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

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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_i) as $S_i = I_i^{0{\cdot}5}$. 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

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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

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see Griffiths 1986). One explanation is that individuals of intermediate-sized species are best able simultaneously to meet a pair of constraints (Hutchinson & MacArthur 1959) such as metabolic efficiency vs. reproductive rate (e.g. Dial & Marzluff 1988; Brown *et al.* 1993; Marquet, Navarrete & Castilla 1995). The distribution of body sizes around this optimal size is hypothesized to result from character displacement. Alternatively, the smallest animals may be the most diverse if diversity is limited primarily by habitat heterogeneity (Morse *et al.* 1985; Lawton 1986; May 1986). The disagreement between this prediction and available data may result from systematic undersampling of small animals (Morse *et al.* 1985; May 1986). More thorough sampling that is evaluated by constructing species accumulation curves for animals of different sizes (Colwell & Coddington 1994; Rosenzweig 1995) would provide a preliminary test of this hypothesis.

The relationship between species richness and body size may result from the relationship between body size and some other variable correlated with species richness, such as number of individuals (Harvey & Lawton 1986; Lawton 1986; Morse *et al.* 1988; Cousins 1991; Tilman & Pacala 1993). Because (i) local diversity is determined by the balance between local immigration and local extinction of species (MacArthur & Wilson 1967) and (ii) rarer species are generally more likely to go extinct (Pimm, Jones & Diamond 1988; Lawton & May 1995), the number of species in a group of interacting species, here assumed to be animals of similar size, may depend on the number of individuals in the group (Lawton 1986; Tilman & Pacala 1993) and their abundance distribution (e.g. MacArthur 1957; Preston 1962; Sugihara 1980; Tokeshi 1990). Alternatively, it has also been suggested that species richness may be more closely related to total biomass in a size class, because it is an index of resource acquisition (Marquet *et al.* 1995).

We determined the relationships among body size, species richness and number of individuals in size classes for grassland arthropods. Arthropods were collected using two sampling methods (sweep nets and pitfall traps) to help control, but not necessarily eliminate, sampling biases. The arthropods are an excellent group for this type of investigation because they are among the most diverse taxa on earth, are easily collected, represent a range of trophic roles and their body sizes span many orders of magnitude. We determined and compared the abundance distributions of different size classes. In order to assess the completeness of our sampling efforts, we constructed species accumulation curves (Colwell & Coddington 1994; Rosenzweig 1995).

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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 cm^3 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 antannae, 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 $\log_2$ biovolume classes. A class of size N included those species ranging in biovolume from 2^{N-1} mm^3 up to and including 2^N mm^3. 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 $\log_2$ scale) that is moved in small increments (0·01 in $\log_2$ 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^{N+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 e^{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 [$\mathrm{Species} - (\mathrm{Species} - \mathrm{a}) * \mathrm{e}^{-\mathrm{b*individuals}}$] 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; $r^2 < 0{\cdot}01$, for all cases $N_{\mathrm{sweep}} = 1225$, $N_{\mathrm{pitfall}} = 92$).

Log species richness and log biovolume had a unimodal relationship for the entire sweep ned (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 $\log_2$ 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:

$$A_{r,i} = A_{1,i}/r^m,$$

where $A_{r,i}$ is the abundance of the r^{th} most abundant species in the ith 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; $m = 1{\cdot}41 + 0{\cdot}10 \ \log_2$ (biovolume), $r^2 = 0{\cdot}67$, $F_{1,13} = 26{\cdot}01$, $P < 0{\cdot}001$; size class -3 omitted]. Omitting size class 12 which was not well sampled (Table 3) did not change this result [$m = 1{\cdot}43 + 0{\cdot}09 \ \log_2$ (biovolume), $r^2 = 0{\cdot}59$, $F_{1,12} = 17{\cdot}42$, $P < 0{\cdot}01$; 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; $P = 0{\cdot}84$).

In sweep data, species richness (S_i) in size classes was related to the number of individuals (I_i) in size

Table 1. Species and individuals within taxonomic and trophic groups

	Sweep net		Pitfall trap	
Group	Species	Individuals	Species	Individuals
Araneida	58	929	1	14
Coleoptera	212	6403	52	11498
Diptera	252	6016	1	1
Hemiptera	89	22660	8	73
Homoptera	109	39476	0	0
Hymenoptera	335	1936	8	639
Lepidoptera	99	1493	0	0
Orthoptera	50	11353	22	496
Miscellaneous	21	259	0	0
Total	1225	90525	92	12721
Detritivore	141	5625	19	8986
Herbivores	577	78508	36	846
Parasites	281	1589	3	5
Predators	226	4803	34	2884
Total	1225	90525	92	12721

classes as a power function $S_i = 1{\cdot}05I_i^{0{\cdot}52}$ ($r^2 = 0{\cdot}85$, $P < 0{\cdot}01$, d.f. = 14) (Fig. 1e). In a multiple regression, Log S_i in sweep data was significantly positively correlated with Log I_i and significantly negatively correlated with the log of biovolume [Log $S_i = 0{\cdot}19 + 0{\cdot}52$ Log $I_i - 0{\cdot}04$ Log (Size), $R^2 = 0{\cdot}93$, $P < 0{\cdot}01$ for overall regression and each term, d.f. = 13]. Therefore, for sweep data, there were significantly more species from the same number of individuals for smaller species. For sweep data, species richness within size classes was related to the number of individuals and the slope of the size classes rank-abundance relationship (m) as Log $S_i = 0{\cdot}42 + 0{\cdot}61$ Log $I_i - 0{\cdot}38m$ ($R^2 = 0{\cdot}95$, $P < 0{\cdot}001$ for overall regression and each term, d.f. = 13). In a multiple regression that included Log I_i, m and Log (size) as predictors, Log S_i did not depend significantly on size ($P = 0{\cdot}58$). Within every taxonomic order, species richness within size classes was a power function of the number of individuals (Orthoptera: exponent = 0·26, $r^2 = 0{\cdot}64$; Araneida: 0·59, 0·77; Hemiptera: 0·29, 0·66; Homoptera: 0·35, 0·92; Coleoptera: 0·48, 0·94; Lepidoptera: 0·46, 0·74; Diptera: 0·57, 0·94; Hymenoptera: 0·63, 0·90). In pitfall data, species richness within size classes was related to numbers of individuals as $S_i = 2{\cdot}23I]_i^{0{\cdot}47}$ ($r^2 = 0{\cdot}77$, $P < 0{\cdot}01$, d.f. = 8) (Fig. 1f) but was independent of body size ($P = 0{\cdot}49$) and slope of rank-abundance relationship ($P = 0{\cdot}52$) when they were included in the regression. For both the entire sweep and pitfall datasets and the eight most abundant taxonomic orders, the species richness of size classes was predicted less well by the total biovolume summed across individuals in the size class (sweep $r^2 = 0{\cdot}15$, pitfall $r^2 = 0{\cdot}58$) than by the number of individuals.

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, $r^2 = 0{\cdot}81$; 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 ($S_{\text{asym},i}$) was almost identical to the relationship between number of individuals and observed species richness (sweep: $S_{\text{asym},i} = 1{\cdot}37I_i^{0{\cdot}50}$, $r^2 = 0{\cdot}74$, $N = 15$, $P < 0{\cdot}01$; pitfall: $S_{\text{asym},i} = 0{\cdot}46I_i^{0{\cdot}50}$, $r^2 = 0{\cdot}72$, $N = 9$, $P < 0{\cdot}01$).

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

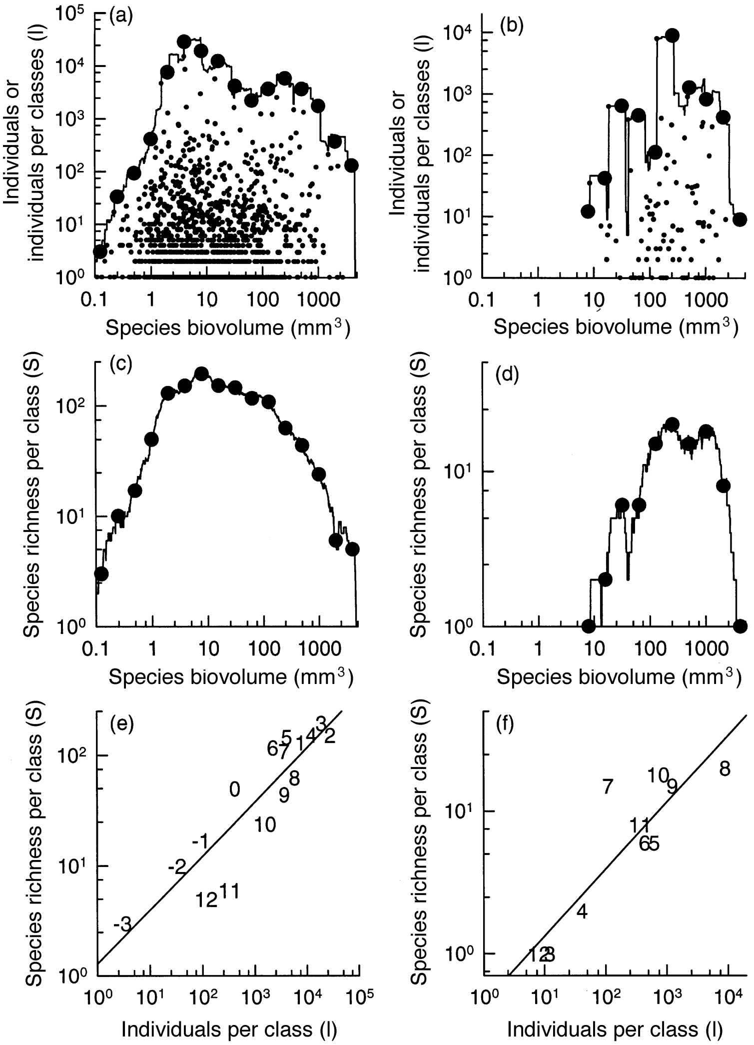

Fig. 1. Body size relationships for sweep net (left column) and pitfall trap (right column) samples. For each graph, the curves represent the distributions obtained from the smoothing procedure described in Methods. The large circles are the numbers of species or individuals in integral N biovolume categories (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).

(Table 2). 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

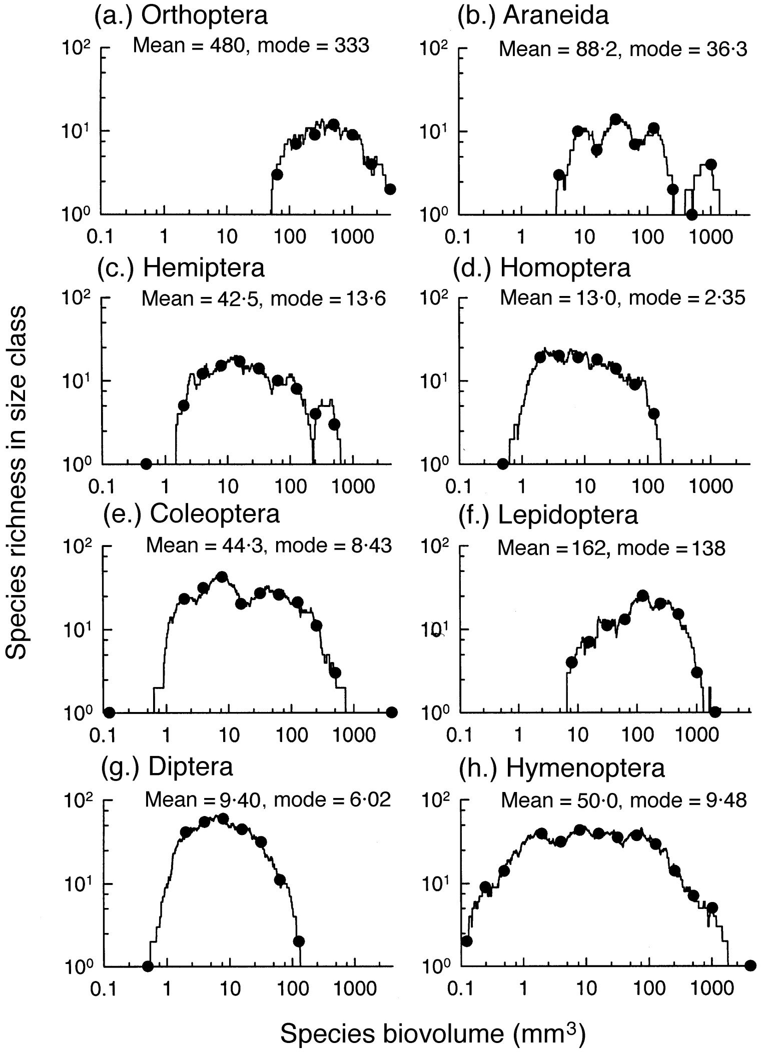

Fig. 2. The relationship between species richness and body size for the eight most abundant orders in sweep net samples [the large circles are the numbers of species or individuals in integral N biovolume categories (from 2^{N-1} to 2^{N} mm^3)] with mean and modal body size (mm^3) for species in the 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

Source	d.f.	SS	MS	F-value	P-value
ORDER	15	133·14	8·87	21·89	0·0001
TROPH	3	1·03	0·34	0·84	0·4704
ORDER*TROPH	8	26·52	3·32	8·18	0·0001
Error	1198	486·32	0·41		

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_i) in size classes, $S_i \sim I_i^{0{\cdot}5}$ (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 the relationship between population sizes and extinc-

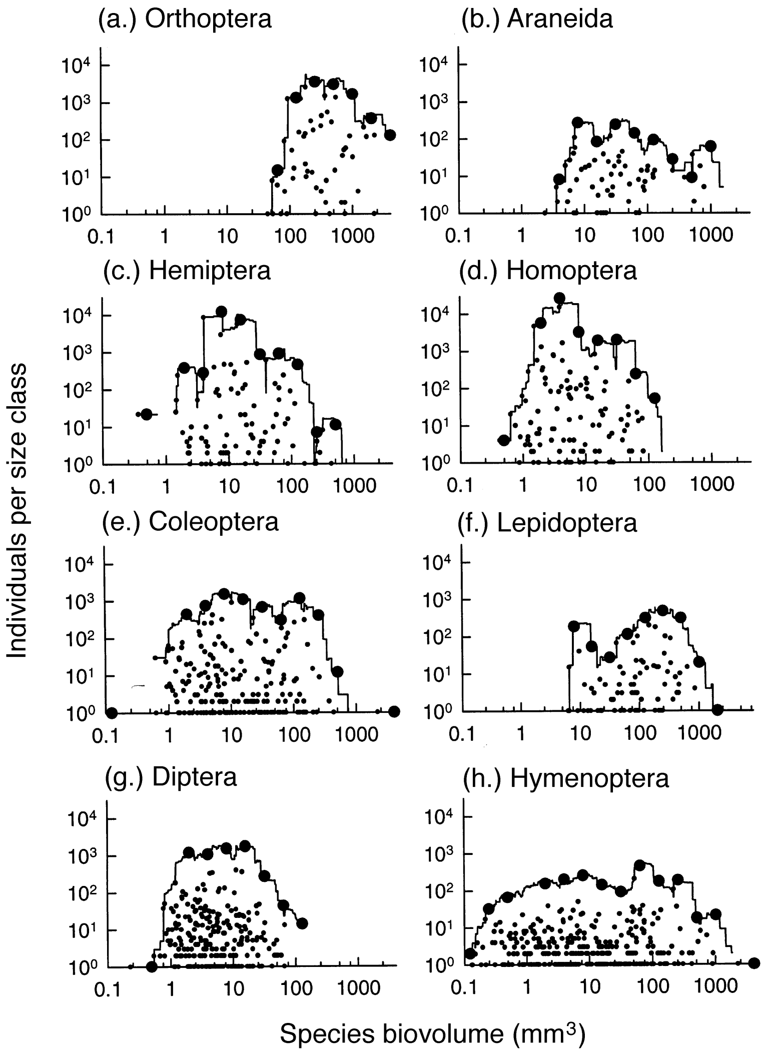

Fig. 3. The relationship between number of individuals and body size for the eight most abundant orders in sweep net samples. The large circles are the numbers of individuals in integral N biovolume categories (from 2^{N-1} to 2^N mm^3). Small dots are the size and abundance of each species.

tion risk (Pimm *et al.* 1988) may be responsible for the species richness and body size relationship.

Abundance distributions of size classes generally had the form $A_{r,i} = A_{1,i}/r^m$ (Fig. 4; Table 3) that others have reported for whole communities (Root 1973; Morse *et al.* 1988; Bassett & Kitching 1991; Siemann *et al.* 1996). These distributions are qualitatively similar to, but steeper than, MacArthur's (1957) model ('overlapping niches') in which the abundance of each species is independently determined to approximate a community with weak interspecific competition. Of course, this similarity does not imply that weak interspecific interactions are the mechanism causing these relationships. Understanding the causes of these distributions is important because they suggest there is a simple, general, size-independent rule governing how resources are divided among species of similar sizes because per capita resource use will be similar within size classes (Peters 1983; West *et al.* 1997).

If (1) the abundance distributions of size classes are of this form, $A_{r,i} = A_{1,i}/r^m$, (2) the distribution of resources within a size class is roughly the same for different size classes (i.e. same m), (3) size classes have the same minimum population size for persistence, and (4) resource division is inequitable or size classes are similar in species richness (see Appendix, eqn A9) then the species richness and number of individuals within size classes within the community should be related as $S_i \sim I_i^{1/m}$ (see Appendix for proof). Together, the slope of the abundance distribution and the number of individuals in a size class were sufficient to predict the number of species in a size class almost exactly ($R > 0{\cdot}95$) for sweep samples because at intermediate size classes, although the number of individuals decreased (Fig. 1a) while the number of species did not (Fig. 1b), the abundance distributions for these classes were relatively more equitable (Fig. 4; Table 3). Slopes of abundance distributions in the pitfall data predict $S \sim I^{0{\cdot}4}$ and we observed $S \sim I^{0{\cdot}47}$. The patterns of relative abundances of species within size

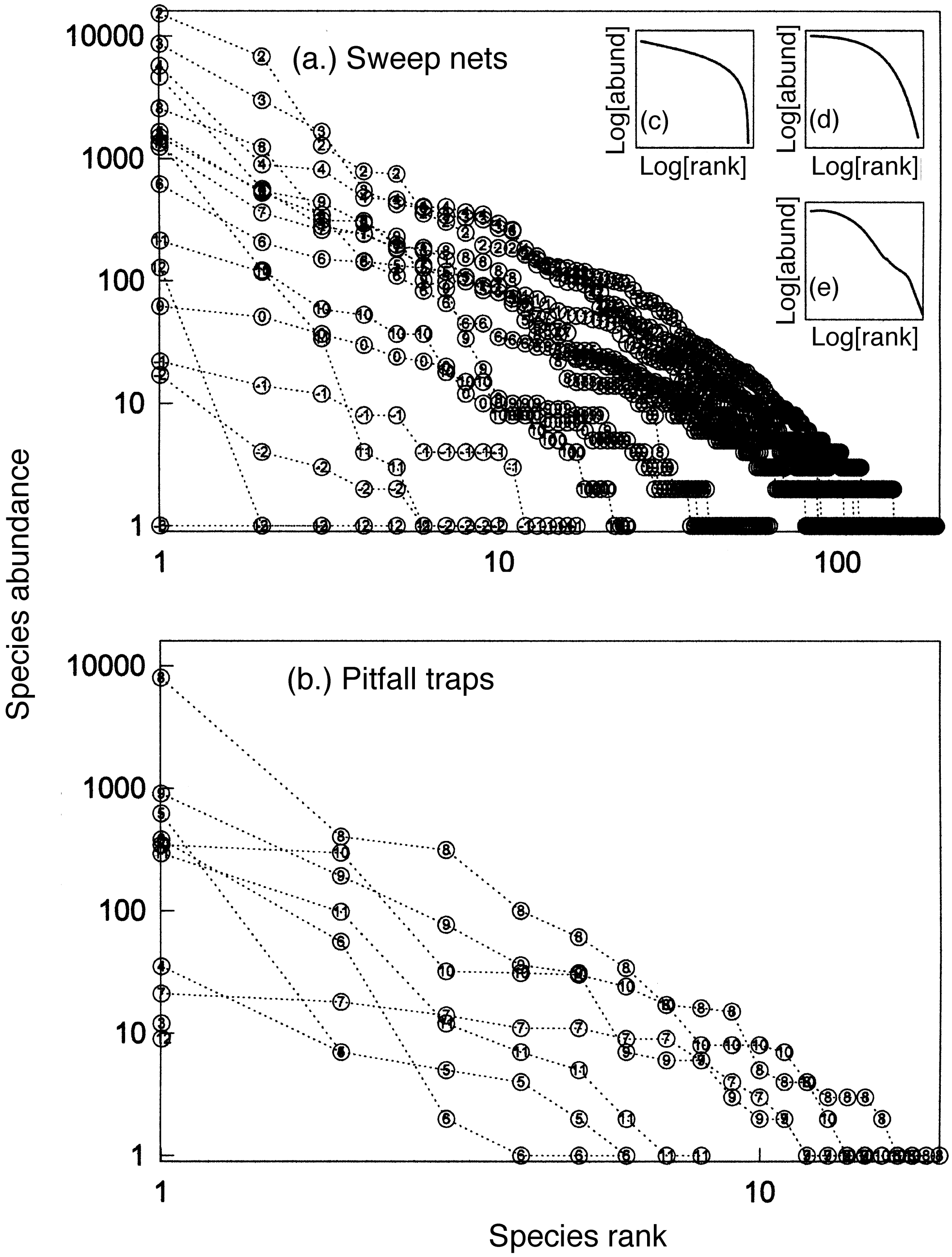

Fig. 4. Rank abundance distributions within integral biovolume size classes for each sampling method [(a) Sweep nets (numbers inside symbols represent the size classes). (b) Pitfall traps] with lines connecting successively rarer species within a size class. The slope and r^2 values for OLS fitted lines (functions of the form [abundance = a/rank^m]) are reported for each size class in Table 3. These data do not appear to follow a broken-stick (c), geometric (d) or log-normal distribution (e) of abundances. A log-series distribution is virtually indistinguishable from the geometric distribution in log[abund] vs. log[rank] space.

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 [abundance = a/rank^m]) are reported for each size class and for each sampling method. NA means that the asymptote was not estimable

		Sweep net				Pitfall trap			
		Species richness		Regression		Species richness		Regression	
Class	Biovolume (mm^3)	Observed	Asymptotic	m	r^2	Observed	Asymptotic	m	r^2
−3	0·125	3	NA	0	1	0	0		
−2	0·25	10	10	1·22	0·94	0	0		
−1	0·5	17	18	1·23	0·87	0	0		
0	1	50	58	1·26	0·93	0	0		
1	2	130	143	1·73	0·97	0	0		
2	4	152	167	2·04	0·98	0	0		
3	8	195	234	1·93	0·97	1	NA		
4	16	153	179	1·96	0·97	2	NA	2·32	1
5	32	146	175	1·63	0·98	6	6	3·22	0·88
6	64	117	126	1·52	0·96	6	27	3·71	0·91
7	128	109	122	1·71	0·96	15	16	1·29	0·78
8	256	63	84	2·26	0·95	20	21	2·95	0·99
9	512	44	47	2·10	0·97	15	16	2·71	0·98
10	1024	24	24	2·06	0·97	18	19	2·22	0·92
11	2048	6	6	3·11	0·90	8	8	2·92	0·97
12	4096	5	15	2·87	0·71	1	NA		
13	8192	1	NA			0	0		

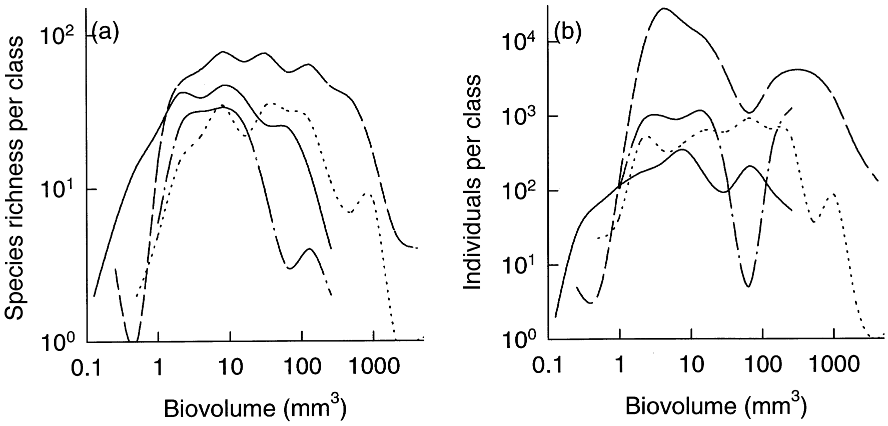

Fig. 5. The relationships between species richness, number of individuals and body size for trophic groups in sweep net samples. Lines are connected through points and rounded (not a statistical fit): solid = parasite; dashed = herbivore; dotted = predator; dot-dashed = detritivore.

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, $S_{\mathrm{asym},i}$ and the number actually caught (Table 3). The relationship between $S_{\mathrm{asym},i}$ and I_i was virtually identical to the relationship between S_i and I_i. Together, these results suggest that the relationships between body size and either S_i or I_i, and between S_i and I_i, 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 $S_i \sim I_i^{0\cdot5}$ 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, $S_i \sim I_i^{0\cdot5}$ 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.

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Appendix

PROOF OF WHY OUR RANK–ABUNDANCE RELATIONS LEAD TO $S_i \sim I_i^{0\cdot5}$

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

$$A_{r,i} = A_{1,i}/r^m \qquad \text{eqn A1}$$

where $A_{r,i}$ is the abundance of the r^{th} most abundant species in the ith size class, $A_{1,i}$ is the abundance of the most abundant species in the ith 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_1) in the first size class is:

$$I_1 = \sum_{r=1}^{S_1} (A_{1,1}/r^m) \qquad \text{eqn A2}$$

where S_1 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_1 species in one size class and n times as many species in the second ($S_2 = nS_1$). In a graph with ln $A_{r,i}$ on the y-axis and ln r 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:

$$\frac{I_2}{I_1} = \frac{\sum_{r=1}^{n \cdot S_1} (A_{1,2}/r^m)}{\sum_{r=1}^{S_1} (A_{1,1}/r^m)}. \qquad \text{eqn A3}$$

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

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

$$\ln A_{1,2} \cong \ln {}_{1,1} + m \ln n \qquad \text{eqn A5}$$

$$A_{1,2} \cong n^{m \cdot} A_{1,1} \qquad \text{eqn A6}$$

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

$$\frac{I_2}{I_1} \cong \frac{[(n^{m \cdot} A_{1,1})(1/1^m + 1/2^m + \cdots + 1/(n \cdot S_1)^m]}{(A_{1,1})(1/1^m + 1/2^m + \cdots + 1/S_1^m)}. \qquad \text{eqn A7}$$

For sufficiently large S_i and/or m the sum:

$$I_i = \sum_{r=1}^{S_i} (1/r^m) \qquad \text{eqn A8}$$

is roughly constant. For our data with average $m = 1{\cdot}94$, 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 ($S_{\max}$), values of the minimum number of species in the least speciose size class ($S_{\min}$) and m can be found so that the sum will vary less than 5%. Fitted sigmoidal curves to these values for a range of $S_{\max}$ from 50 to 500 show that the approximate requirement for less than 5% variation in the sum A8 is:

$$(S_{\min}/S_{\max})\{1 + \exp[(m - 1{\cdot}2)/0{\cdot}2]\} \geqslant 0{\cdot}95. \qquad \text{eqn A9}$$

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

$$I_2/I_1 \cong n^m \cong n^{1{\cdot}94}. \qquad \text{eqn A10}$$

Therefore:

$$S_i \sim I_i^{1/m} = I_i^{0{\cdot}5}. \qquad \text{eqn A11}$$