

Are common species sufficient in describing turnover in aquatic metacommunities along environmental and spatial gradients?

Jani Heino^{a,*} and Janne Soininen^b

^aFinnish Environment Institute, Natural Environment Centre, Ecosystem Change Unit, Biodiversity Change Group, University of Oulu, Finland

^bDepartment of Environmental Sciences, University of Helsinki, Finland

Abstract

Recent findings have suggested that large-scale diversity patterns are primarily driven by widespread species, while rare species are less important in this regard. The degree to which variation in the diversity of local communities in the context of metacommunity ecology concurs with these findings has not been rigorously examined to date. It is also unknown if community turnover along environmental and spatial gradients is mostly attributable to common as opposed to rare species. We examined spatial turnover for three categories of species, all, common, and rare, in seven aquatic metacommunities using simple and partial Mantel tests. We found that variation in turnover along environmental and spatial gradients was generally similar among all, common, and rare species categories, with five of the seven data sets following this pattern. Our findings thus suggest that spatial turnover in aquatic metacommunities can often be adequately described using common species. More importantly, our findings also suggest that turnover–environment relationships can also be described relatively well using information from common species only.

In recent decades, there has been a considerable increase in the number of studies addressing the causes and consequences of biodiversity in nature (Gaston 2000; Tilman 2000). Compared to studies on alpha diversity, studies addressing gamma and beta diversity have increased particularly rapidly. Beta diversity—the turnover of community composition from place to place or from time to time—has been actively studied in recent years (Koleff et al. 2003). Examination of patterns in beta diversity at multiple scales is of great importance because it helps one to understand the ways in which changes in community composition at local scales are mediated to larger spatial and temporal scales. Beta diversity can be measured as variation in community composition across space, with the focus on variability in species composition among disjointed and nonoverlapping sites (Soininen et al. 2007b). Turnover can thus be examined using distance–decay graphs, where all pairwise similarities in community composition are plotted against geographical or environmental distance between the sample pairs. This distance decay of community similarity has been examined widely in recent years (Nekola and White 1999; Soininen et al. 2007b), but this pattern remains inadequately understood for aquatic systems (Shurin et al. 2009; Leprieur et al. 2009).

Moreover, there is not much information about the way in which distance decay is affected by the distribution of common vs. rare species in ecological communities. Ecological communities are typically dominated by rare species that have very restricted ranges (Gaston 2003; Soininen and Heino 2005). Recent research has shown, however, that species richness patterns are primarily driven by widespread species, whereas species with restricted ranges contribute much less to these patterns (Jetz and Rahbek 2002; Lennon

et al. 2004; Mora and Robertson 2005). The richness of widespread species may also be more closely related to environmental variables than that of rare species (Kreft et al. 2006; Rahbek et al. 2007; Gaston 2008). These studies have generally examined patterns across large-scale grids at large geographical extents, whereas research on diversity and turnover patterns across local ecosystems has been given less attention (Pearman and Weber 2007). Furthermore, to our knowledge, no studies have addressed the relationships of turnover of common and rare species to environmental and spatial gradients across metacommunities that consist of interacting metapopulations.

We examined three alternative scenarios concerning the way in which species turnover would be related to environmental and spatial gradients in all, common, and rare species. (1) We assumed that all three groups of species would show similar turnover along environmental and spatial gradients (Fig. 1A). (2) We assumed that all species and common species would exhibit significant spatial turnover, whereas rare species would occur so sporadically across sites that their assemblages would not exhibit significant variation in turnover (Fig. 1B). (3) We assumed that all and rare species would exhibit spatial turnover, whereas common species would occur at so many sites that there would be no considerable variation in their species turnover among sites (Fig. 1C). If scenario 2 or 3 is correct, we would expect an understanding of turnover to require the examination of both common and rare species. By contrast, if scenario 1 is correct, then describing turnover of common species would be sufficient to understand the turnover of entire communities along environmental and spatial gradients. We would like to emphasize, however, that these scenarios are illustrative only, and that the pattern for the turnover of all species is likely to be something between those of common and rare species.

* Corresponding author: jani.heino@ymparisto.fi

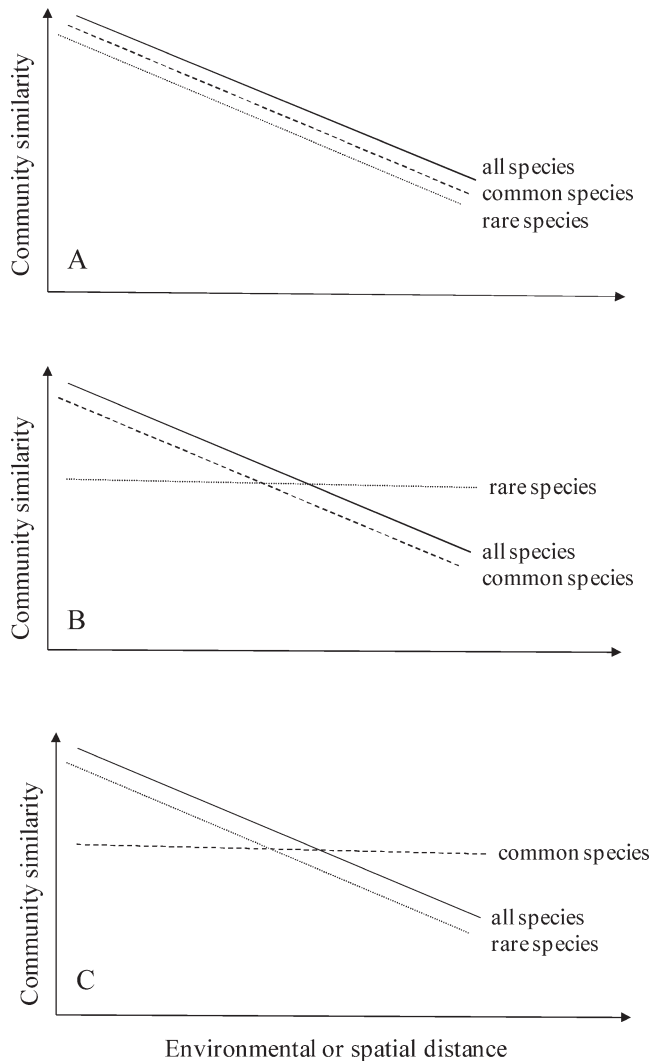


Fig. 1. Three possible scenarios for spatial turnover in all, common, and rare species. (A) All groups of species may show similar distance decay along environmental and spatial gradients. (B) All species and common species show relatively similar variation along environmental and spatial gradients, whereas rare species occur sporadically and show no discernible distance decay. (C) All and rare species show relatively similar variation along environmental and spatial gradients, whereas common species occur at most sites, and there is thus no clear distance decay.

Aquatic metacommunities are suitable objects of study for this type of examination because they are embedded within the hostile terrestrial matrix, are well-bounded, and exhibit wide variation in environmental conditions across sites. However, studies of aquatic metacommunity ecology have until now largely neglected comparisons of spatial turnover patterns shown by common vs. rare species.

Methods

We analyzed data from seven aquatic metacommunities surveyed by us or compiled from the literature. A metacommunity was characterized by a set of sites within a drainage basin, with the exception of stream diatoms and

littoral microcrustaceans. Additional information on the data sets can be found in the original articles (Table 1). Pond phytoplankton and zooplankton were sampled from 25 wetland ponds in the Koutajoki drainage basin in northeastern Finland in 2005 (Soininen et al. 2007a). These data included nearshore samples of planktonic communities and simultaneous sampling of water chemistry. Lake zooplankton were collected from 44 headwater lakes in the Koutajoki drainage basin in 2005 (J. Heino and T. Muotka unpubl.). The samples were taken from five nearshore locations from which pooled samples of zooplankton were compiled. The field and laboratory methods in this work followed those of pond zooplankton. The zooplankton survey was conducted simultaneously with the littoral macroinvertebrate sampling, and the data included measurements of the same environmental variables (Heino 2008a). Littoral microcrustacean data were extracted from the literature (Walseng et al. 2008). These data included littoral samples from 22 Canadian Shield lakes. Although the lakes were not restricted to a single drainage basin, we expected that these communities would exchange colonists relatively efficiently. In fact, many species occupied virtually all of the surveyed lakes in the study area, suggesting that these sites also formed a metacommunity. Littoral macroinvertebrates were collected from 48 headwater lakes in the Koutajoki drainage basin in 2005 (Heino 2008a). The sampling of each lake incorporated five littoral samples that were pooled for the analyses. Stream diatoms were collected from 47 headwater streams and small rivers in northern and eastern Finland in 2001 or 2004 (Heino and Soininen 2005). Despite the fact that the study area, spanning three major drainage basins, was larger than that for the other data sets in this study, we considered diatoms with a high dispersal ability to form a metacommunity also at this scale. This was also evidenced by the fact that many species were detected in all drainage basins. Finally, stream macroinvertebrates were sampled at 34 sites in the Koutajoki drainage basin in 2002 (Heino 2008b).

There are various ways to define common and rare species. For example, Pärtel et al. (2001) considered common species to occur at more than 75% of surveyed sites, while Larsen et al. (2007) defined common species as the 25% with the largest geographic distribution. Although basing the definition of commonness on the percentages of occupied sites would certainly facilitate comparisons among studies, such definitions are problematic for assemblages of small aquatic organisms that are strongly dominated by rare species. Stream diatom assemblages, for example, are dominated by very rare species, and only a very small subset of species occurs at more than 75% of surveyed sites (Soininen and Heino 2005). Therefore, we used an alternative way to delineate common species, which considered common species as the 25% most frequently occurring of all species (Larsen et al. 2007). We thus divided the data sets into three types: (1) species-by-sites matrix with all species included; (2) species-by-sites matrix with 25% of the most frequent species (i.e., common species) included; and (3) species-by-sites matrix with the remaining 75% of species (i.e., rare species) included. An analysis of species composition of the 25%, or even 50%, of

Table 1. Characteristics of the data sets used in the analyses.

Data set	Number of all species in data set	Number of common species in data set	Number of sites	Average number of rare species per site	Environmental variables	Reference
Pond phytoplankton	152	37	25	8.4	8	Soininen et al. (2007a)
Pond zooplankton	54	14	25	13.8	8	Soininen et al. (2007a)
Lake zooplankton	55	14	44	6.8	17	J. Heino and T. Muotka (unpubl.)
Littoral microcrustaceans	72	18	22	16.7	10	Walseng et al. (2008)
Littoral macroinvertebrates	155	41	48	12.9	17	Heino (2008a)
Stream diatoms	254	65	47	16.9	17	Heino and Soininen (2005)
Stream macroinvertebrates	170	44	34	12.9	15	Heino (2008b)

the most infrequent species (i.e., rare species) was not possible because these species were often so sporadic in their distributions that it led to numerous sites with no species. Our delineation of common species also ensured that the proportions of common and rare species in relation to all species remained almost the same across the data sets.

There were two methodological limitations in our analyses. Although we strongly feel that abundance constitutes an important facet of rarity, the use of abundance data is problematic in the present context for a number of reasons. (1) We did not have abundance data for all of the data sets. (2) In the cases for which we had abundance data, we did not have strictly quantitative, but semiquantitative data (for the details of sampling, *see* original papers listed previously). In these kind of data sets, estimation of true abundances might be somewhat distorted. (3) Abundances for different organisms groups in this study are not easily comparable because they were measured using highly different field sampling methods and different methods in the laboratory. (4) Since we are mainly interested in variation in species occupancy along gradients, and not the distribution of species abundances, we feel that presence–absence data are more appropriate here. Thus, we emphasized the rarity measure based on presence–absence data and proportions of sites occupied.

A second methodological limitation of our study was related to the geographical distances between sites used in Mantel tests. One may envisage that watercourse distances are more relevant than overland distances for the dispersal of aquatic organisms (Grant et al. 2009; Brown and Swan 2010). However, we had to use Euclidean overland distances between sites for comparison because we did not have data for watercourse distances. More importantly, because not all lakes and ponds were connected by streams or rivers, we could not measure watercourse distances between sites. Some lentic studies have also found that the use of either overland or watercourse distances between sites makes little difference in community analyses of small aquatic organisms (Beisner et al. 2006; Nabout et al. 2009). However, in lotic studies, watercourse distances may be ecologically more relevant than overland distances (Grant et al. 2009; Brown and Swan 2010).

We used a Mantel test with a Pearson correlation coefficient for each data set to examine community turnover along environmental and spatial gradients (Mantel 1967; Legendre and Legendre 1998). In short, a Mantel test is a correlation of dissimilarity or distance matrices. We first produced distance matrices for environmental, geographical, and biological data. Environmental variables and site coordinates were centered on their respective means and standardized by standard deviate, and among-site Euclidean distances were then calculated between all site pairs separately for environmental variables and site coordinates. We used three different dissimilarity coefficients based on the presence–absence data of biotic communities to calculate pairwise dissimilarities between all site pairs: Sorensen, Jaccard, and Kulczynski (Legendre and Legendre 1998). However, in practice, all three dissimilarity coefficients led to highly similar correlations between the biological dissimilarity and environmental or geographical distance matrices in the Mantel tests. To facilitate comparisons with most other studies, we show the results based on the Sorensen coefficient (Soininen et al. 2007b). In summary, we correlated the biological and environmental distances, and biological and geographical distances between sites using simple Mantel correlations. Moreover, we ran partial Mantel tests where either the environmental or spatial distance matrix was the explanatory matrix, and the other one was the partial matrix. A partial Mantel test examines the influence of environmental distance on biotic distance while controlling for geographical distance and vice versa. This was done to tease apart the pure effects of environment and space on biological matrices. A partial Mantel test is thus equivalent to partial correlation. The significance of the relationships between dissimilarity and distance matrices was assessed using 1000 randomizations. Mantel tests were conducted using Brodgar version 2.5.1 (<http://www.brodgar.com/brodgar.htm>).

We were also interested in testing differences in Mantel r -values between the analyses of common and rare species. We thus tested for differences in the r -values of Mantel tests between data of common and rare species using paired t -test across all the data sets. Although our primary variable of interest was Mantel r -values, we also obtained

Table 2. Results of Mantel tests for community dissimilarities (Sorensen coefficient) against spatial and environmental distances (Euclidean distance). Partial Mantel tests (comparable to partial correlations) were conducted with either environmental distances as the explanatory matrix and spatial distances as the partial matrix (i.e., pure environment), or vice versa (i.e., pure space). * $p < 0.050$.

	Environment	Space	Partial tests	
			Pure environment	Pure space
Pond phytoplankton all	0.161	0.226*	0.095	0.186
Pond phytoplankton common	0.097	0.127	0.059	0.102
Pond phytoplankton rare	0.064	0.073	0.043	0.055
Pond zooplankton all	0.389*	0.496*	0.278	0.424*
Pond zooplankton common	0.163	0.409*	0.035	0.381*
Pond zooplankton rare	0.457*	0.328*	0.393*	0.213
Lake zooplankton all	0.202*	-0.034	0.206*	-0.051
Lake zooplankton common	0.193*	-0.053	0.198*	-0.069
Lake zooplankton rare	0.175*	-0.073	0.182*	-0.088
Littoral microcrustaceans all	0.754*	0.651*	0.629*	0.438*
Littoral microcrustaceans common	0.712*	0.573*	0.582*	0.316*
Littoral microcrustaceans rare	0.702*	0.710*	0.535*	0.550*
Littoral macroinvertebrates all	0.383*	0.109*	0.377*	0.081*
Littoral macroinvertebrates common	0.298*	0.073	0.293*	0.049
Littoral macroinvertebrates rare	0.297*	0.099*	0.291*	0.077*
Stream diatoms all	0.365*	0.418*	0.325*	0.386*
Stream diatoms common	0.381*	0.411*	0.347*	0.378*
Stream diatoms rare	0.306*	0.373*	0.262*	0.340*
Stream macroinvertebrates all	0.273*	-0.054	0.273*	-0.055
Stream macroinvertebrates common	0.217*	-0.037	0.217	-0.037
Stream macroinvertebrates rare	0.176*	0.050	0.177*	0.052

qualitatively similar results from paired *t*-tests for the slopes of linear regressions (i.e., when we regressed biological dissimilarities with environmental or spatial distances).

Results

In general, littoral microcrustaceans showed the strongest Mantel correlation between biological and environmental or spatial distance matrices, followed by pond zooplankton and stream diatoms (Table 2). Weakest correlations were shown by pond phytoplankton and lake zooplankton. Mantel correlations between biotic dissimilarity and environmental or spatial distance matrices were relatively similar among all, common, and rare species categories included in the analysis (Table 2). Both simple and partial Mantel tests supported this reasoning and clearly showed that, in five of the seven data sets, community dissimilarities based on all, common, and rare species varied relatively similarly along environmental and spatial gradients. The exceptions were pond phytoplankton and pond zooplankton data sets, where common species had clearly lower Mantel correlations than all species with regard to environmental variation. In pond phytoplankton, analyses of common and rare species deviated from that of all species. In pond zooplankton, common species deviated from all and rare species. However, overall paired *t*-tests indicated that the Mantel tests' *r*-values did not differ between data of common and rare species across the data sets ($p > 0.05$; both simple and partial Mantel tests' *r*-values tested separately between the two groups of species).

Discussion

Our results partly concur with other studies that have considered the contribution of common and rare species to species richness patterns. It has been shown with large-scale data that common species drive species richness patterns (Jetz and Rahbek 2002; Lennon et al. 2004; Vázquez and Gaston 2004), and that the richness of common species is more closely related to environmental variation than that of rare species (Jetz and Rahbek 2002; Kreft et al. 2006; Rahbek et al. 2007). However, the generality of such conclusions remains to be addressed with other organism groups and across metacommunities. Our findings also suggest that mostly common species drive community turnover in aquatic metacommunities along environmental and spatial gradients. Although we could not analyze very rare species owing to their sporadic occurrences, these species contributed to the matrices of all species and rare species, and their influences on spatial turnover should be seen in the analyses of these data. Yet, it is likely that common species are often sufficient in describing turnover along environmental and spatial gradients. This finding is in agreement with Tuomisto et al. (2003), who found that spatial turnover in compositional dissimilarity was similar among all and abundant species in plants. Moreover, Gaston et al. (2007) found that spatial turnover was mainly driven by widespread species in birds.

There were two notable exceptions to these general patterns. Pond phytoplankton and pond zooplankton did not follow the general pattern observed for other data sets (which showed that all, common, and rare species data showed similar environmental and geographical relationships). These deviating patterns may be attributable to the

characteristics of the littoral plankton communities in ponds. Our littoral samples may have incorporated various rare species originating from benthic habitats, thereby leading to differing environmental and geographical relationships for all, common, and rare species data. Although this explanation may be correct, it is at odds with the finding that lake littoral zooplankton data for all, common, and rare species showed strikingly similar patterns. More data sets on littoral and pelagic plankton communities would be needed to resolve this question.

Our findings may nevertheless have potential implications for community ecology. For examination of community similarity–environment relationships, it is perhaps not necessary to include information about rare species, because as small a proportion of species as 25% of the most frequent ones appears to be enough to describe the pattern. One may, of course, question this assumption, because a researcher cannot know beforehand which species are rare and which are common. Our point here is, however, that samples of small aquatic organisms (e.g., phytoplankton, zooplankton, and macroinvertebrates) are hardly ever close to complete, meaning that most rare species are missed. Thus, our argument is that rare species may be less relevant than common species in studies of the distance decay of community similarity in the aquatic realm, because the signal of spatial turnover is mainly carried by common species. Such a limited attention to common species only is likely to reduce the amount of effort and costs needed to enumerate species in aquatic surveys, and yet the information on common species is likely to relatively accurately describe turnover along spatial and environment gradients. Reductions in cost and effort are especially relevant in situations where the most difficult-to-identify and difficult-to-survey species belong to rare species (Vellend et al. 2008).

These cost-efficient concerns may also be true in the context of environmental assessment, and researchers would perhaps like to concentrate on common and otherwise easily surveyed species when estimating degradation of aquatic ecosystems. However, given that we did not survey anthropogenically altered environmental gradients, we cannot be sure if anthropogenic influences can be detected more easily based on common as opposed to rare species (but see Van Sickle et al. 2007). Finally, although rare species are surely important in the context of conservation (Gaston and Rodrigues 2003), it appears that spatial turnover, an important component of biodiversity, can be relatively reliably determined based on information about common species (Morlon et al. 2008). The generality of this reasoning should, however, be tested using more data from terrestrial and marine systems, as well as those freshwater systems affected by anthropogenic factors.

Acknowledgments

We thank all the colleagues who contributed to collecting and making available the data sets analyzed in this paper. We also thank two anonymous reviewers and Robert W. Sterner for constructive comments on an earlier draft of the paper. The preparation of this paper was supported by grants from the Academy of Finland to J.H. and J.S.

References

- BEISNER, B. E., P. R. PERES-NETO, A. S. LINDSTRÖM, A. BARNETT, AND M. L. LONGHI. 2006. The role of environmental and spatial processes in structuring lake communities from bacteria to fish. *Ecology* **87**: 2985–2991, doi:10.1890/0012-9658(2006)87[2985:TROEAS]2.0.CO;2
- BROWN, B. L., AND C. M. SWAN. 2010. Dendritic network structure constrains metacommunity properties in riverine ecosystems. *J. Anim. Ecol.* **79**: 571–580, doi:10.1111/j.1365-2656.2010.01668.x
- GASTON, K. J. 2000. Global patterns in biodiversity. *Nature* **405**: 220–227, doi:10.1038/35012228
- . 2003. The structure and dynamics of geographic ranges. Oxford Univ. Press.
- . 2008. Biodiversity and extinction: The importance of being common. *Prog. Phys. Geogr.* **32**: 73–79, doi:10.1177/0309133308089499
- , AND A. S. L. RODRIGUES. 2003. Reserve selection in regions with poor biological data. *Cons. Biol.* **17**: 188–195, doi:10.1046/j.1523-1739.2003.01268.x
- , AND OTHERS. 2007. Spatial turnover in the global avifauna. *Proc. R. Soc. Lond. B* **274**: 1567–1574, doi:10.1098/rspb.2007.0236
- GRANT, E. H. C., L. E. GREEN, AND W. H. LOWE. 2009. Salamander occupancy in headwater stream networks. *Freshwat. Biol.* **54**: 1370–1378, doi:10.1111/j.1365-2427.2009.02166.x
- HEINO, J. 2008a. Patterns of functional biodiversity and function–environment relationships in lake littoral macroinvertebrates. *Limnol. Oceanogr.* **53**: 1446–1455.
- . 2008b. Influence of taxonomic resolution and data transformation on biotic matrix concordance and assemblage–environment relationships in stream macroinvertebrates. *Boreal Env. Res.* **13**: 359–369.
- , AND J. SOININEN. 2005. Assembly rules and community models for unicellular organisms: Patterns in diatoms of boreal streams. *Freshwat. Biol.* **50**: 567–577, doi:10.1111/j.1365-2427.2005.01346.x
- JETZ, W., AND C. RAHBK. 2002. Geographic range size and determinants of avian species richness. *Science* **297**: 1548–1551, doi:10.1126/science.1072779
- KOLEFF, P., K. J. GASTON, AND J. J. LENNON. 2003. Measuring beta diversity for presence–absence data. *J. Anim. Ecol.* **72**: 367–382, doi:10.1046/j.1365-2656.2003.00710.x
- KREFT, H., J. H. SOMMER, AND W. BARTHOLOTT. 2006. The significance of geographic range size for spatial diversity in Neotropical palms. *Ecography* **29**: 21–30, doi:10.1111/j.2005.0906-7590.04203.x
- LARSEN, F. W., J. BLADT, AND C. RAHBK. 2007. Improving the performance of indicator groups for the identification of important areas for species conservation. *Cons. Biol.* **21**: 731–740, doi:10.1111/j.1523-1739.2007.00658.x
- LEGENDRE, P., AND L. LEGENDRE. 1998. Numerical ecology. Elsevier.
- LENNON, J. J., K. KOLEFF, J. J. D. GREENWOOD, AND K. J. GASTON. 2004. Contribution of rarity and commonness to patterns of species richness. *Ecol. Lett.* **7**: 81–87, doi:10.1046/j.1461-0248.2004.00548.x
- LEPRIEUR, F., J. D. OLDEN, S. LEK, AND S. BROUSSE. 2009. Contrasting patterns and mechanisms of spatial turnover for native and exotic freshwater fish in Europe. *J. Biogeogr.* **36**: 1899–1912, doi:10.1111/j.1365-2699.2009.02107.x
- MANTEL, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Res.* **27**: 209–220.

- MORA, C., AND D. R. ROBERTSON. 2005. Causes of latitudinal gradients in species richness: A test with fishes of the tropical Eastern Pacific. *Ecology* **86**: 1771–1782, doi:10.1890/04-0883
- MORLON, H., AND OTHERS. 2008. A general framework for the distance decay of similarity in ecological communities. *Ecol. Lett.* **11**: 904–917, doi:10.1111/j.1461-0248.2008.01202.x
- NABOUT, J. C., T. SIQUEIRA, L. M. BINI, AND I. S. NOGUEIRA. 2009. No evidence for environmental and spatial processes in structuring phytoplankton communities. *Acta Oecol.* **35**: 720–726, doi:10.1016/j.actao.2009.07.002
- NEKOLA, J. C., AND P. S. WHITE. 1999. The distance decay of community similarity in biogeography and ecology. *J. Biogeogr.* **26**: 867–878, doi:10.1046/j.1365-2699.1999.00305.x
- PÄRTEL, M., M. MOORA, AND M. ZOBEL. 2001. Variation in species richness within and between calcareous (alvar) grassland stands: The role of core and satellite species. *Plant. Ecol.* **157**: 203–211, doi:10.1023/A:1013938624716
- PEARMAN, P. B., AND D. WEBER. 2007. Common species determine richness patterns in biodiversity indicator taxa. *Biol. Cons.* **138**: 109–119, doi:10.1016/j.biocon.2007.04.005
- RAHBEK, C., N. J. GOTELLI, R. K. COLWELL, G. L. ENTSMINGER, T. F. RANGEL, AND G. R. GRAVES. 2007. Predicting continental-scale patterns of bird species richness with spatially explicit models. *Proc. R. Soc. Lond. B* **274**: 165–174, doi:10.1098/rspb.2006.3700
- SHURIN, J. B., K. COTTENIE, AND H. HILLEBRAND. 2009. Spatial autocorrelation and dispersal limitation in freshwater organisms. *Oecologia* **159**: 151–159, doi:10.1007/s00442-008-1174-z
- SOININEN, J., AND J. HEINO. 2005. Relationships between local population persistence, local abundance and regional occupancy of species: Patterns in diatoms of boreal streams. *J. Biogeogr.* **32**: 1971–1978, doi:10.1111/j.1365-2699.2005.01342.x
- , M. KOKOCINSKI, S. ESTLANDER, J. KOTANEN, AND J. HEINO. 2007a. Neutrality, niches and determinants of plankton metacommunity structure across boreal wetland ponds. *Ecoscience* **14**: 146–154, doi:10.2980/1195-6860(2007)14[146:NNADOP]2.0.CO;2
- , R. MACDONALD, AND H. HILLEBRAND. 2007b. The distance decay of similarity in ecological communities. *Ecography* **30**: 3–12.
- TILMAN, D. 2000. Causes, consequences and ethics of biodiversity. *Nature* **405**: 208–211, doi:10.1038/35012217
- TUOMISTO, H., K. RUOKOLAINEN, AND M. YLI-HALLA. 2003. Dispersal, environment, and floristic variation of Western Amazonian forests. *Science* **299**: 241–244, doi:10.1126/science.1078037
- VAN SICKLE, J., D. P. LARSEN, AND C. P. HAWKINS. 2007. Exclusion of rare taxa affects performance of the *O/E* index in bioassessments. *J. N. Amer. Benthol. Soc.* **26**: 319–331, doi:10.1899/0887-3593(2007)26[319:EORTAP]2.0.CO;2
- VÁZQUEZ, L.-B., AND K. J. GASTON. 2004. Rarity, commonness, and patterns of species richness: The mammals of Mexico. *Glob. Ecol. Biogeogr.* **13**: 535–542, doi:10.1111/j.1466-822X.2004.00126.x
- VELLEND, M., P. L. LILLEY, AND B. L. STARZOMSKI. 2008. Using subsets of species in biodiversity surveys. *J. Appl. Ecol.* **45**: 161–169, doi:10.1111/j.1365-2664.2007.01413.x
- WALSING, B., N. D. YAN, T. W. PAWSON, AND O. SKARPAAS. 2008. Acidity versus habitat structure as regulators of littoral microcrustacean assemblages. *Freshwat. Biol.* **53**: 290–303.

Associate editor: Robert W. Sterner

Received: 09 February 2010

Accepted: 08 July 2010

Amended: 30 July 2010