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Connectivity and nestedness of the meta-community structure of moss dwelling bdelloid rotifers along a stream

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Abstract

We analyzed meta-community structure of bdelloid rotifers colonizing mosses along an 80 meter section of Rio Valnava in NW Italy. Bdelloid rotifers are small animals living associated with a substratum; colonization in bdelloids can be produced by active animals moving along the riverbed, or by passive dormant propagules, moved by wind. To detect which kind of colonization might be stronger at different spatial scales, we designed a spatially nested sampling experiment at three hierarchical levels: (1) single sample, (2) 10 communities inside each pool, (3) complete section of 10 pools. Assessing species richness and species similarity of communities, and coherence and nestedness of bdelloid meta-communities, we found that different forces may drive species composition at different spatial scales: at the largest scale, colonization of propagules may over-ride direct dispersal between pools, while at the scale of the single pool, differential movements of species give a nested structure to the meta-communities. The number of species increased as the level of analysis increased, even though this study was carried out along only a small stream section.

Introduction

Classical analysis of freshwater community structure usually has attempted to recognize environmental features shaping species composition as if such communities were spatially and temporally isolated entities. The connectivity of communities has been considered as a relevant factor influencing species structure only recently (Forbes & Chase, 2002; Cottenie & De Meester, 2003; Cottenie et al., 2003; Kneitel & Miller, 2003). Naturally, with the addition of this new perspective, the scale over which communities are potentially connected – local vs. regional, for example – has also become important (Amarasekare, 2000; Taneyhill, 2000; Mouquet & Loreau, 2002). One of the major innovations arising from these recent studies is the concept of the meta-community, that is, a set of ecological communities at different sites that are potentially connected by dispersal (Leibold and Mikkelson, 2002) and for which species composition is at least partially structured by the interplay of colonization and selective local extinction (Lomolino, 1996; Worthen et al., 1998; Wright et al., 1998; Davidar et al., 2002; Mac Nally et al., 2002, Chase, 2003).

To date, no evaluation of meta-community interaction has been based on freshwater benthic meiofaunal communities. Such communities are very widespread in freshwater habitats of many kinds, including those physically connected by water courses that could serve as effective conduits for species migrations. Hence, meiofaunal communities are excellent systems to evaluate the applicability of meta-community theory. The current work assesses the significance of community connectivity for a series of meiofaunal communities numerically dominated by bdelloid rotifers associated with submerged mosses of a freshwater stream (Linhart et al., 2002a, b).

Bdelloids are small (<1000 μm) animals that live in close association with the substrate and which can move actively by swimming or 'creeping', or be passively transported downstream by drift (Schmid-Araya, 1998a, b; Bilton et al., 2001; Elliott, 2003). Bdelloids can withstand prolonged drought by entering dormancy and can be dispersed in the dormant state to colonize distant areas not directly connected by water (Cáceres & Soluk, 2002; cf. Jenkins & Underwood, 1998 and Bohonak & Jenkins, 2003). Moreover, their small size and low vagility allow study of different communities in a relatively small area. Restricting study to a local area in a single environment can minimize differences in species composition caused by extensive differences in environmental features, disturbance processes or geographic history. Because of these unique characteristics, bdelloid communities are a particularly useful field model for investigation of different meta-community structures.

Here we analyze a series of bdelloid rotifer communities from submerged mosses in pools in a short section of a mid-elevation stream. We propose the following alternative hypotheses: (1) if individual pool community structure is driven primarily by aerial colonization by dormant propagules from distant source communities (which should be rare and random events), inter-community comparisons should show stochastic meta-community structure; (2) if direct (i.e. aquatic) connectivity dominates over only occasional aerial colonization, nearby communities are expected to be more similar in species composition than more distant ones.

Material and methods

Study area

Moss samples were collected in June, July, and August 2003 along a 80 m long section of Rio Valnava (approx. coordinates: 4° 11′ E, 45° 39′ N). The sampling site was near Bercovei cave at an elevation of about 400 m, in the municipality of Sostegno, Biella province, Piedmont Region, NW Italy. The transect was characterized by a sequence of 10 pools, with low flow rate, linearly connected by segments of riffles, each with a higher flow rate. Each pool measured from 1 to 4 m^2 (Table 1) with shoreline edges almost fully covered with submerged mosses; mosses were absent in the riffle segments. Distance between any two adjacent pools varied from 3 to 20 m. Except for this section of 10 pools, mosses were not observed along the stream.

Temperature was about 16 °C, pH around 7 and the rocky substratum at all sampled sites was made of limestone. Moss species was the same too (*Brachythecium* sp.). Macrobenthos or other biotic components at the different sites were not investigated, and we assumed that their effect on bdelloids could have been equal throughout the different sampling sites, due to the high vagility of macrobenthos at the scale of the length of the analyzed transect (Bilton et al., 2001).

We considered 10 continuous pools (called, from upstream to downstream, A–J), and we designed a cumulative spatial analysis at three different nested levels. The first level is for the individual moss sample (local level; single community), the second level is for each pool (intermediate level; 10 communities, one from each moss sample), and the third level is at the stream level (largest level; 10 communities, one from each pool). This spatially nested design should have allowed us to detect hierarchical differences in the structure of the meta-communities at different spatial scales.

Sampling

Each sample of moss had a surface area of 5 cm^2. Samples were kept in small plastic bottles and were directly taken to the laboratory, where they were maintained at 6 °C to keep the animals alive. As soon as possible, but in no case longer than 3 days, living bdelloids were isolated and identified from each sample.

Statistical analyses

The meta-community analysis performed on the data followed Leibold & Mikkelson (2002). This analysis deals with presence of species and disregards the frequency of individuals. The data sets for each of the three scales analysis were arranged

Table 1. Number of sites, number of bdelloid species, and area of each analyzed matrix, with p-values from 200 simulated matrices, counting number of embedded absences for coherence and number of species replacements for nestedness, as described in Leibold & Mikkelson (2002)

Pool	Number of sites	Number of species	Area (m^2)	Coherence p values	Nestedness p values
A	10	9	1.5	*0.000*	0.054
B	10	9	1.0	*0.000*	*0.012*
C	10	7	2.0	*0.002*	*0.010*
D	10	7	1.8	*0.009*	*0.013*
E	10	7	3.0	*0.038*	0.052
F	10	10	2.2	*0.000*	*0.021*
G	10	9	4.0	*0.000*	*0.038*
H	10	8	3.0	*0.002*	0.050
I	10	7	1.2	*0.005*	0.082
J	10	9	3.8	*0.000*	*0.044*
System	10	15		*0.000*	0.696

Cells with '0.000' mean a lower value than '0.001'. Significant p values are in italics.

in ordered presence/absence matrices listing species in columns, and communities in rows. The ranking of rows and columns was obtained by reciprocal averaging (also known as correspondence analysis), so that communities (rows) with the closest lists of species were close each other, and species (columns) with the closest distributions were close each other.

We tested each matrix for coherence and for nestedness. A matrix of species distribution is considered to be coherent when the presences are arranged along the diagonal line of the matrix; coherence is the pre-requisite to detect nestedness (Leibold & Mikkelson, 2002). A pattern of species distribution is considered to be nested when the communities poorer in species are subsamples of the richest ones (Patterson & Atmar, 1986; Fisher & Lindenmayer, 2002).

Coherence was detected through the number of embedded absences in the matrix, while nestedness was detected through the number of absence/presence changes; that is, how many species are replaced in the sequence of communities. Each data set was tested by comparing the absences or replacements with those present in 200 matrices randomly generated by Monte Carlo simulations. Each generated matrix had 2 constraints: (1) the number of presences equal to that of the observed data matrix, and (2) no row or column empty.

First, we tested the nestedness of the whole meta-community of the 10 pools at the system level, and then the nestedness of each pool, at the intermediate level.

Results

At the stream level (largest level), a total of 15 species were identified. At this largest spatial level (10 pools), the meta-community described by the analysis had a coherent pattern of species distribution, but revealed a random spatial turnover of species (Table 1). No nested structure could be recognized (Fig. 1). The rank order of pools in the ordered matrix (Fig. 1) was not related to the downstream position of pools in the field (Spearman $r = 0.563$, n.s.), indicating that close pools were not more similar than distant pools. Mean number of species per pool was 8.2 ± 1.13 (SD), with no significant difference between communities in the downstream position in the field (Spearman $r = 0.061$, n.s.). The number of species present in each pool was independent from the area of the pool (Spearman $r = 0.23$, n.s.).

The analysis at the intermediate level revealed that the species in the 10 meta-communities from each of the 10 pools were distributed non-randomly. Significant values of nestedness were evident. Communities of A, E and H pools were slightly nested (p-value ~ 0.05), and p value for I pool resulted a bit higher than this level. (Table 1),

Philodina rugosa Bryce, 1903	*Pleuretra brycei* (Weber, 1898)	*Habrotrocha bidens* (Gosse, 1851)	*Habrotrocha constricta* (Dujardin, 1841)	*Habrotrocha pulchra* (Murray, 1905)	*Adineta vaga minor* Bryce, 1893	*Habrotrocha gracilis* Montet, 1915	*Philodina flaviceps* Bryce, 1906	*Philodina plena* (Bryce, 1894)	*Rotaria rotatoria* (Pallas, 1766)	*Philodina acuticornis odiosa* Milne, 1916	*Embata hamata* (Murray, 1906)	*Philodina vorax* (Janson, 1893)	*Macrotrachela quadricornifera* Milne, 1886	*Philodina* sp.	pool
▨	▨	▨	▨		▨	▨	▨	▨							H
▨	▨	▨	▨	▨	▨	▨	▨	▨							J
		▨	▨	▨	▨	▨	▨	▨	▨	▨					G
		▨	▨	▨	▨	▨	▨	▨	▨		▨				B
		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨				F
				▨	▨	▨	▨	▨			▨	▨			D
					▨	▨	▨	▨	▨	▨		▨			C or E or I
					▨	▨	▨	▨	▨	▨		▨			C or E or I
					▨	▨	▨	▨	▨	▨		▨			C or E or I
				▨	▨	▨	▨	▨			▨	▨	▨	▨	A

Figure 1. Bdelloid species presence in 10 analyzed pools in the ordered matrix. Communities are ordered in rows and species in columns.

but these values could be due to the low number of cells of our matrices. Nevertheless, all matrices resulting from ordination were typically nested (Fig. 2), except matrix from C pool.

At the local level, the average number of species per sample was 5.7 ± 1.56, without significant differences between pools (ANOVA test: $F_{9,90} = 1.602$, $p = 0.127$).

Discussion

The 15 species found along the stream were not equally present in the 10 pools, and so obviously not all present in the 10 moss samples for each pool. On average 8 species were present in each pool, and adjacent pools did not show same species assemblages. In three cases the pools had the same species, but these pools were not directly connected. Bdelloid rotifers can actively move on the river bed and be spread downstream by drift. Thus the similarity between the pools could be due either to chance or to sampling bias. Thus, and although bdelloid species were apparently randomly distributed, a species structure of the communities along the stream was revealed by application of meta-community analysis.

The analysis run at different scale levels showed that the structure of the bdelloid meta-communities changes according to the scale of investigation, with stochastic distribution at the largest level and nestedness at the intermediate level. At the largest level, each pool could be recognized as a separate system, sharing only few species with other pools. Passive dispersal of bdelloids by wind or rain is possible, and this process should be independent of the connectivity between pools. If this were the case, all pools should present the same composition in species. In contrast, we found a random spatial substitution of species. This could be explained hypothesizing that new invaders could be precluded from successful colonization of a given area by the already established community

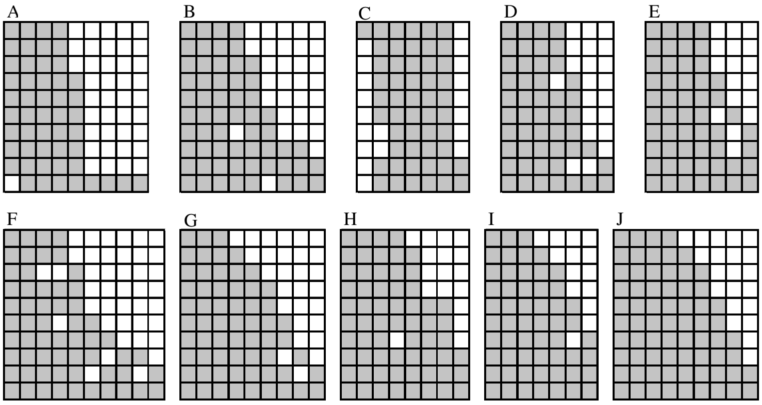

Figure 2. Reciprocal averaging ordered matrices with data from the 10 communities in each pool. Communities are ordered in rows and species in columns.

(Shurin, 2000; Rundle et al., 2002). And a strong priority effect of early founders may drive the species assemblages of the pools to differ. As founder effect may be rare and random, the meta-community structure was random, as well (De Meester et al., 2002).

In contrast, at intermediate level, all pools revealed nested structures. Nestedness could be produced by (1) differential colonization (Loo et al., 2002), or (2) sampling artifact (Cutler, 1994; Fischer & Lindenmayer, 2002). In both cases, some species should be present in every sample from a same pool, while others should be present only in the richest communities. In our system this pattern could be related to different motility. Locally rare species in each pool system were *Embata hamata* and *Rotaria rotatoria*, that are those species that can move more easily by swimming. More common within each pool were the species that move mainly by inching or creeping on the bottom, such as *Adineta* and *Habrotrocha*. In the attempt of relating different locomotory behavior to colonization capability, we could have expected that the swimming species should have been the most widespread inside each pool, while the opposite was found. If swimming of bdelloids is not related to their colonization capability, as seems to be the case from our results, active colonization should be expected through water beds, only.

As noted earlier, we considered two alternative hypotheses, one predicting dominance of colonization by passive dispersal, and the other predicting the structuring influence of active animal movements. In the former case the meta-community would show a random character, and in the latter a statistically significant structure. The hypotheses seem to fit the observed meta-communities if the analysis is run at the largest level or at the intermediate level, respectively.

The meta-community approach for the study of benthic meiofauna evidences patterns and provides interpretation for species distribution that could not be approached through other ecological analysis. Although this study was carried out along a small stream section, 80 m long, the number of species for the three different levels of analysis increased (single moss sample = 5.7, pools = 8.2, stream = 15), analogously to the general feature of scale-dependent diversity found in community ecology at larger geographical scales (Shorrocks & Sevenster, 1995; Cornell, 1999; Lawton, 1999; Gaston, 2000; Arita & Rodriguez, 2002). The characteristics of poor vagility, colonization capability, widespread distribution and minute size make bdelloid rotifer a well suited organism model for these analyses.

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