

## Species richness and the proportion of predatory animal species in temporary freshwater pools: relationships with habitat size and permanence

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### Abstract

The proportion of predatory animal species is often believed not to vary systematically across communities. However, we predict that larger temporary freshwater pools, and pools that are more permanent, will contain a higher proportion of predatory animal species. In 24 temporary rockpools in Northern Israel (supporting communities dominated by ostracods, copepods, cladocerans, flatworms, dipterans and amphibians), the mean proportion of macroscopic predatory species (averaged over a series of samples) increased with increasing pool area. For the highest possible proportion of predatory species (including microscopic species with uncertain diets), the relationship with pool area was not statistically significant. We did not find significant relationships between permanence and the proportion of either macroscopic or all possible predatory species. Larger pools and pools that were more permanent had more species. Species richness and the proportion of macroscopic predators were positively correlated. These patterns imply that species-poor ecosystems are likely to be functionally different from species-rich systems.

### Keywords

Diversity, habitat permanence, habitat size, predator:prey ratios, species richness, temporary habitats, trophic structure.

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### INTRODUCTION

The relationships between habitat characteristics and species richness are a major theme in ecology. However, to understand the functioning of ecosystems, we need to know not only how many, but also what kinds of species are present. The simple division of animal species into predators (animals feeding mainly on other live metazoa) and nonpredators (all other animals) is associated with a wide range of ecological differences; e.g. predators tend to be larger (Warren & Lawton 1987; Cohen *et al.* 1993), have lower population densities (Peters 1983; Silva & Downing *et al.* 1994) and have lower nitrogen:phosphorus ratios (Sterner *et al.* 1996) than nonpredators. Furthermore, over half of a set of published field experiments reviewed by Sih *et al.* (1985) found more than two-fold changes in individual and population-level characteristics of prey in response to manipulations of carnivore density. The expectation that communities with different proportions of predatory species differ in structure and function, has motivated ecologists to look for patterns in the relative numbers of predatory and nonpredatory species across communities.

The numbers of predatory and nonpredatory animal species in communities are positively correlated (Jeffries & Lawton 1985; Gaston *et al.* 1992; Warren & Gaston 1992; Rosenzweig 1995; see also Cohen 1977, 1978; Schoener 1989), and the proportion of predatory species in freshwater communities shows little systematic variation with species richness (Jeffries & Lawton 1985; Warren & Gaston 1992). Explanations for this relationship (reviewed by Warren & Gaston 1992) include random sampling from a regional species pool (Cole 1980; Wilson 1996), niche interactions (that the number of prey species limits the number of niches for predators, or vice versa), the availability of energy at different trophic levels or common factors that determine the diversity of both predators and prey. Deviations from a constant proportion of predatory species suggest nonrandom processes (Wilson 1996). We will examine the relationships of habitat size and permanence to species richness and the proportion of predatory species in the metazoa of a set of temporary freshwater pools. Both habitat size and hydroperiod influence the occurrence of predators in temporary pools (Pearman 1995; Schneider

& Frost 1996; Wellborn *et al.* 1996), and are likely to affect the proportion of predatory species. The pools we studied are unusual in that habitat size and permanence are not strongly correlated, allowing us to separate their relationships with the biota. Our hypotheses are as follows.

**1** Species richness will increase with increasing pool size and permanence. Larger pools may support larger populations with lower extinction rates, may be more attractive to dispersing individuals, may contain more different microhabitats and may have more stable physicochemical conditions. Pools that dry frequently may support only those species able to tolerate desiccation or disperse before the pool dries, and are available to colonists for a shorter time.

**2** The proportion of predatory species will increase with increasing pool size and permanence. Predators often have lower population densities than nonpredators (Silva & Downing 1994), and may therefore have higher extinction rates and produce fewer dispersing individuals (Warren & Gaston 1992). Dispersing predators may also actively select larger pools (Pearman 1995) and may eliminate some of their prey (Blaustein *et al.* 1996; Wellborn *et al.* 1996). We also expect that nonpredators can persist in the absence of predators, but not vice versa. The larger sizes (Warren & Lawton 1987; Cohen *et al.* 1993) and longer generation times (Peters 1983) of predators may limit them to pools that are more permanent (Schneider & Frost 1996). As a consequence, species richness and the proportion of predatory species will be positively correlated. The proportion of predatory species will also be lower than the average reported for lentic habitats.

**3** Both species richness and the proportion of predatory species will increase over time during the wet season. The longer a pool has held water and the more surrounding pools hold water, the more opportunities there will be for colonization, and predators are unlikely to become established until their prey are abundant.

## MATERIALS AND METHODS

### Site description

Our study site is located on the Mount Carmel range (32°43' N, 35°2' E), approximately 500 m above sea level. Rainfall is about 700 mm per year, mainly between December and March, and average minimum and maximum temperatures between October and April are 12°C and 18°C, respectively (Warburg 1986). There are a few trees (*Pinus halipensis* Mill.) and bushes (*Pistacia lentiscus* L.), and a variety of grasses. A small (800 m<sup>2</sup>) area of exposed limestone bedrock contains many temporary pools, from which we selected 25 (spanning the range of

observed sizes) for intensive study. The closeness of the pools in space minimizes the effects of geographical variation.

### Biological samples

Twenty-five pools were sampled on each of five dates (November 9, 1997; December 4, 1997; January 15, 1998; February 12, 1998; and March 22, 1998), provided that standing water was present. Species lists were constructed from sweep samples (taken with a 7 × 10 cm, 210 µm mesh net) examined under a dissecting microscope, plus any species seen in the field but not appearing in samples. Sampling effort (total length of net sweeps) in each pool was proportional to surface area, and was sufficient to detect 80% of species in each pool, based on preliminary yield/effort curves. For species caught in net sweeps, we estimated density as the number of individuals per meter net sweep. Many organisms were identified only as morphological species, as few taxonomic groups of Israeli freshwater fauna are well known and some species are undescribed. Voucher specimens will be deposited in the Tel Aviv University Zoological Museum. We refer to morphological species as “species” for brevity.

We divide animal species into “predators” and “non-predators” (which some other studies refer to as “prey”). Following Jeffries & Lawton (1985) and Warren & Gaston (1992), species that feed predominantly on living metazoa are “predators”, whereas those feeding on dead metazoa, microbial food, plants and detritus are “non-predators”. Omnivores (species that may feed on living metazoa, but not predominantly) are counted as non-predators. We used both general sources (e.g. Merritt & Cummins 1978; Pennak 1978) and more detailed works on particular taxonomic groups (e.g. Fryer 1957 for copepods; Berg 1995 for chironomids) to classify organisms into predators and nonpredators. Some microscopic morphological species (nematodes, rotifers and tardigrades) may have contained more than one biological species, and may have included both predators and nonpredators. We analysed the data twice, first counting these species as predators to obtain the highest possible proportion of predators, then counting them as nonpredators to obtain the proportion of macroscopic predators. We also looked for systematic trends in the proportion of these species (which we will refer to as the proportion of doubtful species) with size and permanence. A regional species list, with trophic categories, number of pools in which each species occurred and mean densities when present, is given in the Appendix.

We recorded the presence or absence of standing water in each pool on 39 days between 30 September 1997 and 22 March 1998. This covers most of the wet season: on 30

September, no pools contained standing water, and on a return visit at the end of April 1998 we found that all pools were again dry. We define permanence as the proportion of visits on which we found standing water above the sediment or rock bed of each pool, and pool size as the maximum surface area estimated using the appropriate simple geometric shape (circle, square, triangle) after several days of heavy rain. Community structure may depend partly on previous as well as current inundations, but visits to the site in previous and succeeding years (L. Blaustein, unpublished data) suggest that the relative permanence and size of the pools does not change much from year to year.

### Statistical methods

We calculated the mean species richness, proportion of predatory species (both macroscopic and highest possible, as described above), and the proportion of doubtful species for each pool, over the sample dates on which each pool contained water. We also examined analogous variables from the set of all species that ever occurred in each pool, but as these gave similar results and were always highly correlated with the means (Pearson correlation coefficients  $\geq 0.77$ ,  $N = 25$  for species richness or 24 for other variables,  $P < 0.0001$  in all cases), we do not discuss them further. Repeated-measures analyses were not possible because most pools were dry on at least one date. The absence of aquatic organisms in the absence of water is not useful information and would have to be treated as missing data, which would result in very small sample sizes.

We used maximum surface area (natural log transformed) and permanence (arcsine square root transformed) as independent variables in multiple regression models for species richness, proportions of predatory species and proportion of doubtful species. Proportions of doubtful and predatory species were arcsine square root transformed. We tested the significance of each independent variable assuming known model structure (i.e. models always included both area and permanence). We also evaluated the effects of interaction terms and other physicochemical variables such as pH and depth on the fit of the model, using Spjøtvoll's test (Miller 1990) to control the Type I error rate under the assumption of unknown model structure (conventional "*F*-to-enter" statistics can greatly inflate the Type I error rate in this situation). We did not find any significant improvements in the model fits, so for brevity we do not report these results. This does not necessarily imply that these other variables are unimportant, as exploratory analyses are necessarily less powerful than tests of models with known structure.

Spatial autocorrelations in the independent variables are a potential confounding factor. For example, if large pools tended to occur close together, they might support similar communities due to local dispersal or similarities in microclimate. We measured the shortest distance between each pair of pools to the nearest 5 cm and calculated normalized Mantel statistics (which, like other correlation coefficients, range between  $-1$  and  $+1$ ) as a measure of the average magnitude of spatial autocorrelation in pool area (natural log transformed) and permanence (arcsine square root transformed). We tested the two-tailed significance of these correlations using 1000 permutations (Fortin & Gurevitch 1993).

We compared the proportion of predatory species in our pools with the mean proportion of predators in lentic habitats given by Warren & Gaston (1992). Warren & Gaston's data include habitats ranging in size and permanence from phytotelmata (water bodies contained within terrestrial plants) to lakes, and are a mixture of single and repeated samples of invertebrates, excluding taxa "such as protozoa and rotifers" (Warren & Gaston 1992). For comparison, we calculated the mean proportions of predators among the macroinvertebrates in our samples, excluding amphibians, rotifers, nematodes and tardigrades. We used Pearson correlation coefficients to examine the relationships between species richness and the proportion of predatory species (both macroscopic and highest possible, arcsine square root transformed).

We used linear least-squares regressions to test for consistent increases in species richness and proportions of predatory species over time (measured in days since the first sample date). Consecutive samples are not entirely independent, because pools may contain the same individuals of long-lived species such as amphibians on consecutive dates. Type I error rates may be somewhat inflated as a result. All analyses were done using JMP for Macintosh Version 3.1 (SAS Institute Inc., Cary, NC) and Matlab Version 4.2d (The Mathworks Inc., Natick, MA).

## RESULTS

### Physical properties

Maximum surface area ranged from 0.15 to 13.0 m<sup>2</sup>, with a mean of 2.7 m<sup>2</sup> (standard deviation 3.9,  $N = 25$ ). Permanence ranged from 0.26 to 0.97, with a mean of 0.73 (standard deviation 0.19,  $N = 25$ ). The Spearman correlation coefficient between surface area and permanence was 0.19 ( $P = 0.37$ ,  $N = 25$ ). Neither surface area (natural log transformed) nor permanence (arcsine square root transformed) was significantly spatially autocorrelated (normalized Mantel statistics:  $r = -0.006$ ,  $P = 0.92$ ,  $N = 25$  for area;  $r = -0.005$ ,  $P = 0.93$ ,  $N = 25$  for permanence).

### Trophic structure and species distributions

Between two and five samples were taken per pool (mean four). Living metazoa were never found in one of the 25 pools, although it contained water on two of the five sample dates, so this pool was dropped from all analyses of proportions of predatory and doubtful species (but retained in analyses of species richness). In the remaining pools, no collections were made on 20 pool × date combinations when there was no water, or too little to sample. This left a total of 100 samples, containing 0–14 species, with a mean of 4.9 (standard deviation 2.9). In total, 29 morphological species were found (see Appendix), of which three were “doubtful” (may have contained several biological species, which may have been predators or nonpredators). Six species were definitely predators (see Appendix). The regional proportion of predators was therefore at least 0.21 (counting only macroscopic predators) but no more than 0.31 (counting all possible predators). Of the 97 samples that contained at least one species, 56 or 32 contained no predators, and one or three contained only predators (counting macroscopic, or all possible predators, respectively). The mean density (excluding zeros) of macroscopic predators tended (although the tendency was not statistically significant, Table 1a) to be lower than the mean density of other species. However, if all possible predators were considered, there was no such tendency (Table 1a). Predatory and nonpredatory species did not differ significantly in the number of pools in which they ever occurred (Table 1b), or the mean size of pools in which they were found (Table 1c).

### Species richness

Larger pools had significantly more species (Fig. 1a, Table 2a), and pools that were more permanent had significantly more species (Fig. 1b, Table 2a). There was a small but significant increase in species richness over time, although

little of the variation in the data was explained by this relationship (Fig. 2a).

### Proportions of doubtful and predatory species

The proportion of doubtful species was not significantly related to either area or permanence (overall model  $R^2 = 0.03$ ,  $P > 0.4$  for both variables). The proportion of macroscopic predatory species was significantly higher in larger pools (Fig. 3a, Table 2b), but was not significantly related to permanence (Fig. 3b, Table 2b). The relationship between the highest possible proportion of predatory species and area was positive but not statistically significant (Fig. 3a, Table 2c). Highest possible proportion of predators was not significantly related to permanence (Fig. 3b, Table 2c). We did not detect an increase in either proportion of predatory species over time (Fig. 2b).

The proportion of predatory species among macroinvertebrate taxa (mean 0.08, 95% confidence limits  $\pm 0.05$ ) was substantially lower than the average proportion of predatory invertebrate species in still freshwater habitats (mean 0.31, 95% confidence limits  $\pm 0.02$ ) from Warren & Gaston (1992). There was a significant positive correlation between species richness and the proportion of macroscopic predatory species ( $r = 0.42$ ,  $P = 0.04$ ,  $N = 24$ ). There was also a positive correlation between species richness and the highest possible proportion of predatory species, but this was not statistically significant ( $r = 0.33$ ,  $P = 0.11$ ,  $N = 24$ ).

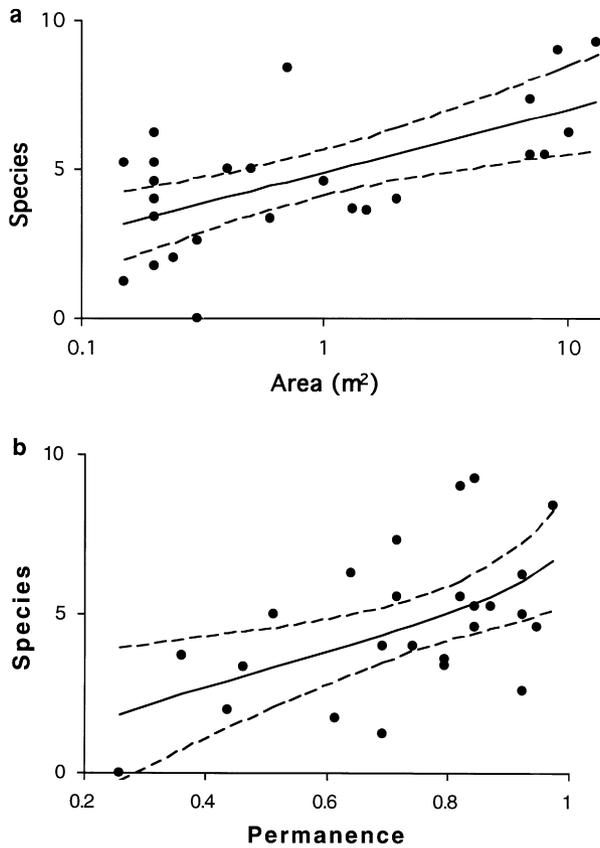
### DISCUSSION

Pools with larger surface area had more species (Fig. 1a). Similar results have been found in other temporary pools (Ward & Blaustein 1994). There are many possible reasons for this, including passive sampling, lower extinction risk due to larger population sizes and

**Table 1** Predator and nonpredator distributions: (a) mean densities per m net sweep (natural log transformed), excluding zeros; (b) number of pools in which species ever occurred; (c) mean area in m<sup>2</sup> of pools in which species ever occurred. In each case, the first value includes only macroscopic predators and the second value includes all possible predators (see Materials and Methods). The Wilcoxon rank sum test statistic  $Z$  and the  $P$  value are given for each comparison.

	Mean	Standard error	N
(a) In mean density ( $Z = -1.90$ or $-0.64$ , $N = 0.06$ or $0.53$ )			
Non-predators	3.55 or 3.37	0.38 or 0.43	20 or 17
Predators	1.87 or 3.01	0.33 or 0.61	4 or 7
(b) Pools found ( $Z = -0.43$ or $-0.12$ , $P = 0.66$ or $0.91$ )			
Non-predators	8.7 or 8.8	1.5 or 1.7	23 or 20
Predators	6.0 or 6.8	1.7 or 1.4	6 or 9
(c) Mean area of pools found ( $Z = 1.48$ or $1.44$ , $P = 0.13$ or $0.15$ )			
Non-predators	4.0 or 3.9	0.5 or 0.6	23 or 20
Predators	6.0 or 5.6	1.4 or 1.1	6 or 9

buffering against fluctuations in physicochemical conditions, and increased diversity of microhabitats (Connor & McCoy 1979; Hart & Horwitz 1991). These factors are



**Figure 1** Relationships of area (a) and permanence (b) with mean species richness. Univariate regression lines with 95% prediction confidence limits are shown. Permanence was arcsine square root transformed for analysis, and back-transformed values are plotted. Area was natural log transformed.

**Table 2** Multiple regression models for (a) species richness, (b) proportion of macroscopic predators and (c) highest possible proportion of predators. Maximum pools surface area ("area") was natural log transformed and permanence ("perm") and proportions of predatory species were arcsine square root transformed.

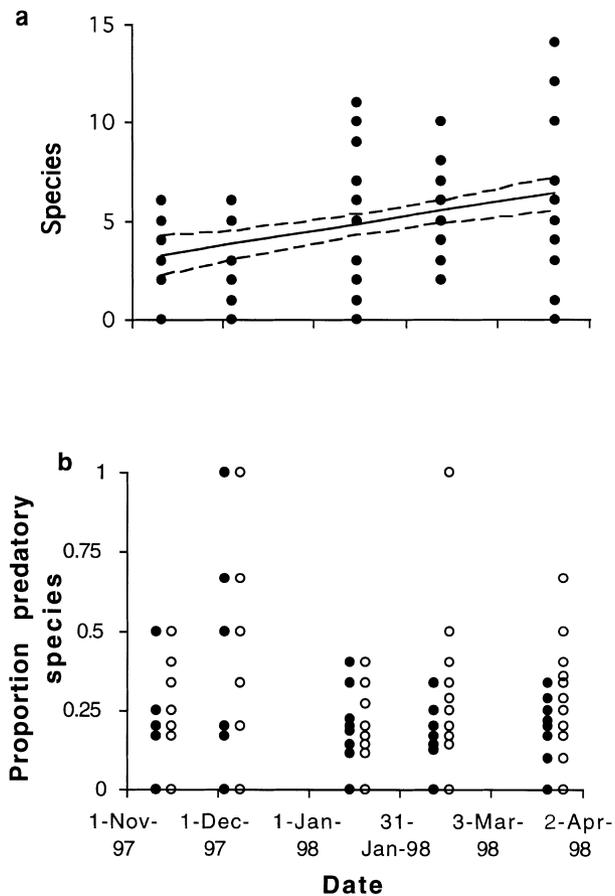
Parameter	Estimate	Standard error	<i>t</i>	<i>P</i>
(a) Species richness (overall fit: $F_{2,22} = 13.95$ , $P = 0.0001$ , $R^2 = 0.56$ ).				
intercept	0.24	1.58	0.15	0.88
area	0.79	0.21	3.69	0.001
perm	4.41	1.48	2.98	0.01
(b) Proportion of macroscopic predators (overall fit: $F_{2,21} = 7.02$ , $P = 0.005$ , $R^2 = 0.40$ ).				
intercept	0.44	0.23	1.90	0.07
area	0.10	0.03	3.74	0.001
perm	-0.14	0.21	-0.68	0.51
(c) Highest possible proportion of predators (overall fit: $F_{2,21} = 1.51$ , $P = 0.24$ , $R^2 = 0.13$ ).				
intercept	0.66	0.23	2.89	0.01
area	0.04	0.03	1.63	0.12
perm	-0.18	0.21	-0.86	0.40

not mutually exclusive, and we will not attempt to separate their contributions. However, simple species-area relationships are not ubiquitous in freshwater ponds: biotic interactions (Barnes 1983) and water chemistry (Friday 1987) are sometimes more important.

In many temporary pools, species richness is strongly affected by hydroperiod (Schneider & Frost 1996). We found that species richness was significantly higher in pools that were more permanent (Fig. 1b, Table 2a). For fully aquatic organisms, the longer a pool contains water, the more species are able to complete their life cycles and thus maintain viable populations. For species with dispersing adults, pools that are more permanent are available to colonists for longer (and some species may be able to select pools that are more permanent).

There was some evidence for a slight increase in species richness over time (Fig. 2a; bearing in mind that consecutive samples are not fully independent). This may be because later in the season, pools that hold water for a long time have been exposed to more colonizers. However, the trend may be weak because temporary pool fauna are generally characterized by high colonization rates (Jeffries 1994), and many taxa can persist in dry sediments and revive quickly when wetted (Jeffries 1989). Thus, species richness may approach a steady state soon after pools are filled.

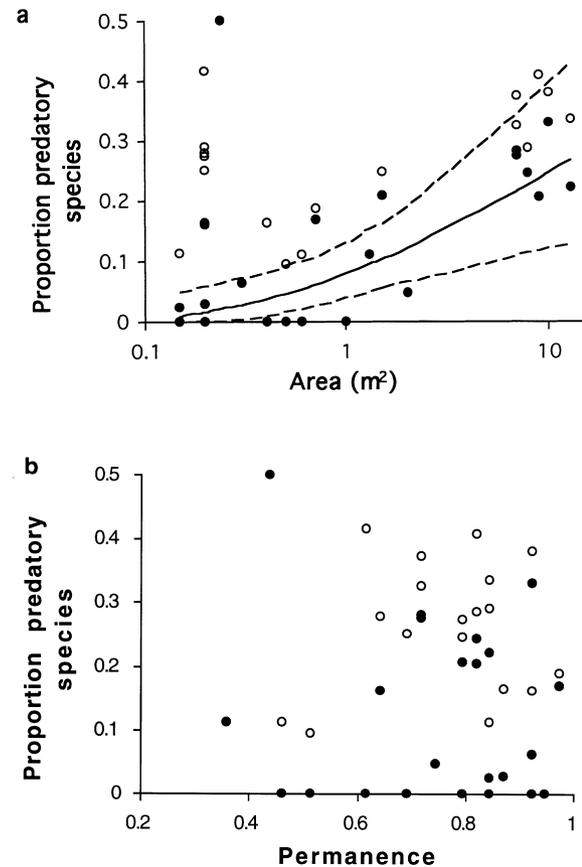
The proportion of predatory species (either macroscopic or all possible predators) did not change significantly over time (Fig. 2b) or with permanence (Fig. 3b). In many temporary pools, the predators are mainly insects, which colonize relatively slowly compared with aquatic organisms emerging from resting stages, so the proportion of predatory species increases with time (Williams 1987). Similarly, food chain length increases over the growing season in rice fields, due to herbivores arriving before predators and parasitoids (Schoenly *et al.*



**Figure 2** (a) Species richness over time, with the least-squares regression line and 95% prediction confidence intervals (regression coefficient = 0.02, standard error = 0.006,  $t = 4.03$ ,  $P = 0.001$ ,  $R^2 = 0.14$ ,  $N = 100$ ). (b) Proportions of macroscopic predators (●) and all possible predators (○, shifted to the right for clarity) over time. Least-squares regression relationships were not significant (macroscopic predators, coefficient =  $-7 \times 10^{-4}$ , standard error =  $7 \times 10^{-4}$ ,  $t = -1.10$ ,  $P = 0.27$ ,  $R^2 = 0.01$ ,  $N = 97$ ; all possible predators, coefficient =  $-2 \times 10^{-4}$ , standard error =  $8 \times 10^{-4}$ ,  $t = -0.27$ ,  $P = 0.79$ ,  $R^2 = 8 \times 10^{-4}$ ,  $N = 97$ . Proportions of predatory species were arcsine square root transformed).

1996). In ponds in northern Wisconsin, relatively few species of predators occur in ponds that dry frequently (Schneider 1997). However, in our pools many of the predators are either fully aquatic and adapted to frequent drying (such as flatworms and the potentially predatory rotifers, nematodes and tardigrades) or rapid colonizers (such as salamanders). Those predators that do occur may thus appear as quickly as the nonpredators, and predators that are not able to survive desiccation or to colonize rapidly are absent from all the pools.

The proportion of macroscopic predatory species increased significantly with surface area (Fig. 3a). The



**Figure 3** Relationships of area (a) and permanence (b) with proportions of predatory species. ●, Proportion of macroscopic predators; ○, highest possible proportion of predators. In (a), the univariate regression relationship with 95% prediction confidence limits is shown for the relationship between area and proportion of macroscopic predators (Table 2b), but not for the highest possible proportion of predators as this relationship was not statistically significant in multiple regression (Table 2c). Neither proportion of predatory species was significantly related to permanence (Table 2b and c). Proportions of predators were arcsine square root transformed for analysis, and back-transformed values are plotted. Area was natural log transformed and permanence was arcsine square root transformed.

partial regression coefficient for highest possible proportion of predatory species was also positive (Table 2c), but not significantly greater than zero. The proportion of doubtful species was not significantly related to either area or permanence. These species (rotifers, nematodes and tardigrades) are all very small, and it is not surprising that their distributions are not strongly related to area or permanence. Even in small pools, they may have large populations with low extinction risk, and can make use of microhabitats on a much finer scale than larger organisms (Shorrocks *et al.* 1991). Their short life cycles will allow them to quickly respond to drying. The other predators

(flatworms, amphibians and beetle larvae) are much larger. Both beetles (e.g. Pearman 1995) and salamanders (L. Blaustein *et al.* unpublished work) are likely to select larger pools for oviposition, and all these species are likely to have much lower local population sizes and longer generation times than the “doubtful” species. Therefore, if the “doubtful” species are not predators we would expect a stronger relationship between the proportion of predatory species and pool area than if the “doubtful” species are predatory. The true relationship is probably intermediate between the extremes we examined.

We suggested that the proportion of predatory species might increase with pool size either because predators have lower population densities and thus tend to occur in fewer, larger pools than nonpredators, or because species-poor communities without predators are likely, but communities without nonpredators will be rare. The mean density of macroscopic predators was significantly lower than the mean density of other species, but there was no evidence for this if all possible predators were considered (Table 1a). In either case, predators were not found in significantly fewer (Table 1b) or larger (Table 1c) pools than nonpredators. We found few samples in which there were predators without prey, but many in which there were nonpredators without predators (presumably because it is much more difficult for predators to survive without prey than for prey to survive without predators). As the number of species per pool was low, the influence of these predator-free communities on the overall relationship will be large. This probably accounts for the much lower proportions of macroinvertebrate predatory species in our pools than in lentic freshwater habitats generally (Warren & Gaston 1992), and for the positive correlation between species richness and the proportion of macroscopic predatory species in our data. Similar patterns have been found in other species-poor communities. Very small terrestrial islands in the Bahamas have very few species, and generally lack predators, whereas larger islands have more species, including predators (Schoener 1989; species richness not stated, but apparently low). The proportion of carnivores among montane mammals of the Southern Rocky Mountains increases with increasing species richness (Patterson *et al.* 1984; regional pool of 26 species). Among aquatic insects inhabiting water trapped in Costa Rican bromeliads, predators are absent from smaller plants (Srivastava 1998; regional pool of 35 species). The proportion of predatory species among invertebrates living in moss patches in northern England decreased over 6 months with experimental habitat fragmentation (Gilbert *et al.* 1998; mean 23.2 species per sample), and more isolated patches of stinging nettle (*Urtica dioica*) in northern Germany supported relatively fewer predatory species (Zabel &

Tscharntke 1998; maximum <30 species per sample, although some unidentified organisms were not included). However, studies involving large numbers of species generally find little systematic variation in the proportion of predatory species (or related statistics) with species richness (Cohen 1977, 1978; Jeffries & Lawton 1985; Schoener 1989; Gaston *et al.* 1992; Warren & Gaston 1992; Rosenzweig 1995; see also Mikkelsen 1993; although species richness is not stated). The disparity between results from studies with low and high species richness can be explained by an asymptotic relationship between species richness and the proportion of predatory species. Random sampling from a regional species pool with the constraint that there must be some nonpredators in each local community can generate this kind of pattern (Deb 1995), although specifying the probability of occurrence for each species is difficult, as observed frequencies (Cole 1980; Wilson 1996) may include the effects of local assembly rules (Warren & Gaston 1992), whereas equal probabilities ignore other factors affecting frequency of occurrence (Wilson 1995).

Similar relationships have been predicted between habitat area and food chain length. When species richness is low, sequential dependencies (a predator cannot colonize unless its prey are already present) could lead to strong relationships between habitat size and food chain length (Holt 1996). However, when the number of species is very large, these constraints are unlikely to be important, and food chain length will only increase very slowly with habitat size (Cohen & Newman 1991). Sequential dependencies may also lead to steeper species-area relationships for species at higher trophic levels, but are less likely to have large effects on community structure when consumers can survive on many different resources (Holt *et al.*, 1999). Despite this, resource diversity may still affect the occurrence of generalist consumers. For example, Ritchie (1999) showed that a generalist rodent herbivore (the prairie dog, *Cynomys parvidens*) in Utah has lower extinction rates in habitat patches with more species of plants, possibly because higher plant diversity increases the chance that at least one resource is abundant in any given year. However, in some taxa such as beetles (Becker 1975), carnivores tend to have broader diets than herbivores, and consequently their occurrence may be less limited by the presence of suitable resources.

There is some evidence that other ecosystem properties show asymptotic relationships with species richness (Tilman *et al.* 1997). This suggests that communities with very few species may function differently from communities with moderate to high species richness, and are more likely to be severely affected by the loss of a given proportion of species. There are also implications for the

scaling of ecological experiments. If many ecosystem processes approach an asymptote at fairly low species richness, experiments involving a moderate number of species may be useful in understanding the functioning of much more speciose systems.

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#### BIOSKETCH

Matthew Spencer is interested in the trophic structure of communities, and its consequences for population dynamics, conservation and ecotoxicology.

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#### APPENDIX

Morphological species found at least once in any pool. Trophic groups are “N” for nonpredators, “P” for predators and “D” for doubtful. “sp.” indicates that we are confident that only one biological species was present even if it could not be identified to species level. Mean density (individuals per m net sweep), excludes zeros, and was not determined (indicated by “–”) for species that were observed but never caught in net sweeps. Pools found is the number of pools in which the species ever occurred. See Materials and Methods for more details.

Morphological species	Trophic group	Mean density	Pools found
Ostracoda:			
<i>Heterocypris</i> sp.	N	614	22
<i>Pomatocypris</i> sp.	N	74	15
<i>Eucyprinotus</i> sp.	N	103	17
<i>Ilyocypris</i> sp.	N	77	17
Ostracoda sp. 1	N	17	4
Ostracoda sp. 2	N	–	1
Copepoda:			
<i>Eucyclops serratus</i> Fischer	N	19	15
Harpacticoidea sp.	N	2	1
<i>Arctodiaptomus similis</i> Baird	N	1	1
Cladocera:			
<i>Pleuroxus</i> sp.	N	204	17
<i>Macrothrix hirsuticornis</i> Norman & Brady	N	105	13
<i>Ceriodaphnia</i> sp.	N	183	2
Conchostraca:			
<i>Cyzicus</i> sp.	N	3	2
Tardigrada	D	59	5
Rotifera D	317	6	
Nematoda	D	41	14
Annelida:			
Oligochaeta sp.	N	17	3

## Appendix Continued:

Morphological species	Trophic group	Mean density	Pools found
Turbellaria:			
<i>Mesostoma</i> sp.	P	6	10
Turbellaria sp. 1	P	16	10
Turbellaria sp. 2	P	4	3
Insecta:			
Chironomidae larvae	N	11	17
<i>Dasyhelea</i> sp. larvae	N	128	19
Ephidridae larvae	N	15	6
<i>Culex</i> sp. larvae	N	7	1
Dytiscidae sp. larvae	P	5	2
Corixidae sp. adults	N	–	1
Syrphidae larvae	N	–	2
Caudata:			
<i>Salamandra salamandra inframaculata</i> (L.) larvae	P	–	9
<i>Triturus vittatus vittatus</i> (Jenyns) adults	P	–	2