

METACOMMUNITY STRUCTURE: SYNERGY OF BIOTIC INTERACTIONS AS SELECTIVE AGENTS AND DISPERSAL AS FUEL

KARL COTTENIE^{1,3} AND LUC DE MEESTER²

¹National Center for Ecological Analysis and Synthesis, 735 State Street, Suite 300, Santa Barbara, California 93101 USA

²Laboratory of Aquatic Ecology, Katholieke Universiteit Leuven, Ch. De Bériotstraat 32, B-3000 Leuven, Belgium

Abstract. The relative importance of regional and local processes in determining community structure is a long-standing problem in community ecology. This is especially problematic in communities from highly connected habitats, which undergo two opposing forces: differences in environmental conditions of the habitats lead to divergence of the communities, while the dispersal of individuals leads to convergence of the communities. Using a transplant experiment, we experimentally showed that biotic interactions have a predictable, deterministic impact on zooplankton community structure in a metacommunity of highly interconnected shallow ponds. Fish predation and presence of abundant macrophyte cover rapidly structured regional communities of zooplankton, both in terms of relative abundances and of cladoceran species richness. Moreover, we could use the relations between the experimentally manipulated environmental conditions and the observed experimental communities to successfully classify the contrasting local communities found in the original neighboring ponds, thus directly relating the experimental results to the actual field situation. Notwithstanding the observed strong impact of local biotic conditions, we also showed that dispersal had an influence on community structure and species richness. Dispersal increased species richness of cladocerans by three species and influenced zooplankton community structure. Moreover, dispersal actually made the response to local conditions more deterministic.

Key words: *alternative equilibria; community structure; dispersal; enclosure; fish predation; local vs. regional processes; macrophyte cover; metacommunity; shallow lakes; species richness; transplant experiment; zooplankton.*

INTRODUCTION

A central theme in community ecology is the relative importance of local vs. regional processes in determining local community structure (Ricklefs 1987). Local processes such as competition, predation, resource constraints, disturbance, and chance events are known to influence local community structure and diversity. Regional processes such as differences in habitat age, differences in rates of speciation and immigration, and differences in the history of extinction (Schluter and Ricklefs 1993) are more difficult to incorporate in ecological studies since they act on a much larger scale, both spatially and temporally. To unravel this question, generally an indirect observational method is used, in which mean local richness is plotted as a function of the regional richness for several regions (Ricklefs 1987, Cornell and Lawton 1992, Caley and Schluter 1997, Shurin et al. 2000). If local processes are important in determining species richness, this function will reach an upper limit (saturation curve). If regional processes are important, then local richness will be a linear function of regional richness, suggesting dispersal limitation. This has resulted in equivocal support for either process (Holt 1993). Moreover, the interpre-

tation of such saturation curves is fraught with difficulties (Huston 1999, Srivastava 1999, Shurin et al. 2000). In contrast to the theory of saturation curves, metacommunity models, which define metacommunities as groups of distinct local communities coupled by dispersal of their constituent members (Holt 1991), stress the positive aspect of dispersal. Connected communities are more similar to each other, due to the subsidizing of individuals from species that would normally go extinct because of local factors (rescue effect in source-sink dynamics; Brown and Kodric-Brown 1977).

We used an experimental approach to study this interaction of local and regional processes in structuring local community structure. We conducted a transplant experiment approach similar to a set-up commonly used by evolutionary biologists to quantify genetic adaptation to local conditions (e.g., Carvalho 1987, De Meester 1996, Declerck et al. 2001). Our model system is a set of highly interconnected ponds (Michels et al. 2001a, b), with strongly contrasting zooplankton communities associated with environmental variables such as water transparency (Cottenie et al. 2001). Cottenie and colleagues (Cottenie and De Meester 2003, Cottenie et al. 2003) have shown with observational data that both dispersal and local environmental variables influence zooplankton community structure and diversity. To also assess experimentally the strength of local

Manuscript received 3 January 2003; revised 7 July 2003; accepted 11 July 2003. Corresponding Editor: J. E. Havel.

³ E-mail: cottenie@nceas.ucsb.edu

interactions in the face of high dispersal rates, we performed an enclosure experiment in the downstream pond of two interconnected ponds with widely different community structures. Despite the continuous addition of individuals from the upstream pond, the downstream pond shows a different community structure (Cottenie et al. 2003). It is thus crucial in the understanding of this system to determine the factors that override the effect of dispersal. While keeping the initial abiotic conditions of the water constant over all enclosures placed in the downstream pond, we manipulated fish predation pressure and macrophyte cover in a factorial experiment. We chose these treatments because the relation between water transparency and zooplankton community structure is a dynamic process (Scheffer 1998) mostly mediated by planktivorous fish predation and macrophyte shelter. Because the downstream pond continuously receives species from the upstream pond, we inoculated the enclosures with a mixture of species from the two different ponds, which contrasts to other fish/no-fish limnology experiments (e.g., Brett and Goldman 1997). We also used a condition in which an enclosure was inoculated with only the community from the resident, downstream pond, without species from the upstream pond. The environmental treatment for this condition consisted of no fish predation and no macrophytes. By comparing the results with enclosures exposed to similar environmental treatments but receiving species from both the upstream and the downstream pond, it is possible to check for the effect of dispersal on species composition under the established conditions.

METHODS

The pond system in the nature reserve “De Maten” (Genk, Belgium) consists of 34 highly interconnected ponds that are ecologically very different (Cottenie et al. 2001). A mean of 3600 zooplankton individuals/h disperse through overflows and rivulets between any two connected ponds in this system, which corresponds to a population turnover time of 13 d (Michels et al. 2001b). In the summer of 2000, we selected two ponds that were directly interconnected with a 120 m long rivulet, but with ecologically contrasting characteristics. Pond 13 (2.9 ha area, 1 m mean depth), the upstream pond of the two, is a clear-water pond with an abundant vegetation of submerged macrophytes (70–80% of lake area) and intermediate total fish predation pressure (total catch of planktivorous and benthivorous fish species per fyke per night is 0.35 kg). Pond 12 (3.0 ha, 1 m mean depth), the downstream pond, is typically turbid, characterized by high fish predation pressure on zooplankton (total catch per fyke per night is 3.50 kg), and contains no submerged macrophytes (Cottenie et al. 2001; S. Declerck, unpublished data).

Fifteen enclosures were fixed to wooden poles inserted in the sediment and positioned in a sheltered area of the downstream Pond 12 on 18–19 July 2000.

Each enclosure was 1.0 m diameter \times 1.0 m high, woven laminated polyethylene with a closed bottom, without water transfer between enclosure and lake. The upper parts of the enclosures were 30 cm above the water surface to eliminate contamination of the enclosures with lake water (and consequently new individuals) and with fish. As a result, the depth in the enclosures was 70 cm. The enclosures were filled with lake water from Pond 12 (600 L each) filtered through a net with a mesh size of 64 μ m, thus effectively removing individuals of the cladoceran, copepod, and larger rotifer species. Half of the collected zooplankton community from Pond 12 (i.e., corresponding to 4500 L filtered lake water) was concentrated in a bucket, mixed gently, and distributed in equal proportions to the 15 enclosures on 19 July. On 20 July, we filtered 4500 L of pond water from Pond 13 and retained only the filtered zooplankton community. The filtered zooplankton community was similarly concentrated in a bucket, mixed gently, and distributed in equal proportions to 12 of the 15 enclosures; the remaining three enclosures received only an inoculum of species from the resident community (RC), Pond 12.

We employed a total of five different treatments, with three replicate enclosures each. Four treatments were a full factorial combination of the presence or absence of both fish and macrophytes. These were randomly allocated to the 12 enclosures inoculated with a mixed community of zooplankton from Pond 12 and Pond 13 on 20 July. In six enclosures, two individuals of *Lepomis gibbosus* (mean total length 7.3 cm) were added, and, in each of six enclosures, five strands of *Polygomonum amphibium* were added. *Lepomis gibbosus* is very common in the pond system studied, whereas *Polygomonum amphibium* is abundant in Pond 13 (Cottenie et al. 2001). Four treatments were thus inoculated with mixed communities and different environments: fish/macrophytes (FM), fish/no macrophytes (FN), no fish/macrophytes (NM), and no fish/no macrophytes (NN). The fifth treatment was inoculated with the community from Pond 12 only and did not receive macrophytes or fish: the resident community (RC). This treatment is thus similar to the no fish/no macrophytes treatment, except that the latter received an additional inoculum from the Pond 13 community.

All enclosures and Pond 12 and 13 were sampled four times after setting up the treatments (20, 24, 31 July, and 14 August). The total water column was sampled at 4–5 different places per enclosure with a tube sampler (6.5 cm diameter \times 1.0 m high). From each combined sample, 15 L were filtered through a net with 64- μ m mesh size, concentrated in 60 mL bottles, and fixed with sugar formaldehyde (final concentration of 7%). The sampling devices were thoroughly rinsed between sampling the different enclosures. From each sample, two subsamples (totaling 6 mL) were taken with a wide-bore pipet, and all individuals were identified and counted for each subsample. The following

identification levels and keys were used: cladocerans to the species level with Flößner (1972), Flößner and Kraus (1986), and Smirnov (1996), copepods to the order level plus life stage (nauplii), rotifers to species or genus level with Koste (1978), and macroinvertebrates (mainly water mites and juvenile insects belonging to Ephemeroptera, Heteroptera, and Coleoptera) as a single group.

Data were expressed in number of individuals per taxon per liter and square-root transformed to reduce the effect of high densities of a few taxa. Redundancy analysis (RDA, CANOCO 4.0 for Windows, with scaling 2 that focuses on interspecies correlations; ter Braak and Smilauer 1998) was used to analyze the data. RDA has been recently used in other community studies (Legendre and Anderson 1999, Shurin 2001) and has the advantage of treating the community as a multivariate entity. The focal data set consisted of the square-root transformed taxa densities of the 15 enclosures, whereas the explanatory variables were coded as five binary variables indicating the five different treatments. The variance in zooplankton community structure explained by the experimental manipulation was obtained, together with the associated F ratio. The significance of this value was computed with a permutation test under the reduced model, with 999 new permutations. The RDA results were visualized with a two-dimensional biplot giving the position of the different enclosures based on their zooplankton community structure, which best corresponded to the different treatments. We also computed the significance of these first two axes independently, similar to the procedure outlined above. The obtained relation between zooplankton taxa and enclosure treatments was also used to add the samples from Pond 12 and 13 as supplementary points (ter Braak and Smilauer 1998). This allowed us to investigate where the original communities lie in the results obtained in our experiment and thus better explore the relevancy of our experimental results.

To determine the effect of the experimental manipulations on species richness, we only considered cladoceran species richness, since this was the only taxonomic group for which individuals were always determined to species level. Cladoceran species richness was determined as the number of cladoceran species in the 6-mL subsample counted. A two-way ANOVA with fish predation and macrophyte presence was followed by the conservative Scheffé post-hoc test (Sokal and Rohlf 1995) to determine which treatments differed from one another. A two-sample t test (Sokal and Rohlf 1995) was performed to assess whether the resident community treatment (RC) differed significantly from the no fish/no macrophyte (NN) treatment, to test the effect of dispersal. For both tests, the parametric assumptions of normality and homogeneity of variances were checked and were met.

RESULTS

The results show that, already on the second sampling day after adding the Pond 13 communities to the enclosures (24 July), significantly different communities developed in the enclosures, but with lower density values than in the pond communities (results not shown). After 25 d (14 August) the densities in the field, and the pattern of differences remained stable (Fig. 1). The total variance in zooplankton community structure explained by treatments is 63.3% (F ratio = 4.316, P = 0.001), with the first two axes already explaining 51.2% of the variance in zooplankton community structure or 80.8% of the total explained variance. The first axis (26.4% of the variance in zooplankton community structure, F ratio = 3.583, P = 0.001) discriminated between the enclosures with and without fish. Enclosures with fish had small species (e.g., *Chydorus sphaericus*, *Alonella nana*, *Bosmina longirostris*, rotifer taxa) while enclosures without fish had large species (e.g., *Eurycerus lamellatus*, *Simocephalus vetulus*, *Daphnia galeata*). The second axis (24.8% of the variance in zooplankton community structure, F ratio = 5.074, P = 0.001) discriminated between enclosures with and without macrophytes. This corresponded to enclosures with macrophyte-associated species (e.g., *Sida cristalina*, *Chydorus sphaericus*, *Alonella nana*, *Eurycerus lamellatus*, *Simocephalus vetulus*) and enclosures with pelagic species (e.g., *Bosmina longirostris*, *Daphnia galeata*, *Daphnia ambigua*, cyclopoid copepods). The community that developed in the enclosures with fish and without macrophytes is similar to the resident community of the pond in which the experiment was done (see the a posteriori addition of the samples taken from P12 in Fig. 1) and reflects the ecological conditions in this pond (turbid water, high fish predation pressure, and no macrophytes; Cottenie et al. 2001). The community of the upstream pond (from which the immigrating community was derived, P13) takes an intermediate position between the communities in the enclosures with fish and macrophytes and the communities with macrophytes but without fish. This pond is indeed in the clear-water state and is characterized by abundant submerged vegetation and intermediate levels of fish predation (Cottenie et al. 2001).

The experimental manipulation also had a significant effect on cladoceran species richness (see Fig. 2, significance of the full two-way ANOVA: $F_{3,8} = 10.79$, $P = 0.003$). The FN treatment exhibited significantly lower species richness than the other three treatments (see Fig. 2, post-hoc comparisons). The richness in the mixed treatment without fish and macrophytes (NN) was significantly higher than in the RC enclosures. These two treatments are both without fish and macrophytes, but the RC treatment initially only received species from Pond 12 ($t = -6.36$, $df = 4$, $P = 0.003$).

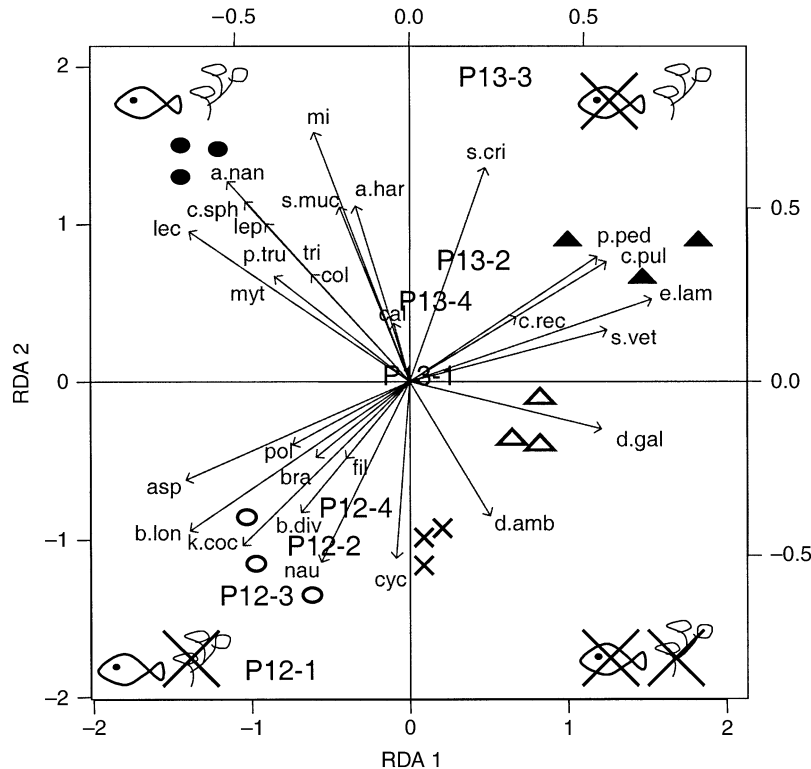


FIG. 1. Results of the redundancy analysis (RDA) testing for the significance of effects of the presence of fish and macrophytes on zooplankton community structure in situ enclosures (see *Methods* for details). The different enclosures are represented by symbols indicating the treatment they received: solid ovals = fish/macrophytes; filled triangles = no fish/macrophytes; open triangles = no fish/no macrophytes; open ovals = fish/no macrophytes; ×'s refer to enclosures with resident community only. The samples from the two original ponds are added as supplementary variables: P13-*x* = Pond 13, P12-*x* = Pond 12, with *x* corresponding to four sampling dates. The scaling on the lower and left axes refers to the position of the enclosures; the scaling on the upper and right axes refers to position of the species. The relative species composition in the enclosures can be determined from the relation between the position of the enclosures and the species arrows: orthogonal projection of an enclosure on a species arrow determines the relative abundance of this species in the enclosure, if the particular species arrow is long. Thus the fish/macrophytes enclosures are characterized by small, macrophyte-associated species such as lec = *Lecane*, c.sph = *Chydorus sphaericus*, a.nan = *Alonella nana*, lep = *Lepadella*, s.muc = *Scapholeberis mucronata*, mi = macroinvertebrates, and a.har = *Acroperus harpae*; the no fish/macrophytes enclosures are characterized by mostly larger, macrophyte-associated species such as s.cri = *Sida cristallina*, p.ped = *Polyphemus pediculus*, c.pul = *Ceriodaphnia pulchella*, e.lam = *Eurycerus lamellatus*, and s.vet = *Simocephalus vetulus*; the no fish/no macrophyte enclosures are characterized by large pelagic species such as d.gal = *Daphnia galeata* and d.amb = *Daphnia ambigua*; the fish/no macrophytes enclosures are characterized by small pelagic species or life stages such as nau = nauplii, k.coc = *Keratella cochlearis*, b.lon = *Bosmina longirostris*, asp = *Asplanchna*, cyc = cyclopoid copepods, and b.div = *Brachionus diversicornis*. The species with small arrow lengths are myt = *Mytilina*, p.tru = *Pleuroxus truncatus*, tri = *Trigonellus*, col = *Colurella*, cal = calanoid copepods, c.rec = *Camptocercus rectirostris*, fil = *Filinia*, bra = *Brachionus angularis*, and pol = *Polyarthra*.

DISCUSSION

Our results show that, starting from a mixed community, the full spectrum of community composition found in the upstream and downstream pond could be quickly reached by merely manipulating the presence of fish predation pressure and macrophyte cover. This direct link between manipulated and actual communities aids in determining the applicability, and thus strength, of the experiment for the real situation. For instance, our results suggest that the species in Pond 13 undergo an intermediate fish predation, as the actual Pond 13 results lie between the no fish/macrophyte and fish/macrophyte enclosures (Fig. 1). This corresponds

to the actual fish densities: there is fish predation present but moderate compared to that in Pond 12. These results also indicate that the effects of potential biases (enclosure effects) were small during this short-term experiment or consistent across the different enclosures sampled. Also, sampling bias caused by undersampling the small rotifers and fast-swimming copepods were consistent across the different enclosures. Our results suggest that the development of a community adapted to no fish/no macrophyte conditions in the enclosures was more constrained in the RC treatment than in the mixed inoculum treatment. The communities found in the RC enclosures remained more similar to the com-

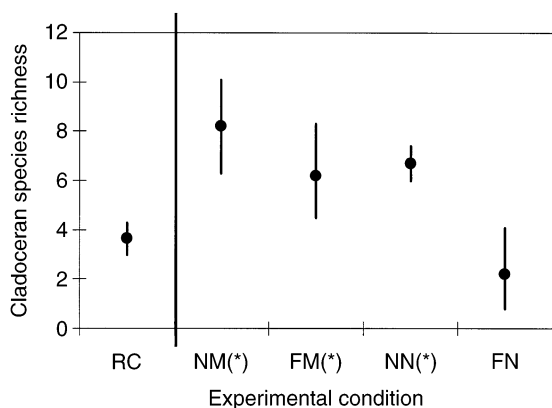


FIG. 2. Cladoceran species richness in the different experimental conditions (means \pm 2 SE): RC = resident community (species of only Pond 12 without fish and macrophytes), NM = no fish/macrophytes, FM = fish/macrophytes, NN = no fish/no macrophytes, FN = fish/no macrophytes. Asterisks indicate that these experimental conditions were significantly different from RC ($P < 0.05$) with the Scheffé method of multiple comparisons.

munities in the presence of fish (FN, the situation in the resident pond) than to the communities that developed from the mixed inoculum in the absence of fish and macrophytes (NN). This can be seen even more clearly in the difference in cladoceran diversity in the resident community and the no fish/no macrophyte treatment. Three cladoceran species were not present in the RC enclosures, but were present in the NN enclosures. These species were present in the samples of Pond 13 (*Simocephalus vetulus*, *Eurycercus lamellatus*, and *Sida cristallina*), while being absent in the samples of Pond 12, indicating that these species were derived from the inoculum from Pond 13. If the local environment conditions would change in Pond 12, dispersal in space (from neighboring ponds) or time (hatching from the dormant propagule bank) would be necessary to deliver the species best adapted to these new environmental conditions. The perfect match of the natural communities in Pond 12 and 13 and the communities that developed in the enclosures initiated with a mixed inoculum (mimicking dispersal) and exposed to conditions corresponding to those in the ponds is strongly suggestive of dispersal indeed also being effective in this highly connected system, reflecting that the different communities form a metacommunity.

Our results unequivocally point to local environmental factors determining local community structure, both as relative abundances and as species richness, in the zooplankton metacommunity studied, with the high dispersal rates enhancing the response to local selective factors. This interpretation is consistent with studies by Shurin (2000, 2001) that show that regional dispersal rates may strongly influence the capacity of local communities to adjust to changing local environmental conditions. The observation that fish predation pressure

and macrophyte cover have such a strong impact on zooplankton community structure is also consistent with a whole body of literature emphasizing the impact of predation on aquatic ecosystems (Carpenter and Kitchell 1993) and the theory of alternative equilibrium states with turbid and clear-water states in shallow lakes (Scheffer 1998). Our results show that local selective factors may have a very rapid and deterministic impact on local community structure of zooplankton in systems in which dispersal is not limiting (Ricklefs 1987, Jenkins and Buikema 1998). However, our results also illustrate the importance of the role of dispersal in influencing community structure and diversity. This outcome is in line with the increasing interest in the role of spatial scale of ecological processes. It has been shown theoretically (Durrett and Levin 1994, Hassel et al. 1994, Tilman and Kareiva 1997, Loreau and Mouquet 1999) and experimentally (Amezcuca and Holyoak 2000, Kerr et al. 2002) that local dispersal can promote diversity within a community. Although there are obvious differences, the parallel with evolutionary responses and local adaptation in natural populations is also striking. In natural populations, local factors drive evolutionary divergent selection. In this process, dispersal on the one hand tends to homogenize populations, but on the other hand also increases genetic variation within populations and therefore the ability to adapt. Similarly, in the metacommunity system of "De Maten," dispersal is a necessary condition to deliver the potential building blocks (the fuel supplied by the regional species pool) of a local community. Biotic interactions then select the species best adapted to the different local environmental conditions (actual species pool). Although strong dispersal may homogenize communities, our results on the highly connected metacommunity of "De Maten" indicate that local species sorting seems to be powerful in the face of very substantial dispersal rates.

ACKNOWLEDGMENTS

We thank Natuurpunt v.z.w. and especially the warden Willy Peumans for allowing access to the nature reserve "De Maten" and their cooperation. We thank Lies Neys, Erik Michels, and Frank van de Meutter for practical help during the experiment, and Jonathan Shurin, Luc Brendonck, Steven Declerck, Erik Jeppesen, David Jenkins, John Havel, and two anonymous reviewers for valuable remarks on earlier versions of the manuscript. K. Cottenie was research assistant of the Fund for Scientific Research—Flanders (Belgium) (F.W.O) and a Postdoctoral Associate at the National Center for Ecological Analysis and Synthesis, a center funded by NSF (Grant #DEB-0072909), the University of California, and the Santa Barbara campus. This project was financially supported by the National Fund of Scientific Research—Flanders, grant G.0358.01, and by EU project BIOMAN, EVK2-CT-1999-00046.

LITERATURE CITED

Amezcuca, A. B., and M. Holyoak. 2000. Empirical evidence for predator-prey source-sink dynamics. *Ecology* **81**: 3087–3098.

- Brett, M. T., and C. R. Goldman. 1997. Consumer versus resource control in freshwater pelagic food webs. *Science* **275**:384–386.
- Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* **58**:445–449.
- Caley, M. J., and D. Schluter. 1997. The relationship between local and regional diversity. *Ecology* **78**:70–80.
- Carpenter, S. R., and J. F. Kitchell. 1993. The trophic cascade in lakes. Cambridge University Press, Cambridge, UK.
- Carvalho, G. R. 1987. The clonal ecology of *Daphnia magna* (Crustacea: Cladocera). II. Thermal differentiation among seasonal clones. *Journal of Animal Ecology* **56**:469–478.
- Cornell, H. V., and J. H. Lawton. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology* **61**:1–12.
- Cottenie, K., and L. De Meester. 2003. Connectivity and cladoceran species richness in a small interconnected pond system. *Oikos* **48**:823–832.
- Cottenie, K., E. Michels, N. Nuytten, and L. De Meester. 2003. Zooplankton metacommunity structure: regional vs. local processes in highly interconnected ponds. *Ecology* **84**:991–1000.
- Cottenie, K., N. Nuytten, E. Michels, and L. De Meester. 2001. Zooplankton community structure and environmental conditions in a set of interconnected ponds. *Hydrobiologia* **442**:339–350.
- Declerck, S., C. Cousyn, and L. De Meester. 2001. Evidence for local adaptation in neighbouring *Daphnia* populations: a laboratory transplant experiment. *Freshwater Biology* **46**:187–198.
- De Meester, L. 1996. Local genetic differentiation and adaptation in freshwater zooplankton populations: patterns and processes. *Ecoscience* **3**:385–399.
- Durrett, R., and S. Levin. 1994. The importance of being discrete (and spatial). *Journal of Theoretical Biology* **46**:363–394.
- Flößner, D. 1972. Krebstiere, Crustacea; Kiemen- und Blattfüßer, Branchiopoda; Fischläuse, Branchiura. *In Die Tierwelt Deutschlands* 60. Teil G. Fisher Verlag, Jena, Germany.
- Flößner, D., and K. Kraus. 1986. On the taxonomy of the *Daphnia hyalina-galeata* complex (Crustacea: Cladocera). *Hydrobiologia* **137**:97–115.
- Hassel, M. P., H. N. Comins, and R. M. May. 1994. Species coexistence and self-organizing spatial dynamics. *Nature* **370**:290–292.
- Holt, R. D. 1991. From metapopulation dynamics to community structure: some consequences of spatial heterogeneity. Pages 149–165 *in* M. E. Gilpin and I. Hanski, editors. *Metapopulation dynamics: empirical and theoretical investigations*. Academic Press, London, UK.
- Holt, R. D. 1993. Ecology at the mesoscale: the influence of regional processes on local communities. Pages 77–88 *in* R. E. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, Illinois, USA.
- Huston, M. A. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos* **86**:393–401.
- Jenkins, D. G., and A. L. Buikema, Jr. 1998. Do similar communities develop in similar sites? A test with zooplankton structure and function. *Ecological Monographs* **68**:421–443.
- Kerr, B., M. A. Riley, M. W. Feldman, and B. J. M. Bohannan. 2002. Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. *Nature* **418**:171–174.
- Koste, W. 1978. Rotatoria die rädertiere mitteleuropas. Monogononta. Gebrüder Brontraeger, Berlin, Germany.
- Legendre, P., and M. J. Anderson. 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs* **69**:1–24.
- Loreau, M., and N. Mouquet. 1999. Immigration and the maintenance of local species diversity. *American Naturalist* **154**:427–440.
- Michels, E., K. Cottenie, L. Neys, K. De Gelas, P. Coppin, and L. De Meester. 2001a. Geographical and genetic distances among zooplankton populations in a set of interconnected ponds: a plea for using GIS modelling of the effective geographical distance. *Molecular Ecology* **10**:1929–1938.
- Michels, E., K. Cottenie, L. Neys, and L. De Meester. 2001b. Zooplankton on the move: first results on the quantification of dispersal in a set of interconnected ponds. *Hydrobiologia* **442**:117–126.
- Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. *Science* **235**:167–171.
- Scheffer, M. 1998. *Ecology of shallow lakes*. Chapman and Hall, London, UK.
- Schluter, D., and R. E. Ricklefs. 1993. Convergence and the regional component of species diversity. Pages 230–240 *in* R. E. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities*. University of Chicago Press, Chicago, Illinois, USA.
- Shurin, J. B. 2000. Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. *Ecology* **81**:3074–3086.
- Shurin, J. B. 2001. Interactive effects of predation and dispersal on zooplankton communities. *Ecology* **82**:3404–3416.
- Shurin, J. B., J. E. Havel, M. A. Leibold, and B. Pinel-Alloul. 2000. Local and regional zooplankton species richness: a scale-independent test for saturation. *Ecology* **81**:3062–3073.
- Smirnov, N. N. 1996. Cladocera: the Chydorinae and Syciinae (Chydoridae) of the world. Guides to the identification of the microinvertebrates of the continental waters of the world. SBP Academic Publishing, Amsterdam, The Netherlands.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry: the principles and practice of statistics in biological research*. W. H. Freeman, New York, New York, USA.
- Srivastava, D. S. 1999. Using local-regional richness plots to test for species saturation: pitfalls and potentials. *Journal of Animal Ecology* **68**:1–16.
- ter Braak, C. J. F., and P. Smilauer. 1998. *Canoco reference manual and user's guide to Canoco for Windows: software for canonical community ordination*. Version 4. Microcomputer Power, Ithaca, New York, USA.
- Tilman, D., and P. Kareiva. 1997. *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton, New Jersey, USA.