

Disturbance alters habitat isolation's effect on biodiversity in aquatic microcosms

Örjan Östman, Jamie M. Kneitel and Jonathan M. Chase

Östman, Ö., Kneitel, J. M. and Chase, J. M. 2006. Disturbance alters habitat isolation's effect on biodiversity in aquatic microcosms. – *Oikos* 114: 360–366.

Isolated habitats generally have fewer species at local spatial scales than more connected habitats. However, over larger spatial scales, the response of species richness to variation in the degree of isolation is variable. Here, we hypothesized that the effects of habitat isolation on patterns of regional level species richness may depend at least in part on the level of disturbances those habitats receive. We tested this hypothesis in a microcosm experiment using an aquatic community consisting of container dwelling protists and rotifers by manipulating disturbance and dispersal to experimental regions factorially. In disturbed regions, regional species richness was lower in regions with isolated patches compared to regions where patches were experimentally connected by dispersal. A likely mechanism for this result is that dispersal from adjacent undisturbed local patches allowed disturbance-intolerant species a temporary refugia, thereby allowing regional coexistence of disturbance-tolerant and intolerant species. In contrast, without disturbances (and thus no temporal heterogeneity) it is likely that dispersal homogenized communities, leading to overall lower richness with higher dispersal. Our results emphasize the importance of simultaneously considering multiple limiting factors, disturbance and dispersal in this case, as well as the spatial scale of the response, in order to fully understand factors that control biodiversity.

Ö. Östman, J. M. Kneitel and J. M. Chase, *Dept of Biology, Washington Univ. in St. Louis, Campus Box 1229, St. Louis, MO 63130, USA. Present address for ÖÖ: Dept of Ecology and Evolution, Uppsala Univ., Norbyvägen 18 D, SE-752 36 Uppsala, Sweden (orjan.ostman@ebc.uu.se). Present address for JML: Dept of Biological Sciences California State Univ. Sacramento. 6000 J Street Sacramento CA 95819-6077 USA.*

A multitude of environmental and historical factors simultaneously interact to create patterns of biodiversity (Ricklefs 1987, 2004, Gaston 2000). However, to date, the majority of experimental and theoretical studies consider one factor at a time (but see Wilson and Tilman 2002, Levine 2003, Kneitel and Chase 2004, Scholes et al. 2005), and often find that species diversity can show different patterns in response to the same environmental factors. For example, in a review of studies on the effect of disturbance on diversity, Mackey and Currie (2001) found little generality in the shape of the relationship. This has led to a general sentiment among

community ecologists that there are few general patterns of biodiversity, and that instead, contingency predominates (Lawton 1999, 2000, Simberloff 2004).

A broader perspective, considering the separate and interactive effects of multiple factors acting simultaneously, may lead to a deeper understanding of the perceived contingencies in community ecology. For example, in an experiment manipulating predators, resources, and disturbances on a protist community, Kneitel and Chase (2004) found that the effect of a single factor on diversity was dependent on the level of the other factors. Wilson and Tilman (2002) found similar

Accepted 16 January 2006
Subject Editor: Tim Benton

Copyright © OIKOS 2006
ISSN 0030-1299

interactive effects of disturbance and productivity on plant diversity in an old-field, as did Scholes et al. (2005) in experimental microcosms of protists.

Rates of dispersal among localities (subpopulations) can have different effects on species diversity depending both on the spatial scale under consideration and the interactive environmental variables. Habitat isolation, and the resultant lower rates of dispersal among localities, generally reduces species richness at local spatial scales (Turner et al. 1996, Harrison 1997, 1999, Gonzalez et al. 1998, Laurance et al. 2002, Chase 2003, Kneitel and Miller 2003, Ims et al. 2004), although some notable experiments found no such effects (Forbes and Chase 2002, Hoyle and Gilbert 2004). For cumulative species richness at larger spatial scales (regional species richness), however, the effect of habitat isolation on species richness is variable in both theoretical and experimental investigations. Sometimes isolation decreases regional diversity (Warren 1996a, 1996b, Gonzalez et al. 1998, Kneitel and Miller 2003), whereas other times isolation increases regional diversity (Harrison 1997, 1999, Amarasekare 2000, Forbes and Chase 2002, Chase 2003, Fukami 2004).

We hypothesize that the influence of habitat isolation on local and regional species richness may depend, at least in part, on the rates of disturbance in those habitats. By disturbance, we refer to a temporary process that substantially increases mortality rates of all or a subset of species. Without (or with minimal) disturbance, isolation can often have opposing effects on local and regional species richness, by decreasing local, but increasing regional species richness (Harrison 1997, 1999, Chase 2003). At local scales, species richness is expected to decrease with increasing isolation because of decreased probability of rescue effects (*sensu* Brown and Kodric-Brown 1977) and decreased immigration that can counteract negative population growth rates (i.e. source-sink dynamics, Mouquet and Loreau 2003). At the regional scale, habitat isolation can lead to higher total species richness. Decreased connectance can prevent competitively dominant species from colonizing all localities (Amarasekare 2000, Forbes and Chase 2002, Mouquet and Loreau 2003), and allow historical effects on species composition to persist (Chase 2003, Fukami 2004). In both cases, higher rates of dispersal homogenize community composition among localities and decrease regional species richness.

The effects of habitat isolation on species richness may differ when periodic disturbances occur in local communities, so long as those disturbances do not act on the entire region simultaneously. We hypothesize that at local scales, disturbances will have a stronger negative effect on species richness in isolated habitats because in connected habitats, disturbance-intolerant species will be able to recolonize from undisturbed habitats. At a regional scale, habitat isolation is also likely to decrease

species richness in regions with periodic disturbances, because disturbances reduce the species richness of each local habitat, in particular, eliminating disturbance-intolerant species, and recolonizations are infrequent. However, when habitats are connected through dispersal, disturbance intolerant species can persist in undisturbed spatial refuges, and we predict that both disturbance intolerant and tolerant species can coexist in regions that are connected, increasing regional species richness (Connell 1978, Sousa 1984, Wilson and Tilman 2002, Shea et al. 2004).

In sum, we hypothesize that when disturbances are infrequent or absent, local species richness should decrease and regional species richness should increase in habitats that are more isolated. Alternatively, when disturbances among local communities are more frequent, we hypothesize that isolation will decrease both local and regional species richness. Here, we present the results from a microcosm experiment manipulating disturbance by drying and manipulating dispersal by transfer among communities of a naturally co-occurring community of container (i.e. treehole) dwelling protozoan and rotifer species (Kneitel and Chase 2004). In all, we find support for our hypothesis that the effects of habitat isolation on patterns of local and regional species richness depends on the disturbances those habitats experience.

Material and methods

We collected naturally occurring container protozoan and rotifer species by placing twelve 500-ml plastic bowls with well-water and white oak (*Quercus alba*) leaves for one week in the forest at Washington University's Tyson Research Center (38°31'N, 90°33'W) outside of St. Louis, Missouri. Protozoan and rotifer communities that establish in these bowls are indistinguishable from those that occur in natural tree-hole communities (Kneitel and Chase 2004). We combined these bowls into a single large container to create a regional species pool, and inoculated each experimental patch with this diverse (~20 species (initial species richness was not monitored)) array of organisms.

Experimental local patches were established in 45 ml (85 mm diameter × 8 mm depth) petri dishes; three petri dishes were grouped to create a regional community. In each petri dish, we inoculated 40 ml of water from the container with the entire species pool together with 25 mg of ground dry oak leaves as a resource. Each region received one of four treatments in a 2 × 2 factorial design with dispersal and disturbance as main effects (Fig. 1). All treatments were replicated four times for a total of 16 regions and 48 local patches (petri dishes).

Dispersal was implemented in one of two treatments: (1) no dispersal, or (2) daily transfer of individuals among patches within regions (Fig. 1). Dispersal treat-

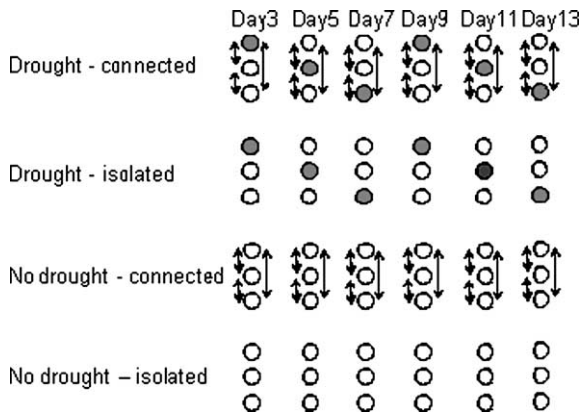


Fig. 1. Schematic figure of the experimental set-up. Shaded circles represent patches (petri dishes) where drought occurred, whereas open circles represent patches with no drought. A region consisted of three petri dishes with the same treatment, and there was dispersal between all three patches in a region where dispersal was imposed (arrows). Each treatment was replicated four times.

ments were imposed by gently stirring the water within each dish and transferring 2 ml of water with a sterilized pipette into a 15 ml test tube. Two ml of water from the test tube was then put back in each of the petri dishes in the region. Thus, on average 3.3% of the individuals in a petri dish were transferred to the other petri dishes every day of the experiment. This average is probably higher than what is found in natural systems, but was chosen to ensure that relatively rare species also could disperse. For common species, the exact dispersal rate was not very important because there was a high probability of dispersal for these species. In natural communities, protists can disperse in a variety of ways, including airborne spores, and we could not exclude such dispersal between our petri dishes in the laboratory. However, in subsequent experiments, we placed 5 dishes with water and sterilized media directly adjacent to 5 dishes with a diverse inocula of species, and after 20 days, found no colonization of the empty dishes, leading us to conclude that dispersal in our experiment was primarily through our manipulations.

Disturbances (droughts) were imposed by allowing petri dishes to naturally evaporate and dry at fixed intervals. Such drying is a common disturbance to these communities in nature (Bradshaw and Holzapfel 1988, Kneitel and Chase 2004). Disturbance was manipulated by either 1) adding approximately 15 ml of deionized water daily over the course of the experiment to counteract evaporation, or 2) allowing water to evaporate and dry at ~6 d intervals (some water was added to these treatments because natural evaporation rates were faster). Within each disturbed region, petri dishes dried asynchronously with two days between consecutive dryings within the region (Fig. 1). We did not have any treatment with synchronous disturbance, but such a

treatment is likely to have similar effect to our non-dispersal treatment because there would not be any refuges for disturbance intolerant species. After a petri dish dried, it remained dry for 24 h and then refilled with 40 ml of deionized water. To avoid increased emigration from petri dishes which were to dry, only 1 ml water was transferred from and to petri dishes the day prior to drying. In addition, dispersal was suspended during the time a dish was dry and not reinstated until one day after the water had been refilled. Both adding deionized water (temporary dilution of nutrients) and dispersal (physical disturbance and homogenization within petri dishes due to stirring) can also be regarded as relatively minor disturbances. However, these disturbances likely have a negligible effect on mortality, and thus we do not expect that these methodologies confound our results.

The first patch of each region dried on day 3 of the experiment, and the experiment ran for 17 days (Fig. 1). This time scale allowed for each Petri dish in a disturbed regional community to dry twice. Protozoa and rotifers have a generation time from less than 12 h to 5 days, allowing them to re-establishing between droughts (6 days, compare McGrady-Steed and Morin 1996), and to recover following the last drought (3–7 days). All communities were sampled on day 17 by first gently stirring the water and extracting 1 ml of water (using a sterilized pipette) into a Sedgewick rafter cell. Individuals were identified and enumerated under a phase-contrast microscope using standard methods (Kneitel and Miller 2003, Kneitel and Chase 2004). Because it is very difficult to identify some protozoans and rotifers to specific species, some individuals were identified to higher taxonomic units (e.g. genus, Fig. 2).

Local species richness was calculated as the number of taxonomic units that occurred in each petri dish, and the average local richness of each regional was calculated for analyses. Regional species richness was calculated as the total number of species observed in all of the three petri dishes in a regional. Community dissimilarity was calculated by comparing the difference in species composition as 1-Jaccard's index of similarity among patches within a regional. Because dissimilarity ranges from 0 (identical communities) to 1 (completely different communities), these data were arcsine square-root transformed prior to analysis to avoid distributions being bounded. Two-way analysis of variance (ANOVA) was used to analyze the effects of drought and dispersal. All data were first assured to fit the assumptions of parametric statistics (e.g. normality, equal variances). Total protist abundance differed substantially among treatments, from 60 to 1500 per sample, which can artificially inflate species richness measurements (Gotelli and Colwell 2001); therefore, we also tested with rarefied data. However, rarefaction also accounts for relative abundance, a more even species distribution gives a

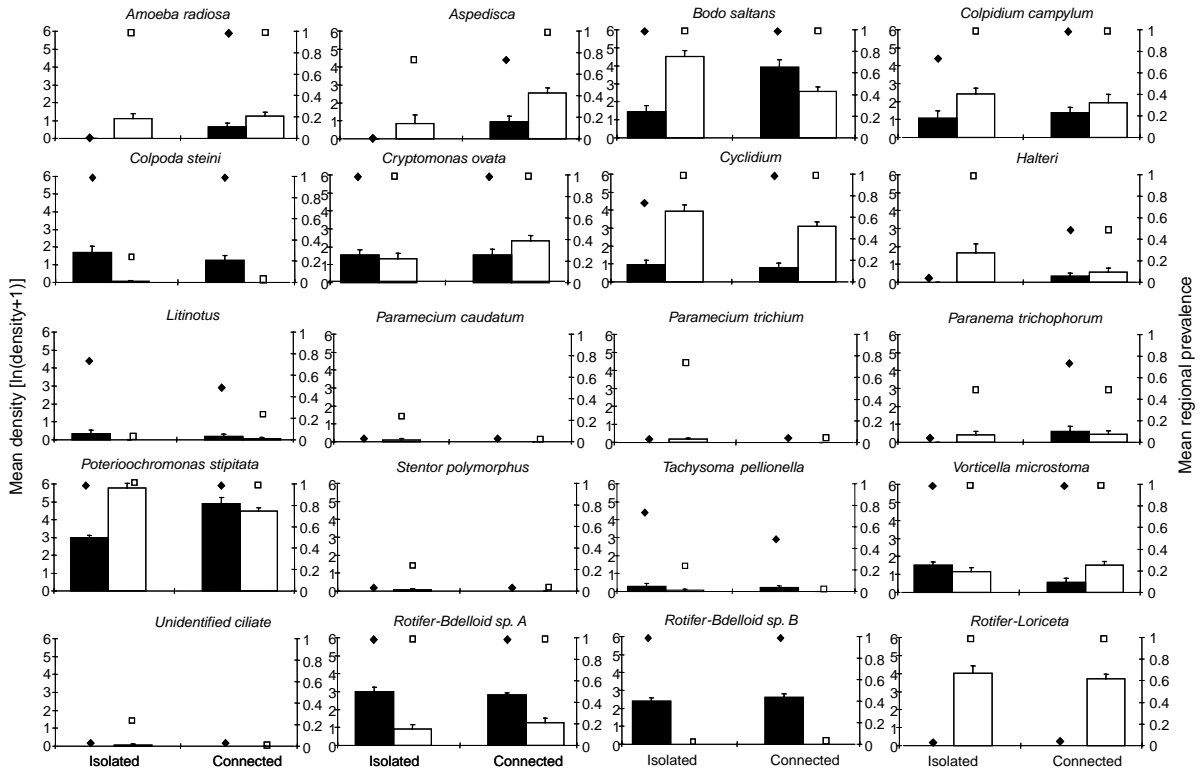


Fig. 2. Mean density [average of $\log_e(\text{number/ml} + 1)$] on the first y-axis and mean regional prevalence (0 not found in any replicate, 1 found in all replicates) on the second y-axis for the different protozoan and rotifer species found in the study. Bars represent densities, whereas squares and diamonds represent regional prevalence. Disturbed communities are represented by black bars and diamonds, whereas non-disturbed communities are represented by open bars and squares. Rotifers are identified as such, whereas all other species are protozoan species. Error bars are 1 standard error.

higher species richness after rarefaction than an uneven distribution. This is a drawback in our study where variation in total abundance was almost entirely due to a few species (Fig. 2). To partly overcome this problem we excluded the two most common species from the rarefaction analyses, *Poterioochromonas stipitata* and *Bodo saltans*, which are very small in size compared to the other species. Moreover, these two species were present in almost all petri dishes and therefore had very little effect on variation in species richness.

The number of protozoans and rotifers individuals counted per petri dish varied from 39 to 436, and per region from 155 to 875 (excluding *P. stipitata* and *B. saltans*). Therefore, we rarefied with 39 and 155 individuals respectively for analyses. Rarefied species richness was the average species richness from 1000 iteration per sample using the software EcoSim ver 7.0 (Gotelli and Entsminger 2001).

Results

Local species richness was lower in regions that were isolated ($F_{1,12} = 4.7$; $P = 0.05$; Fig. 3a) and disturbed

($F_{1,12} = 6.9$; $P = 0.02$; Fig. 3a), but there was no interaction between isolation and disturbance ($F_{1,12} = 0.5$; $P = 0.5$). However, the disturbance effect was largely driven by abundance differences. When rarefied, disturbance had no effect ($F_{1,12} = 0.15$; $P = 0.7$) but there was an isolation effect ($F_{1,12} = 6.4$; $P = 0.02$).

At the regional community scale, there was an interaction between the effect of disturbance and habitat isolation on species richness ($F_{1,12} = 11$; $P = 0.006$, rarefied data: $F_{1,12} = 6.0$; $P = 0.03$). In disturbed regions, isolation decreased species richness ($F_{1,6} = 14$; $P = 0.01$; Fig. 3b, rarefied data: $F_{1,6} = 16$; $P = 0.007$). In undisturbed regions, isolation tended to increase species richness with isolation ($F_{1,6} = 2.5$; $P = 0.08$; Fig. 3b), which however was not apparent when data were rarefied ($F_{1,6} = 1.7$; $P = 0.2$).

There was also a significant interaction between disturbance and isolation on compositional similarity ($F_{1,12} = 11$; $P = 0.006$). In undisturbed regions, there was greater similarity in species composition among patches connected with dispersal ($F_{1,6} = 6.7$; $P = 0.04$; Fig. 3c). Communities became less similar in species composition when there was dispersal among patches in disturbed regions ($F_{1,6} = 28$; $P = 0.002$; Fig. 3c).

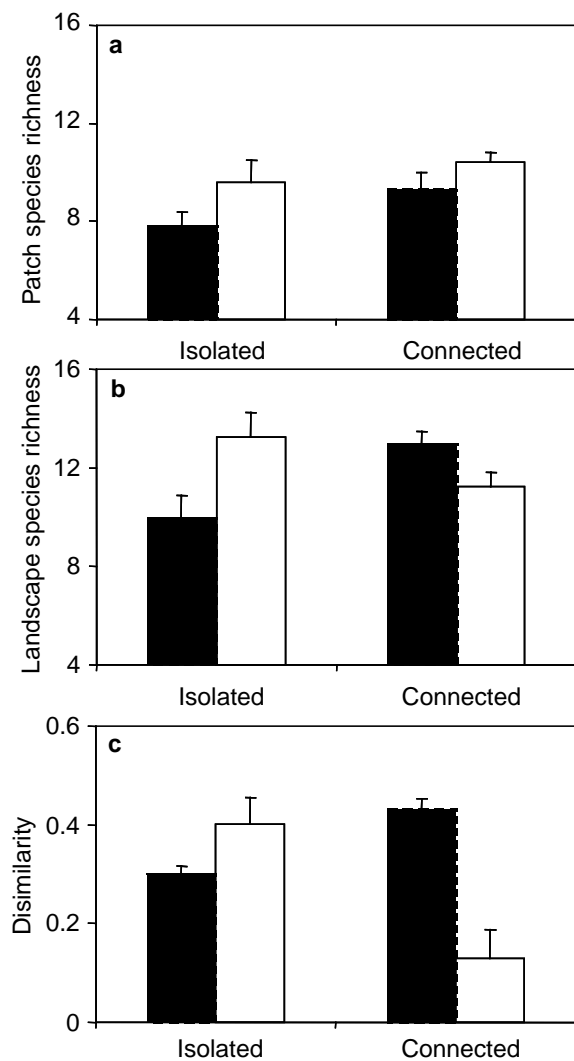


Fig. 3. Effects of habitat isolation and disturbance on (a) local species richness, (b) regional species richness, and (c) community similarity. Disturbed communities are represented by black bars, and non-disturbed communities by open bars. Error bars are 1 standard error.

Dispersal in undisturbed treatments favored species that had intermediate abundances (e.g. *Aspidisca*, *Cryptomonas ovatas*, *Vorticella microstoma*, *Bdelloid* sp. A), whereas species with high abundances decreased (e.g. *B. saltans*, *Colpidium campylum*, *Cyclidium*, *Halteria*, *P. stipitata*) and species with low abundances went extinct (e.g. *Paramecium* sp., *Colpoda steini*, *Tachysoma pellionella*, *Stentor polymorphus*) (Fig. 2). In the drought treatments, dispersal favored most species, except for *V. microstoma*. (Fig. 2). Several species unable to survive in the no-drought treatments (e.g. *C. steini*, *Litinothus*, *T. pellionella*, *Bdelloid* sp. B) were able to exist in regions with droughts, independent of dispersal (Fig. 2).

Discussion

Our results support the hypothesis that the effects of habitat isolation on patterns of species richness at both local and regional scales will depend, at least in part, upon the occurrence of local disturbances. At local scales, we found that habitat isolation reduced species richness (Fig. 3a). Dispersal increased regional species richness when local patches received periodic disturbances, but not in regions without disturbances.

In the absence of dispersal, drought-intolerant species likely could not recolonize patches following their local drought-induced extinction (Kneitel and Chase 2004) or the drought frequency was too high for some species to recover (Mosisch 2001). Consequently, drought had a major impact on species composition (Fig. 2). Species richness was also lower in isolated patches and regions where drought occurred (Fig. 3), which may partly be explained by an abundance effect. Decreased species richness in response to disturbances is frequently observed in natural aquatic systems (Therriault and Kolasa 2001, Baber et al. 2004). McGrady-Steed and Morin (1996) suggested that the difference in species diversity of protists in disturbed and undisturbed communities could be predatory abundance. While we found no evidence for rotifer abundance (which can sometimes consume smaller protozoans) to decline with disturbances, there was a distinct shift in rotifer composition (Fig. 2); this shift in composition may have had an impact on protist community structure.

The joint effects of dispersal and disturbances resulted in spatial refugia for disturbance-intolerant species, allowing species to persist at the regional community scale, even though they could not persist in any locally disturbed patch (e.g. *Amoeba radiosa*, *Aspidisca*, *Halteria*, *Peranema trichophorum*). Dispersal among disturbed patches caused communities to be less similar, whereas dispersal among non-disturbed patches caused communities to be more similar. This was likely driven by the spatio-temporal heterogeneity that disturbances caused at the regional community scale. Moreover, the variation caused by drought treatments may have created a greater likelihood for source-sink dynamics to affect species richness (Pulliam 1988, Boulton 2003, Magoulick and Kobza 2003). However, from our study it is not possible to separate the role of recolonizations from source-sink dynamics.

In the absence of disturbances, dispersal increased species richness at the patch scale, but had rather weak effects at the regional level. Although our study did not allow us to conclusively discern possible mechanisms for these results, the increase in species richness at a patch scale was partly due to several species increased in density and patch occupancy with dispersal in the no-drought treatments (e.g. *Aspidisca*, *C. ovata*, *V. microstoma*, *Bdelloid A*, Fig. 2). However, this

increase in patch occupancy had no effect on regional species richness because they occurred in all replicates of the non-dispersal treatment. This suggests that dispersal may have increased local species richness by preventing extinctions through rescue effects (Brown and Kodric-Brown 1977). In contrast, some rare species (*Paramecium* sp., *C. steini*, *T. pellionella*, *S. polymorphus*) were not found in the dispersal treatment (Fig. 2), which was perhaps due to competitive exclusion, which may have had large effect on the species richness on a regional scale but relative little effect on a patch scale.

Our results are consistent with previous studies testing the effects of dispersal on local and regional species diversity. For example, Forbes and Chase (2002) found decreased regional richness with higher connectance among mesocosms of zooplankton from permanent (non-drying) ponds, as did Chase (2003) in surveys of natural permanent ponds. In a micro-ecosystem of moss-inhabiting invertebrates, Gonzalez et al. (1998) (see also Gilbert et al. 1998) provided some of the best evidence to date of regional isolation (experimental fragmentation) decreasing both local and regional species richness. However, in a subsequent experiment on a similar system using identical methodology, Hoyle and Gilbert (2004) found no effects of habitat isolation on local and regional species richness. This variation may have been due to interactions with disturbances, similar to what was found in the present study. Indeed, Hoyle and Gilbert (2004) suggested that the differences in the results between the two experiments might be that the first experiment was performed during a particularly dry year, and that such drought may have necessitated high dispersal in order to maintain local and regional species richness (Gonzalez and Chaneton 2002).

The design of our experiment was somewhat similar to those in Warren (1996a) who manipulated disturbance rate and dispersal among protist communities, although he found no significant effect of habitat connectance or interactions with disturbance. There were several important differences between our experiment and Warren's (1996a), which may help to explain the more pronounced effect that we observed: (1) our disturbance (drought) is one that this community would naturally experience in natural container ecosystems (Bradshaw and Holzapfel 1988), and protist and rotifer species differentially respond to that drought (Kneitel and Chase 2004). Warren (1996a) used extremely high temperatures as a disturbance, equally killing all individuals of all species; such disturbance is not likely to occur in natural communities of these protists. As a result of disturbances differentially selecting for drought tolerant species, we found higher dissimilarities among local communities in regions where disturbances were applied. (2) Our community, although brought into the laboratory, consisted of naturally co-occurring species of protozoans and rotifers, whereas Warren's (1996a)

experiment was on a group of organisms from disparate sources, which did not necessarily coexist naturally. (3) We had fewer treatment combinations (2 levels of dispersal and disturbance), and so we had more power to detect interactions between the treatment combinations. (4) The initial and final richness of our communities were higher than Warren's (1996a) study. Nevertheless, despite these differences, the similarity in the overall results of our study with Warren's (1996a) results suggests that the differential response to habitat isolation under different disturbance regimes might be a relatively general process.

Human alterations to the environment include fragmentation, which among other things, increases habitat isolation (Harrison and Bruna 1999, Fahrig 2003) and changes the disturbance regime (Pickett and White 1985). In some cases, these factors are altered simultaneously. For example, wood extraction practices fragment forests, increasing habitat isolation (Laurance et al. 2002, Bury 2004), but simultaneously decrease fire frequency (Bury 2004, Brown and Gurevitch 2004). Similarly, when wetlands are drained, this increases the isolation among remaining bodies of water; these remaining bodies are often made deeper for recreation purposes, and thus do not dry as shallower wetlands often do (Prince 1997, National Research Council, 2001). Sometimes even habitat isolation itself will affect disturbance rates, e.g. fragmentation of forests may increase wind fallen trees but decrease fire frequency (Boulinier et al. 1998, Laurance et al. 2002). Thus, our results may allow us to better interpret and predict how patterns of species richness may change as these anthropogenic factors occur.

Finally, our results may provide insights for conservation strategies and reserve design. For example, in habitats with frequent disturbances, we suggest that it might be more important to ensure high dispersal (e.g. through corridors) than in less frequently disturbed habitats, where connectance could in some cases, actually decrease species richness on the regional scale. In our quest to understand how the natural world will respond to increasing human impacts, we suggest that great insights will come from considering multiple stressors and multiple spatial scales simultaneously.

Acknowledgements – We would like to thank members of the J. M. Chase lab: L. Blaustein, T. Knight, J. Losos and R. Ricklefs for their comments and discussion. Ö. Östman was supported by a postdoctoral fellowship from the Swedish Research Council, J. M. Kneitel was supported by a postdoctoral fellowship from the Tyson Research Center, Washington University.

References

- Amarasekare, P. 2000. Coexistence of competing parasitoids on a patchily distributed host: local vs spatial mechanisms. – *Ecology* 81: 1286–1296.

- Baber, M. J., Fleishman, E., Babbitt, K. J. et al. 2004. The relationship between wetland hydroperiod and nestedness patterns in assemblages of larval amphibians and predatory macroinvertebrates. – *Oikos* 107: 16–27.
- Boulinier, T., Nichols, J. D., Hines, J. E. et al. 1998. Higher temporal variability of forest breeding bird communities in fragmented regions. – *Proc. Natl Acad. Sci. USA* 95: 7497–7501.
- Boulton, A. J. 2003. Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. – *Freshwater Biol.* 48: 1173–1185.
- Bradshaw, W. E. and Holzapfel, C. M. 1988. Drought and the organization of tree-hole communities. – *Oecologia* 74: 507–514.
- Brown, J. H. and Kodric-Brown, A. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. – *Ecology* 58: 445–449.
- Brown, K. A. and Gurevitch, J. 2004. Long-term impacts of logging on forest diversity in Madagascar. – *Proc. Natl Acad. Sci. USA* 101: 6045–6049.
- Bury, R. B. 2004. Wildfire, fuel reduction, and herpetofaunas across diverse landscape mosaics in northwestern forests. – *Conserv. Biol.* 18: 968–975.
- Chase, J. M. 2003. Community assembly: when should history matter? – *Oecologia* 136: 489–498.
- Connell, J. H. 1978. Diversity in tropical rainforests and coral reefs. – *Science* 199: 1302–1310.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. – *Annu. Rev. Ecol. Evol. Syst.* 34: 487–515.
- Forbes, A. E. and Chase, J. M. 2002. The role of habitat connectivity and landscape geometry in experimental zooplankton metacommunities. – *Oikos* 96: 433–440.
- Fukami, T. 2004. Community assembly along a species pool gradient: implications for multiple-scale patterns of species diversity. – *Popul. Ecol.* 46: 137–147.
- Gaston, K. J. 2000. Global patterns in biodiversity. – *Nature* 405: 220–227.
- Gilbert, F., Gonzalez, A. and Evans-Freke, I. 1998. Corridors maintain species richness in the fragmented regions of a microecosystem. – *Proc. R. Soc. Lond. B* 265: 577–582.
- Gonzalez, A. and Chanton, E. J. 2002. Heterotroph species extinction, abundance and biomass dynamics in an experimentally fragmented microecosystem. – *J. Anim. Ecol.* 71: 594–602.
- Gonzalez, A., Lawton, J. H., Gilbert, F. S. et al. 1998. Metapopulation dynamics, abundance, and distribution in a microecosystem. – *Science* 281: 2045–2047.
- Gotelli, N. J. and Colwell, R. K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. – *Ecol. Lett.* 4: 379–391.
- Gotelli, N. J. and Entsminger, G. L. 2001. EcoSim: Null models software for ecology. Version 7.0, – Acquired Intelligence Inc. & Kesity-Bear <http://homepages.together.net/~gentmin/ecosim.htm>.
- Harrison, S. 1997. How natural habitat patchiness affects the distribution of diversity in Californian serpentine chaparral. – *Ecology* 78: 1898–1906.
- Harrison, S. 1999. Local and regional diversity in a patchy landscape: native, alien, and endemic herbs on serpentine. – *Ecology* 80: 70–80.
- Harrison, S. and Bruna, E. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? – *Ecography* 22: 225–232.
- Ims, R. A., Leinaas, H. P. and Coulson, S. 2004. Spatial and temporal variation in patch occupancy and population density in a model system of an arctic *Collembola* species assemblage. – *Oikos* 105: 89–100.
- Hoyle, M. and Gilbert, F. 2004. Species richness of moss landscapes unaffected by short-term fragmentation. – *Oikos* 105: 359–367.
- Kneitel, J. M. and Miller, T. E. 2003. Dispersal rates affect species composition in metacommunities of *Scarracenia purpurea* inquilines. – *Am. Nat.* 162: 165–171.
- Kneitel, J. M. and Chase, J. M. 2004. Disturbance, predator and resource interactions alter container community composition. – *Ecology* 85: 2088–2093.
- Laurance, W. F., Lovejoy, T. E., Vasconcelos, H. L. et al. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. – *Conserv. Biol.* 16: 605–618.
- Lawton, J. H. 2000. Community ecology in a changing world. – *Eco. Inst., Oldendorf/Luhe*.
- Levine, J. M. 2003. A patch modeling approach to the community-level consequences of directional dispersal. – *Ecology* 84: 1215–1224.
- Mackey, R. L. and Currie, D. J. 2001. The diversity-disturbance relationship: is it generally strong and peaked? – *Ecology* 82: 3479–3492.
- Magoulick, D. D. and Kobza, R. M. 2003. The role of refugia for fishes during drought: a review and synthesis. – *Freshwater Biol.* 48: 1186–1198.
- McGrady-Steed, J. and Morin, P. J. 1996. Disturbance and the species composition of rain pool microbial communities. – *Oikos* 76: 93–102.
- Mosisch, T. D. 2001. – Effects of desiccation on stream epilithic algae. – *N. Z. J. Mar. Freshwater Res.* 35: 173–179.
- Mouquet, N. and Loreau, M. 2003. Community patterns in source-sink metacommunities. – *Am. Nat.* 162: 544–557.
- National Research Council. 2001. Compensating for wetland losses under the Clean Water Act, – *Natl Acad. Press, Washington, D.C.*
- Pickett, S. T. A. and White, P. S. 1985. The Ecology of natural disturbance and patch dynamics. – *Academic Press*.
- Prince, H. 1997. Wetlands of the American Midwest: a historical geography. – *Univ. Chicago Press*.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. – *Am. Nat.* 132: 652–661.
- Ricklefs, R. E. 1987. Community diversity – relative roles of local and regional processes. – *Science* 235: 167–171.
- Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. – *Ecol. Lett.* 7: 1–15.
- Scholes, L., Warren, P. H. and Beckerman, A. P. 2005. The combined effects of energy and disturbance on species richness in protist microcosms. – *Ecol. Lett.* 8: 730–738.
- Shea, K., Roxburgh, S. H. and Rauscher, E. S. J. 2004. Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. – *Ecol. Lett.* 7: 491–508.
- Simberloff, D. 2004. Community ecology: is it time to move on? – *Am. Nat.* 163: 787–799.
- Sousa, W. P. 1984. The role of disturbance in natural communities. – *Annu. Rev. Ecol. Syst.* 15: 353–391.
- Therriault, T. W. and Kolasa, J. 2001. Desiccation frequency reduces species diversity and predictability of community structure in coastal rock pools. – *Isr. J. Zool.* 47: 477–489.
- Turner, I. M., Chua, K. S., Ong, J. S. Y. et al. 1996. A century of plant species loss from an isolated fragment of lowland tropical rain forest. – *Conserv. Biol.* 10: 1229–1244.
- Warren, P. H. 1996a. Dispersal and destruction in a multihabitat system: an experimental approach using protist communities. – *Oikos* 77: 317–325.
- Warren, P. H. 1996b. The effects of between-habitat dispersal rate on protist communities and metacommunities in microcosms at two spatial scales. – *Oecologia* 105: 132–140.
- Wilson, S. D. and Tilman, D. 2002. Quadratic variation in old-field species richness along gradients of disturbance and nitrogen. – *Ecology* 83: 492–504.