



Increasing isolation reduces predator:prey species richness ratios in aquatic food webs

Rachel S. Shulman and Jonathan M. Chase

R. S. Shulman (rshulman@lifesci.ucsb.edu) and J. M. Chase, Dept of Biology, Washington Univ. in St. Louis, St. Louis, MO 63130, USA. Present address for RSS: Dept of Ecology, Evolution & Marine Biology, Univ. of California, Santa Barbara, Santa Barbara, CA 93106, USA.

The number of species that live in a habitat typically declines as that habitat becomes more isolated. However, the influence of habitat isolation on patterns of food web structure, in particular the ratio of predator to prey species richness, is less well understood. We placed aquatic mesocosms at varying distances from ponds that acted as sources of potential colonists; then we examined how isolation affected the ratio of predator:prey species richness in the communities that assembled. In the final sampling, a total of 21 species (12 prey and 9 predators) of insects, crustaceans, and amphibians had colonized the mesocosms. We found that total species richness, as well as the richness of predators and prey, declined with increasing isolation. However, predator richness declined more rapidly than prey richness with increasing isolation, which lead to decreasing predator:prey ratios. This result conflicts with prior demonstrations of invariant predator:prey ratios in freshwater communities.

Communities that experience lower rates of dispersal from the regional species pool, as often is the case in isolated habitats, tend to have lower local species richness than those with higher dispersal rates (reviewed by Cadotte 2006). It is also well known that predators tend to be disproportionately influenced by habitat isolation relative to prey, owing to their typically larger area requirements and lower population sizes (reviewed by Holt and Hoopes 2005). Less clear, however, is whether there are underlying mechanisms in local food webs that act to readjust prey species richness following disproportionate losses of predators. This type of correction would be expected if the ratio of predator to prey species richness was an invariant property of food webs controlled by local assembly rules (Warren and Gaston 1992). However, if the predator:prey richness ratio is not held constant by underlying rules, then richness ratios may decline with increasing habitat isolation (Watts and Didham 2006).

If the structure of food webs is an invariant property of a local community (Cohen 1977, Briand and Cohen 1984, Jeffries and Lawton 1985, Pimm et al. 1991, Warren and Gaston 1992), then disproportionate

reductions in predator species richness with habitat isolation should be followed by concomitant adjustments in prey richness, and predator:prey ratios should remain constant. Such constancy is thought to be generated by underlying assembly rules (Weiher and Keddy 1999), whereby the number of prey species in a local community constrains the number of predator species, or vice versa. For example, in a meta-analysis of studies examining the responses of plants and vertebrates to habitat fragmentation, Mikkelsen (1993) suggested that, across systems, the predator:prey ratio did not change as the total number of species declined due to fragmentation.

Alternatively, if dispersal from source pools within the region has a strong influence on local communities, and food web structure is not held constant by local rules (Cole 1980, Warren 1995, Wilson 1996, Thompson and Townsend 2000), disproportionate reductions in predator richness with habitat isolation might decrease predator:prey richness ratios. One reason for this expectation is that the smaller population sizes of predators relative to prey (i.e. due to energetic requirements) leads to higher extinction rates of

predators (Schoener 1989). Many empirical studies support the prediction that habitat isolation has a disproportionate effect on predator richness relative to prey richness in subsets of the community (reviewed by Holt and Hoopes 2005). However, whether these disproportionate effects lead to altered predator:prey richness ratios at the level of the entire community remains unclear.

In this study, we examined how habitat isolation affects predator:prey richness ratios in small freshwater pond communities. Habitat isolation in ponds has been implicated as an important determinant of patterns of species richness and composition among a variety of taxa (Maguire 1963, Lehtinen et al. 1999, Shurin 2001, Wilcox 2001, Forbes and Chase 2002, Cohen and Shurin 2003, Jenkins et al. 2003, Chase and Ryberg 2004, McCauley 2006). However, just like the more general studies discussed above, studies in freshwater ponds have found mixed results with regards to predator:prey richness ratios. In some cases, predator:prey ratios in ponds appear to be constant (Jeffries and Lawton 1985, Warren and Gaston 1992, Jeffries 2002, Donald and Anderson 2003, Urban 2004). For example, in an important experimental study, Jeffries (2002) manipulated the ratio of predator:prey richness in experimental ponds and found that, although the identity of species often changed after perturbation, the predator:prey ratio of species richness remained constant. Alternatively, other studies have shown variable predator:prey richness ratios in ponds (Spencer et al. 1999, Bilton et al. 2001).

Material and methods

Study system and experimental design

We chose three fishless, shallow, permanent ponds at Washington Univ.'s Tyson Research Center (Eureka, MO, USA) as source replicates. All of these ponds were constructed by Washington Univ. researchers between 1965 and 1975. The three ponds are separated by a distance >1000 m from each other and from any other ponds on the site. They are of relatively similar size (400–800 m²) and depth (1–2 m), and have similar underlying soil conditions and surrounding terrestrial habitats (oak–hickory forest) (Sexton and Phillips 1986). At the time of the experiment, β -diversity of macro-invertebrates and amphibians across these three ponds was 0.64 (α/γ : 41/64), suggesting that they shared a large proportion of their species (Chase unpubl.).

We manipulated isolation from the source pool of potential colonists at three levels by placing mesocosms along a linear transect at three distances from each of the three source ponds: <5 m, 50 m and 100 m. Each distance treatment (three levels) was replicated across

three spatial blocks (i.e. the three ponds), for a total of three replicates per treatment; that is, each pond received one replicate of each of the three distance treatments. Mesocosms were 60 l plastic tubs filled with 50 l of nutrient-poor well water. Previous experiments at the Tyson Research Center have demonstrated that a diverse array of pond organisms readily colonize these experimental mesocosms, including amphibians (Anura: Hylidae), insects (Diptera, Coleoptera, Ephemeroptera, Hemiptera, Odonata) and crustaceans (Cladocera, Copepoda) (Chase unpubl.). To each of the mesocosms, we added 10 g of mixed oak (*Quercus* spp.) and hickory (*Carya* spp.) leaves as a source of nutrients and detritus at the base of the food web. The mesocosms were naturally replenished with rain water throughout the course of the experiment, and two pairs of small (5 mm in diameter) holes drilled 2.5 cm from the top of the mesocosms allowed excess rainfall to drain with minimal loss of organisms. We established the experiment on 6 June 2004. Vegetative debris and terrestrial insects that had fallen into the mesocosms were removed during each observation period (below).

Sampling

Over the course of the experiment, we established a temporal sampling regime that allowed us to assess whether species composition within the mesocosms had stabilized. Although many of the taxa that colonize these mesocosms are somewhat difficult to identify in situ, the communities were composed of so few individuals that we could not destructively sample them multiple times without potentially altering future dynamics. As such, we set up a non-destructive temporal sampling regime in which one observer (RSS) conducted weekly visual censuses of macroscopic taxa observed in each mesocosm. The accuracy of visual censuses was strengthened by an on-site catalogue of the subset of pond organisms that readily colonize mesocosms at the Tyson Research Center (Chase and Shulman unpubl.). Microscopic organisms such as zooplankton and taxonomically challenging organisms such as Chironomids were identified to family and subfamily, respectively, during visual censuses with the aid of a magnifying glass. Because these organisms were not identified to species in the field and because they represented only a small proportion of the total taxa observed (3 out of 21 taxa), we excluded them from analyses used to determine whether the communities had stabilized. While we recognize that our results would have been reinforced by a more destructive temporal sampling regime, comparisons between our visual censuses of taxa one day prior to the final, destructive sampling and the taxa actually recovered from this final sampling suggest that invertebrate

species were identified accurately during the visual censuses. After analyzing the visual census data and determining that communities were relatively stable through time and that there were no treatment differences in temporal species turnover (Statistical Analysis), we ended the experiment by destructively sampling the mesocosms on 13 August 2004. This allowed us to more definitively identify and count individuals for calculations of species richness, abundances, and community composition.

We destructively sampled the mesocosms in two ways: (1) we sampled macroinvertebrates and amphibians by sweeping a 10×10 cm net (0.33 mm mesh) from one end of each mesocosm to the other until no individuals were sampled in at least five sweeps; we preserved these samples in 70% ethanol and later identified them to species (excluding Chironomids, which were identified to sub-family) under a dissecting microscope using standard (Merritt and Cummins 1996) and region-specific keys (Whiteman and Sites 2003) and (2) we sampled crustacean zooplankton by pulling a 30 μ m mesh zooplankton net (10 cm \varnothing) once vertically through the water column; we preserved the contents in acid lugols solution for later identification and enumeration under a dissecting microscope (Balcer et al. 1984). Microscopic rotifers and protozoa were not analyzed. All sampling equipment was thoroughly rinsed with 70% ethanol and tap water between mesocosms.

Each species was categorized as either 'prey' (those species that feed predominantly on algae, microbes, and/or detritus, i.e. non-predators) or 'predator' (those species that feed predominantly on living metazoans; Jeffries and Lawton 1985, Warren and Gaston 1992) using categorizations from taxonomic keys (Balcer et al. 1984, Merritt and Cummins 1996, Whiteman and Sites 2003).

Statistical analysis

We analyzed data from our visual censuses to discern whether any treatment differences observed in the final destructive sample may have been simply due to the longer time it might take for more isolated communities to stabilize relative to communities closer to the source pond (i.e. due to lower colonization rates in more isolated habitats). We calculated Jaccard's index of community similarity for each mesocosm and used repeated-measures ANOVA to determine whether there was a distance, distance \times time interaction, or pond identity effect on Jaccard's index from one census period to the next over the last three censuses.

Using data from the final destructive census, we conducted one-way ANOVAs to test for the effect of distance from the source pond on total species richness,

predator richness, prey richness, and the ratio of predator to prey species richness. The predator:prey richness ratio was calculated by dividing the total number of species classified as predators by the total number of species classified as prey. Since isolation is well known to influence the abundance of individuals, we considered the possibility that observed treatment differences in species richness correlated with variation in abundance. Because we uniformly and destructively sampled each mesocosm (i.e. each mesocosm was sampled with the same effort), rarefaction allows us to test whether any differences in the abundance of species might have contributed to variation in species richness via a sampling effect, wherein communities with greater numbers of individuals have higher richness. To explore this potential mechanism, we conducted one-way ANOVAs to test for the effect of distance from the source on rarefied richness values. Additionally, we investigated whether isolation influenced the relative abundance of taxa by conducting one-way ANOVAs to test for the effect of isolation on total, predator, and prey evenness (PIE; Hurlbert 1971), as well as total abundance, prey and predator abundance, and the ratio of predator to prey abundance. Since we replicated each distance treatment (<5 m, 50 m and 100 m) across three ponds, pond identity was included as a random block effect in all ANOVAs. Significant ANOVAs were followed by Tukey's HSD for pairwise comparisons among the distance treatments, as well as sequential Bonferroni tests. All ANOVAs were performed using SYSTAT, ver. 10.2.01. Rarefaction curves and evenness were calculated using EcoSim, ver. 7 (Gotelli and Entsminger 2004).

Results

Community similarity between censuses was, on average, greater than 60% for each treatment over the last three weeks of the experiment (Jaccard's similarity: <5 m $-0.64 + 0.18$; 50 m $-0.87 + 0.05$; 100 m $-0.79 + 0.12$), and there was no distance, distance \times time interaction, or pond identity effect on Jaccard's similarity over the last three weeks (all $p > 0.29$). Thus, it was unlikely that treatment differences observed at the end of the experiment were due to the longer time it might take for more isolated communities to stabilize. As a result, we only present the results from the final sampling of the experiment in which we destructively sampled species richness and abundances.

In total, 21 taxa (12 prey, 9 predator) were found in the mesocosms during the final, destructive sampling (Table 1). Increasing distance from the source pond decreased total species richness both before ($F_{2,4} = 17.36$, $p = 0.01$) and after rarefaction ($F_{2,4} = 14.28$,

Table 1. Species and their mean abundances at the three distances from the source pond.

Order	Family	Genus	Species	Mean abundance (\pm SD)		
				<5 m	50 m	100 m
Anura	Hylidae	<i>Hyla</i>	<i>versicolor</i>	13.7 \pm 23.7	0.0	0.0
Coleoptera	Dytiscidae	<i>Acilius</i>	<i>fraternus</i>	3.0 \pm 1.0	0.0	0.0
Coleoptera	Dytiscidae	<i>Copelatus</i>	<i>chevrolati</i>	1.7 \pm 2.1	0.0	0.0
Coleoptera	Dytiscidae	<i>Copelatus</i>	<i>glyphicus</i>	0.3 \pm 0.6	0.0	0.0
Coleoptera	Dytiscidae	<i>Coptotomus</i>	<i>venustu</i>	29.0 \pm 21.7	1.0 \pm 1.0	0.0
Coleoptera	Dytiscidae	<i>Hygrotus</i>	<i>nubilus</i>	0.3 \pm 0.6	0.0	0.0
Coleoptera	Dytiscidae	<i>Thermonectus</i>	<i>basillaris</i>	0.3 \pm 0.6	0.0	0.0
Coleoptera	Dytiscidae	<i>Uvarus</i>	<i>lacustris</i>	8.7 \pm 8.3	0.0	0.0
Coleoptera	Noteridae	<i>Suphisellus</i>	<i>puncticollis</i>	3.3 \pm 3.2	0.0	0.0
Copepoda	Cyclopoida	<i>Acanthocyclops</i>	<i>robustus</i>	476.7 \pm 825.6	0.0	0.0
Copepoda	Cyclopoida	<i>Diacyclops</i>	<i>bicuspidatus</i>	1041.3 \pm 1244.8	0.0	0.0
Diptera	Chaoboridae	<i>Chaoborus</i>	<i>americanus</i>	14.0 \pm 2.0	0.0	0.0
Diptera	Chironomidae	<i>Chironomini</i> (sub-family)	spp.	23.0 \pm 8.0	18.3 \pm 18.5	5.3 \pm 9.2
Diptera	Culicidae	<i>Aedes</i>	<i>vexans</i>	17.7 \pm 16.6	226.0 \pm 32.6	233.7 \pm 17.2
Diptera	Culicidae	<i>Anopheles</i>	<i>quadrimaculatus</i>	109.3 \pm 12.2	13.3 \pm 16.7	0.0
Diptera	Culicidae	<i>Anopheles</i>	<i>punctipennis</i>	0.0	8.7 \pm 15.0	0.0
Diptera	Culicidae	<i>Culex</i>	<i>pipiens</i>	44.7 \pm 16.3	74.3 \pm 33.6	151.7 \pm 26.0
Diptera	Culicidae	<i>Culex</i>	<i>restuans</i>	3.0 \pm 5.2	0.0	4.3 \pm 7.5
Diptera	Culicidae	<i>Toxorhynchites</i>	<i>rustibus</i>	0.0	0.3 \pm 0.6	31.0 \pm 54.0
Diptera	Stratiomyiidae	<i>Stratiomys</i>	<i>barbata</i>	0.0	0.0	4.0 \pm 7.0
Hemiptera	Notonecta	<i>Notonectidae</i>	<i>undulata</i>	0.0	0.7 \pm 1.1	0.0

$p=0.02$). Increasing distance also decreased predator species richness before ($F_{2,4}=48.25$, $p<0.01$; Fig. 1a) and after rarefaction ($F_{2,4}=25.77$, $p<0.01$; Fig. 1b). Distance from the source pond marginally decreased prey species richness before ($F_{2,4}=5.26$, $p=0.07$; Fig. 1a) and after rarefaction ($F_{2,4}=4.92$, $p=0.08$; Fig. 1b). The ratio of predator:prey species richness declined with increasing distance ($F_{2,4}=7.98$, $p=0.04$; Fig. 2). Although total evenness and prey evenness were unaffected by isolation (both $p>0.70$), predator evenness declined with increasing isolation ($F_{2,4}=42.71$, $p<0.01$). Total abundance, predator abundance, prey abundance, and the ratio of predator to prey abundance did not vary with isolation (all $p>0.15$). Block effects were non-significant (all $p>0.45$).

Discussion

Although both predator and prey species richness declined with isolation, predator richness declined more rapidly than prey richness, which lead to decreasing predator:prey richness ratios. While previous studies in ponds have shown that some predatory taxa experience declines in species richness and abundance with increasing isolation (notonectid backswimmers and dytiscid diving beetles, Wilcox 2001; odonate dragonflies, McCauley 2006), ours is the first to show that the more rapid loss of predators with isolation lead to shifts in trophic ratios. This result conflicts with previous studies on pond food webs that have suggested

that that local processes act to maintain constant predator:prey ratios (Jeffries and Lawton 1985, Warren and Gaston 1992, Jeffries 2002, Donald and Anderson 2003, Urban 2004).

Our result that predator richness decreased more rapidly than prey richness with isolation may have resulted from a combination of one or more mechanisms. First, predators may be more vulnerable to stochastic extinctions in isolated habitats than prey because predators tend to have lower population densities (Mikkelsen 1993, Gilbert et al. 1998, Gonzalez et al. 1998, Terborgh et al. 2001). Second, predators might have been more dispersal-limited than their prey, which would impose stricter limits on the potential pool of predator colonists. Additionally, if predators are more influenced by isolation and they have a top-down effect on prey abundance and/or richness, it is possible that spatial refugia from predation could have arisen farther from the source, allowing certain prey species to be impacted less (or positively impacted) by isolation (Shurin and Allen 2001). This mechanism is consistent with the response of several prey taxa in our study that showed increased abundance in more isolated mesocosms (Table 1).

Mass (Shmida and Wilson 1985) and/or rescue effects (Brown and Kodric-Brown 1977) may have contributed to increased richness closer to the source pool simply by increasing the numbers of individuals of different species dispersing to those more proximate localities (i.e. source-sink dynamics; Pulliam 1988). Additionally, habitat selection might have influenced this pattern if individuals perceived habitats

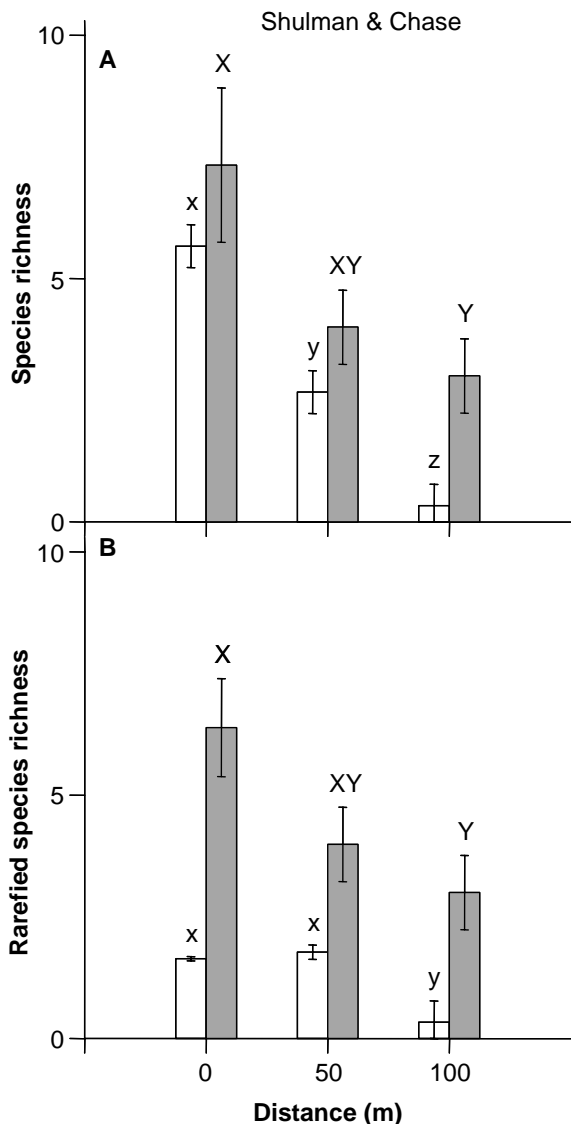


Fig. 1. Distance effect on the means (± 1 SE) of species richness. Open bars are predator species richness and gray bars are prey species richness. Letters correspond to pairwise comparisons among the distance treatments for either predators (lower-case) or prey (upper-case). (A) raw species richness data, (B) rarefied data.

as differentially suitable (Resetarits et al. 2005). Analysis of the richness data after we controlled for differences in the abundances of individuals (using rarefaction) suggests that the decline in predator richness from <5 m to 50 m was at least partially due to declines in the number of predator individuals (Fig. 1B). However, the effect of the distance treatment on prey richness was independent of prey abundance (Fig. 1B), suggesting that the less rapid decline of prey species richness with increasing isolation was likely due to factors other than

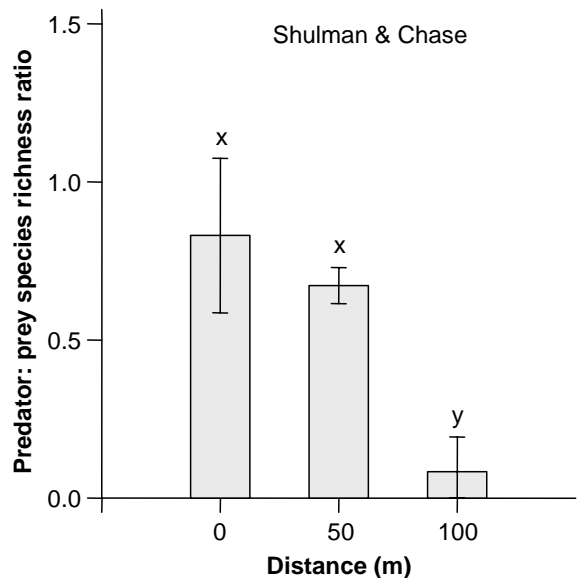


Fig. 2. Distance effect on the means (± 1 SE) of the predator:prey species richness ratio. Letters correspond to pairwise comparisons among the distance treatments.

source–sink or rescue effects, such as spatial heterogeneity in predation.

Our results were largely influenced by the response of two trophically-distinct groups of taxa: (1) coleopterans (beetles), the majority of which were predators (i.e. dytiscids) and (2) dipterans (flies), which were generally classified as prey (Table 1). Coleopterans were found at highest abundances in mesocosms closest to the source, while the abundance of dipterans appeared to be generally less influenced by the isolation gradient (Table 1). Interestingly, these coleopterans spend both their larval and adult stages in aquatic systems, only sporadically entering the terrestrial realm as adults to disperse among ponds, whereas dipterans have a terrestrial adult stage (Merritt and Cummins 1996). This divergence in life-history might have contributed to declining predator:prey ratios with increasing isolation if dipterans have a higher probability of encountering more isolated habitats. Further exploration of how the terrestrial habitat influences the dispersal of aquatic organisms in different trophic levels – especially those with complex life cycles (Wilbur 1980) – will be necessary to resolve the role of space on the structure of these food webs.

While the abundances of most predator species declined with increasing distance from the source pond, the numbers of certain prey species, particularly *Aedes* and *Culex* mosquitoes (Diptera: Culicidae), greatly increased with increasing distance from the source pond (Table 1). We suspect that the distance treatment may have influenced mosquito abundance by

spatially distributing mosquito predators and competitors (reviewed by Blaustein and Chase 2007). Higher levels of predation and/or interspecific competition in more species-rich mesocosms closer to the source pond may have increased mortality of mosquitoes in those mesocosms. This pattern might have been enhanced by the behavior of adult mosquitoes, which have been shown to reduce oviposition in habitats with predators (Stav et al. 1999) or high levels of interspecific competition (Mokany and Shine 2003). Because mosquitoes are important disease vectors (Spielman and D'Antonio 2001), we suggest that investigation of the role of spatial factors on mosquito populations would be a fruitful avenue for future research.

Although controversial (Cole 1980, Warren 1995, Wilson 1996, Thompson and Townsend 2000), it has often been argued that certain structural properties of food webs, such as the ratio of predator to prey species, are invariant and arise from underlying community assembly rules (Cohen 1977, Briand and Cohen 1984, Jeffries and Lawton 1985, Pimm et al. 1991, Warren and Gaston 1992). However, our results support a growing body of literature investigating how communities are structured in spatially explicit landscapes that suggests predators and prey should respond differentially to variation in isolation (reviewed by Holt and Hoopes 2005). Because local and regional factors interact to structure natural communities, a more robust understanding of the role of isolation on food web structure will require simultaneous consideration of how spatial processes control local trophic structure and how local food web interactions mediate the impact of spatial processes (Brose et al. 2004).

Acknowledgements – We thank L. Blaustein, T. Knight, J. Shurin and members of the Chase lab for helpful discussions and comments. We also thank Tyson research community and staff for help with experimental setup and logistical support. This research was supported by an HHMI Fellowship from Washington Univ. to R. S. S., by the Tyson Research Center, and by an NSF REU supplement (DEB 024180) to J. M. C.

References

- Balcer, M. D. et al. 1984. Zooplankton of the Great Lakes. – Univ. of Wisconsin Press.
- Bilton, D. T. et al. 2001. Size, permanence and the proportion of predators in ponds. – *Arch. Hydrobiol.* 151: 451–458.
- Blaustein, L and Chase, J. M. 2007. Interactions between mosquito larvae and species that share the same trophic level. – *Annu. Rev. Entomol.* 52: 489–507.
- Briand, F. and Cohen, J. E. 1984. Community food webs have a scale-invariant structure. – *Nature* 307: 264–266.
- Brose, U. et al. 2004. Unified spatial scaling of species and their trophic interactions. – *Nature* 428: 167–171.
- Brown, J. H. and Kodric-Brown, A. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. – *Ecology* 58: 445–449.
- Cadotte, M. W. 2006. Dispersal and species diversity: a meta-analysis. – *Am. Nat.* 167: 913–924.
- Chase, J. M. and Ryberg, W. A. 2004. Connectance, scale-dependence, and the productivity–diversity relationship. – *Ecol. Lett.* 7: 676–683.
- Cohen, J. E. 1977. Ratio of prey to predators in community food webs. – *Nature* 270: 165–167.
- Cohen, G. M. and Shurin, J. B. 2003. Scale-dependence and mechanisms of dispersal in freshwater zooplankton. – *Oikos* 103: 603–617.
- Cole, B. J. 1980. Trophic structure of a grassland insect community. – *Nature* 288: 76–77.
- Donald, D. B. and Anderson, R. S. 2003. Resistance of the prey-to-predator ratio to environmental gradients and to biomanipulations. – *Ecology* 84: 2387–2394.
- Forbes, A. E. and Chase, J. M. 2002. The role of habitat connectivity and landscape geometry in experimental zooplankton metacommunities. – *Oikos* 96: 433–440.
- Gilbert, F. et al. 1998. Corridors maintain species richness in the fragmented landscapes of a microecosystem. – *Proc. R. Soc. Lond. B* 265: 577–582.
- Gonzalez, A. et al. 1998. Metapopulation dynamics, abundance, and distribution in a microecosystem. – *Science* 281: 2045–2047.
- Gotelli, N. J. and Entsminger, G. L. 2004. EcoSim: null models software for ecology, ver. 7. – Acquired Intelligence & Kesey-Bear. <<http://garyentsminger.com/ecosim/index.htm>>.
- Holt, R. D. and Hoopes, M. F. 2005. Food web dynamics in a metacommunity context: modules and beyond. – In: Holyoak, M. et al. (eds), *Metacommunities: spatial dynamics and ecological communities*. Univ. of Chicago Press, pp. 68–93.
- Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. – *Ecology* 52: 577–585.
- Jeffries, M. J. 2002. Evidence for individualistic species assembly creating convergent predator:prey ratios among pond invertebrate communities. – *J. Anim. Ecol.* 71: 173–184.
- Jeffries, M. J. and Lawton, J. H. 1985. Predator-prey ratios in communities of freshwater invertebrates: the role of enemy free space. – *Freshwater Biol.* 15: 105–112.
- Jenkins, D. G. et al. 2003. Consequences of prairie wetland drainage for crustacean biodiversity and metapopulations. – *Conserv. Biol.* 17: 158–167.
- Lehtinen, R. M. et al. 1999. Consequences of habitat loss and fragmentation for wetland amphibian assemblages. – *Wetlands* 19: 1–12.
- Maguire, B. 1963. The passive dispersal of small aquatic organisms and their colonization of isolated bodies of water. – *Ecol. Monogr.* 33: 161–185.

- McCauley, S. J. 2006. The effects of dispersal and recruitment limitation on community structure of odonates in artificial ponds. – *Ecography* 29: 585–595.
- Merritt, R. and Cummins, K. W. (eds) 1996. An introduction to the aquatic insects of North America (3rd ed.). – Kendall-Hunt Publishing.
- Mikkelsen, G. M. 1993. How do food webs fall apart? A study of changes in trophic structure during relaxation on habitat fragments. – *Oikos* 67: 539–547.
- Mokany, A. and Shine, R. 2003b. Competition between tadpoles and mosquito larvae. – *Oecologia* 135: 615–620.
- Pimm, S. L. et al. 1991. Food web patterns and their consequences. – *Nature* 350: 669–674.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. – *Am. Nat.* 132: 652–661.
- Resetarits, W. J. Jr. et al. 2005. Habitat selection, species interactions, and processes of community assembly in complex landscapes: a metacommunity perspective. – In: Holyoak, M. et al. (eds), *Metacommunities: spatial dynamics and ecological communities*. Univ. of Chicago Press, pp. 374–398.
- Sexton, O. J. and Phillips, C. 1986. A qualitative study of fish–amphibian interactions in three Missouri ponds. – *Trans. Missouri Acad. Sci.* 20: 25–35.
- Schoener, T. W. 1989. Food webs from the small to the large. – *Ecology* 70: 1559–1589.
- Shmida, A. and Wilson, M. V. 1985. Biological determinants of species diversity. – *J. Biogeogr.* 12: 1–20.
- Shurin, J. B. 2001. Interactive effects of predation and dispersal on zooplankton communities. – *Ecology* 82: 3404–3416.
- Shurin, J. B. and Allen, E. G. 2001. Effects of competition, predation, and dispersal on species richness at local and regional scales. – *Am. Nat.* 158: 624–637.
- Spencer, M. et al. 1999. Species richness and the proportion of predatory animal species in temporary freshwater pools: relationships with habitat size and permanence. – *Ecol. Lett.* 2: 157–166.
- Spielman, A. and D’Antonio, M. 2001. *Mosquito: a natural history of our most persistent and deadly foe*. – Hyperion Books.
- Stav, G. et al. 1999. Experimental evidence for predation risk sensitive oviposition by a mosquito, *Culiseta longiareolata*. – *Ecol. Entomol.* 24: 202–207.
- Terborgh, J. et al. 2001. Ecological meltdown in predator-free forest fragments. – *Science* 294: 1923–1926.
- Thompson, R. M. and Townsend, C. R. 2000. Is resolution the solution? The effect of taxonomic resolution on the calculated properties of three stream food webs. – *Freshwater Biol.* 44: 413–422.
- Urban, M. C. 2004. Disturbance heterogeneity determines freshwater metacommunity structure. – *Ecology* 85: 2971–2978.
- Warren, P. H. 1995. Estimating morphologically determined connectance and structure for food webs of freshwater invertebrates. – *Freshwater Biol.* 33: 213–221.
- Warren, P. H. and Gaston, K. J. 1992. Predator–prey ratios: a special case of a general pattern. – *Proc. R. Soc. Lond. B* 338: 113–130.
- Watts, C. H. and Didham, R. K. 2006. Influences of habitat isolation on invertebrate colonization of *Sporodanthus ferrugineus* in a mined peat bog. – *Restor. Ecol.* 14: 412–419.
- Weiher, E. and Keddy, P. 1999. *Ecological assembly rules: perspectives, advances, retreats*. – Cambridge Univ. Press.
- Whiteman, N. K. and Sites, R. W. 2003. Lentic beetles of the Missouri Prairie Region: habitat and regional associations, with keys to the hydradephaga. – *Trans. Am. Entomol. Soc.* 129: 185–243.
- Wilbur, H. M. 1980. Complex life cycles. – *Annu. Rev. Ecol. Syst.* 11: 67–93.
- Wilcox, C. 2001. Habitat size and isolation affect colonization of seasonal wetlands by predatory aquatic insects. – *Isr. J. Entomol.* 47: 459–475.
- Wilson, J. B. 1996. The myth of constant predator: prey ratios. – *Oecologia* 106: 272–276.