body size relationships

Evan Siemann, David Tilman & John Haarstad

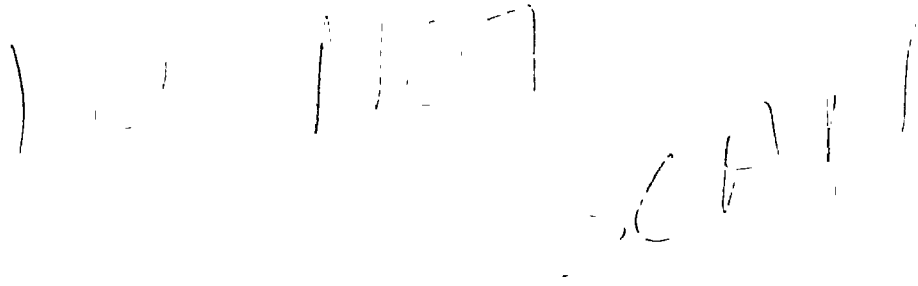
Department of Ecology, Evolution and Behavior, University of Minnesota, St Paul, Minnesota 55108, USA

BIOLOGICAL diversity, population size and body size are interdependent¹⁻⁸, but there is little consensus on the nature or causes of these relations. Here we analyse the most thoroughly sampled ecological community to date, a grassland insect community sample containing 89,596 individuals of 1,167 species. Each taxonomic order had a distinct body size at which both species richness and number of individuals were highest, but these peak sizes varied more than 100-fold among five major orders. These results suggest that there may be fewer undiscovered small insect species than previously thought. Moreover, we found a surprisingly strong, simple, but unreported, relation between species richness (S) and the number of individuals (I) within size classes, $S = I^{0.5}$. Because this held across numerous body types and a 100,000-fold body-size range, there may be a general rule that is independent of body size for the relations among interspecific resource division, abundance and diversity.

Local diversity comes from the balance between immigration of new species and local extinction⁹. Immigration rate depends on the number of species already present⁹ and dispersal ability, which is likely to be dependent on body size¹⁰. Extinction rate depends on population abundances and their distribution, with rare species more likely to become extinct as a result of population fluctuations¹¹. Because of this, species richness (S) should depend on the number of individuals (I) within a group of interacting species, here assumed to be species of similar body size, especially within taxonomic orders^{12,13}. The number of rare species also depends on the abundance distribution (for example, log-normal¹⁴, broken-stick¹⁵), as will the precise relation between S and I .

Assuming a minimum population size for population persistence, and abundances following a broken-stick model¹⁵, it has been shown¹⁶ that $S = cI^{0.5}$, where c is a case-specific constant. The relation $S = cI^{0.25}$ has previously been derived¹⁴ for a canonical log-normal distribution. For our data we investigate the effect on species richness of the total number of individuals in each size class¹⁷. We also examine the relations among species richness, number of individuals, and body size.

We sampled insects 7–9 times throughout the 1992 growing season in each of 48 grassland fields and savannahs at Cedar Creek, Minnesota, and determined the abundance and computed the biovolume of each species (for methods see Fig. 1 legend). These data are especially powerful because they include numer-



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ous simultaneously sampled taxonomic orders spanning a broad range of body sizes.

For our entire fauna, peak species richness occurred at the intermediate body size that led to the maximum number of individuals (Fig. 1A, B). The same pattern occurred within each of the five most abundant orders, although peak body sizes differed (Fig. 2A, B). Decreases in numbers of individuals at small body sizes within each order were not caused by size-biased sampling because these decreases occurred in all orders,

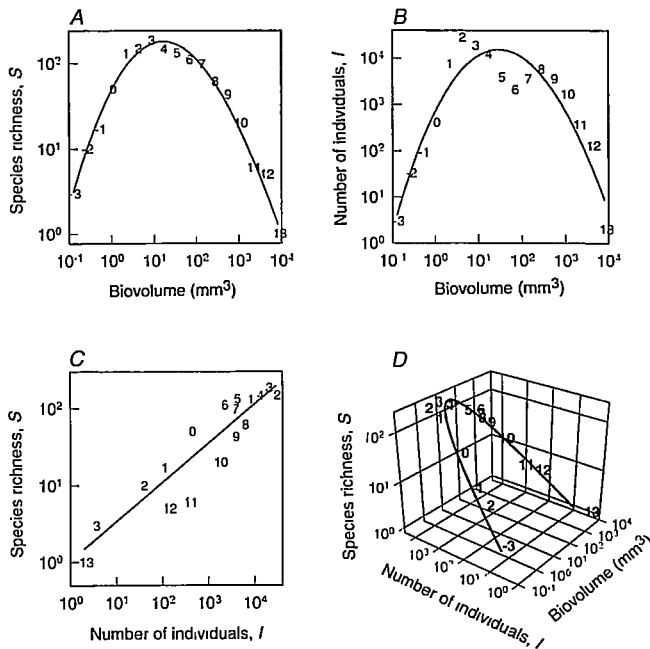


FIG. 1 A, Relation between species richness (S) per \log_2 biovolume class and biovolume (B) fitted by the extreme value function $\ln S = a + b \exp(-\exp\{-(\ln B - c)/d\}) - [(\ln B - c)/d] + 1$, an asymmetric peak function; $a = -55.3$, $b = 60.5$, $c = 2.81$, $d = 13.9$, $r^2 = 0.98$, $N = 17$, $P < 0.01$. Note that numbers shown identify $2^{\text{number}} \text{mm}^3$ size classes (for example, the -1 shows where organisms of size 2^{-1}mm^3 , or $1/2 \text{mm}^3$, fell on the graph). B, Relation between number of individuals (I) within \log_2 biovolume classes and biovolume with fitted parameters of $a = 284.6$, $b = 294.3$, $c = 3.37$, $d = 23.8$, $r^2 = 0.88$, $N = 17$, $P < 0.01$. C, Relation between species richness (S) and number of individuals (I) within \log_2 biovolume size classes, fitted by regression with $S = 1.05 I^{0.51}$, $r^2 = 0.85$, $N = 17$, $P < 0.01$. For the five most abundant orders: Coleoptera, $S = 1.03 I^{0.48}$, $r^2 = 0.95$, $N = 10$, $P < 0.01$; Diptera, $S = 1.21 I^{0.57}$, $r^2 = 0.94$, $N = 8$, $P < 0.01$; Hemiptera, $S = 1.28 I^{0.35}$, $r^2 = 0.91$, $N = 11$, $P < 0.01$; Hymenoptera, $S = 1.10 I^{0.63}$, $r^2 = 0.91$, $N = 14$, $P < 0.01$; and Orthoptera, $S = 1.14 I^{0.26}$, $r^2 = 0.63$, $N = 7$, $P < 0.05$. D, Relation between species richness and number of individuals within \log_2 biovolume classes and biovolume using fitted curves from A and B.

METHODS. Insects were sweep sampled from 48 grassland fields and savannahs at Cedar Creek, Minnesota, 7–9 times each throughout the 1992 growing season, with 100 sweeps per sample. In total, 89,596 individuals of 1,167 species were captured and enumerated. Sweep-net samples give excellent estimates of relative abundance within orders²⁹, and good estimates of relative abundance between orders³⁰. Our conclusions require only that measures of abundance be relative. All specimens were manually sorted and identified to species (89.8% of specimens) or morphospecies within known genera or families. Species biovolume, an index of biomass, was calculated as the average product of length (from tip of head to tip of abdomen), width (maximum width of body or head) and thickness (maximum thickness of body or head) for 5 specimens in the oldest life stage for each species, even though body size increases greatly during development. Most species (84%) only occurred as adults in our samples. To minimize counting a species twice, all larvae were examined by outside experts and, if they might have been the same species as an adult insect, we counted them as a single species.

even though peak body sizes differed 100-fold. Estimates of total species richness from species accumulation curves (Fig. 3) gave results almost identical to those using observed species richness (S). Thus differences in species richness among size classes were real, and not artefacts of sampling effort^{18,19}.

For our entire fauna, the dependence of S on I was best fit by $S = 1.05 I^{0.51}$ (Fig. 1C; $r^2 = 0.85$, $N = 17$, $P < 0.01$). Similar relations occurred in the five most abundant orders (see Fig. 1 legend). A size class with 10 times as many individuals had, on average, 3.2 times as many species. Smaller-bodied size classes had slightly more equitable abundance distributions, and slightly but consistently more species from the same number of individuals (Fig. 1C). Examined in three dimensions, S , I and biovolume formed a parabola (Fig. 1D), which collapsed to the $S = 1.05 I^{0.51}$ line when projected onto the S and I plane. Because processes such as competition, predation, herbivory and dispersal are size depen-

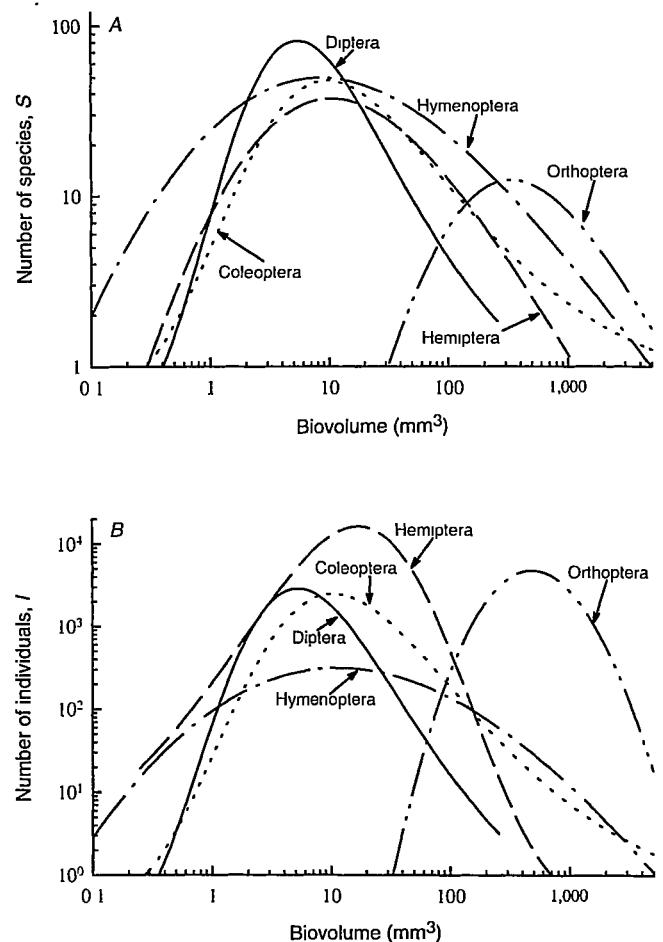


FIG. 2 A, The relation between species richness in \log_2 biovolume classes and biovolume for the five most abundant and speciose orders in our samples. The curve for each order is from the fitted extreme value function (Fig. 1). Coleoptera, $a = -0.44$, $b = 4.3$, $c = 2.27$, $d = 2.22$, $r^2 = 0.91$, $N = 10$, $P < 0.01$; Diptera, $a = -0.99$, $b = 5.4$, $c = 1.69$, $d = 1.8$, $r^2 = 0.93$, $N = 8$, $P < 0.01$; Hemiptera, $a = -8.8$, $b = 12.5$, $c = 2.35$, $d = 3.13$, $r^2 = 0.97$, $N = 11$, $P < 0.01$; Hymenoptera, $a = -10.8$, $b = 14.6$, $c = 2.13$, $d = 7.0$, $r^2 = 0.96$, $N = 14$, $P < 0.01$; Orthoptera, $a = -5.6$, $b = 8.12$, $c = 5.80$, $d = 3.13$, $r^2 = 0.99$, $N = 7$, $P < 0.01$. B, The relations between number of individuals of all species in each \log_2 biovolume class and biovolume. Coleoptera, $a = -0.99$, $b = 8.8$, $c = 2.35$, $d = 2.3$, $r^2 = 0.88$, $N = 10$, $P < 0.01$; Diptera, $a = -2.32$, $b = 10.3$, $c = 1.66$, $d = 2.0$, $r^2 = 0.93$, $N = 8$, $P < 0.01$; Hemiptera, $a = -0.94$, $b = 10.6$, $c = 2.82$, $d = -2.3$, $r^2 = 0.84$, $N = 11$, $P < 0.01$; Hymenoptera, $a = -49.9$, $b = 55.7$, $c = 2.44$, $d = 12.1$, $r^2 = 0.89$, $N = 14$, $P < 0.01$; Orthoptera, $a = 306.2$, $b = 314.5$, $c = 6.16$, $d = 12.0$, $r^2 = 0.96$, $N = 7$, $P < 0.01$.

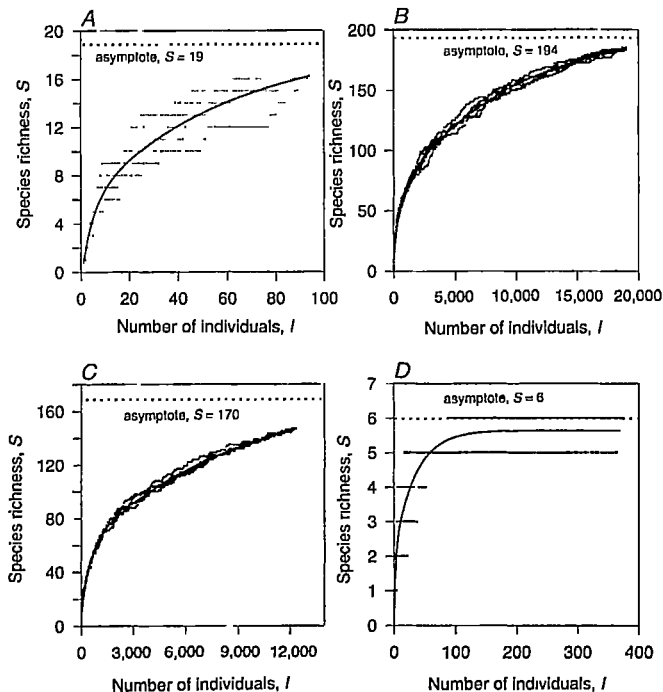


FIG. 3 Species accumulation curves¹⁸ show the effect of sampling effort on observed species richness. For each size class, increasingly larger random subsamples from the set of all individuals of all species in the size class were drawn to construct a species accumulation curve, with a maximum of 500 such random draws per curve. The resulting curve for each size class was fitted with an asymptotic, negative exponential function to estimate the asymptote, which is the number of species estimated with infinite sampling effort¹⁸. Only the smallest size class had no asymptote. The relation of asymptotic species richness ($S_{as,mp}$) and number of individuals (I) was virtually identical to the relation of S and I ; $S_{as,mp} = 0.95 I^{0.63}$, $r^2 = 0.80$, $N = 16$, $P < 0.01$. The accumulation curves for four size classes are shown. A, Size class -1 (0.25–0.5 mm³); B, size class 3 (4–8 mm³); C, size class 4 (8–16 mm³); D, size class 11 (1,024 to 2,048 mm³).

dent^{3,6,10}, it is surprising that the relation of numbers of individuals to species richness is not dependent on body size.

Intriguingly, our results are consistent with May's¹⁶ approximation $S = cI^{1/5}$, but our abundance distributions within size classes were not broken-stick. Rather, they followed the power function $A_r = A_1/r^m$, reported for whole communities¹⁴, where A_r is the abundance of the r th most abundant species in the size class; for our data, $m = 1.94$. It can be shown (E.S. *et al.*, manuscript in preparation) that $S = cI^{1/5}$ if size classes have power-function abundance distributions with equal m , if all size classes have the same minimum population size below which extinction occurs, and if the division of resources within each size class is inequitable ($m > 1.5$). This gives $S \sim I^{1/5.4} = I^{1/5}$. Thus $S = I^{1/5}$ suggests that the same rules determine diversity and abundance across a 100,000-fold range in insect body sizes.

Most studies have found unimodal relations between species richness and body size^{2,3,6,20,21}, and between number of individuals and body size^{1,3,6,22–24}. Although hypotheses incorporating trade-offs, for example between metabolic efficiency and reproductive rate^{25,26}, predict unimodal relations between species richness and body size, none predicts that the number of individuals should peak at the same intermediate size. The differences among modal sizes of the five insect orders suggest that shared physiologies and/

or morphologies from the common genetic heritage of an order limit related organisms to similar sizes.

Global diversity based on currently described species is a unimodal function of body size⁶. May⁶ proposed that actual global diversity may be highest at the smallest sizes, with small species fantastically undersampled, representing many millions of undescribed species. Our data suggest that undescribed species are more likely to be of intermediate sizes within any taxonomic group, which is supported by studies of tropical forest canopy beetles^{1,8,21}. This seems to support May's alternative hypothesis that diversity peaks at some intermediate body size⁶, and would seem to suggest that global diversity is closer to the lower end of the estimate 10–50 million species⁷. However, if $S = I^{1/5}$ holds for nematodes, bacteria and viruses, it would suggest these phenomenally abundant small-bodied taxa might constitute most of the Earth's diversity, giving a total global diversity towards the higher end of May's estimate. Any such extrapolations are speculative until we know if the patterns we report for insects hold for other groups, and how the geographical turnover of species depends on body size^{27,28}. Such relationships, once observed in other communities, would provide vital clues to the diversity of life on Earth, and the causes of this diversity. □

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CORRESPONDENCE AND MATERIALS. Requests to be addressed to E.S. (e-mail address: evan@ter.umn.edu).