



# The role of metacommunity processes in shaping invertebrate rock pool communities along a dispersal gradient

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Explaining the variance of local communities in a spatial-environmental matrix is one of the core interests of ecology today. Recent progress in metacommunity theory has made a substantial contribution to this field, however good empirical data in support of available theories are still relatively scarce. In this study we sampled a cluster of 36 temporary rock pools four times during one season to assess invertebrate metacommunity structure and dynamics and to search for steering processes and variables. Both Mantel tests and redundancy models indicate that local abiotic factors were dominant over spatial factors in explaining community structure and both were acting independently. Spatial variables were only important for passive dispersers and significantly explained 11% of variation in this community component. Pools connected by temporary overflows hosted more similar communities of passive dispersers than unconnected ones while community dissimilarity significantly increased with inter-pool distance. A negative curvilinear relation was discovered between taxon richness and isolation in passive dispersers, providing some support for existing theoretical models of Mouquet and Loreau. Of different metacommunity perspectives, a combination of species sorting and mass effects best explains the observed patterns. Additionally, priority effects and monopolization may buffer against the homogenising effects of dispersal and contribute to the distinctness of isolated communities. This is one of the first studies to present evidence for spatial patterns in aquatic communities on such a small spatial scale (a rock ledge of  $\pm 9000 \text{ m}^2$ ). Bridging the gap between theory and observed patterns in natural systems is one of the main challenges for future metacommunity research. Small aquatic habitats such as pitcher plants and freshwater rock pools may well have an important role to play as model systems to study ecological processes in a natural spatially explicit environment.

Community structure and  $\alpha$  diversity are largely determined by the interplay of local processes (e.g. competition, predation, parasitism, abiotic environment) and interactions with the landscape and the regional species pool (dispersal, migration) (Ricklefs 1987, Cornell and Lawton 1992). The relative importance and interaction between local and regional processes is the subject of considerable debate (Shurin 2001, Rajaniemi et al. 2006). The importance of the spatial context, such as isolation and connectivity of different habitat patches, is a recurring theme in ecology. First recognized in island biogeography (MacArthur and Wilson 1967), it gave rise to both classic (Levins 1970) and modern, spatially realistic, metapopulation theory (Hanski 2001, Hanski and Gaggiotti 2004). The meta-view developed for populations has recently also found its way into community ecology. Communities linked by dispersal are consequently defined as metacommunities (Gilpin and Hanski 1991, Wilson 1992). Four perspectives dominate metacommunity thinking today, differing in the assumption whether migration is high enough to alter local population abundances and whether patches are homogeneous or not (reviewed by Leibold and Miller 2004, Holyoak et al. 2005). The patch dynamics view focuses on the importance of local, within patch, dynamics, assuming that dispersal rates are low and patches are homogenous. The species sorting view

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emphasizes the importance of local environmental factors, assuming that with sufficient dispersal, species will be “sorted” among different patches, using the local environment as a filter. Mass effects (Holt 1993, Mouquet and Loreau 2002) only come into play when dispersal rates are high enough to change population abundances. Finally, Hubbell (2001) proposed a neutral model, assuming no differences between environments or species. A synthesis for these views is still lacking (Leibold and Miller 2004) although some elements of synthesis have recently been developed by Leibold et al. (2004).

Knowledge of dispersal strategies and rates in plants and animals is essential to understand species distribution and coexistence patterns. Aquatic invertebrates have developed a diverse array of dispersal strategies. While many adult aquatic insects can disperse actively, most zooplankton species are able to colonise new water bodies very quickly, solely relying on passive dispersal (Louette and De Meester 2005). Connecting waterways between lentic systems can act as important dispersal pathways; illustrated by Michels et al. (2001) for zooplankton and by Van de Meutter et al. (2006) for macroinvertebrates. Cottenie et al. (2003) showed that in this system of highly connected ponds (scale 1 km<sup>2</sup>), local environmental factors were structuring the zooplankton communities despite high dispersal rates, providing support for the species sorting view. Different experimental studies also subscribe the importance of wind as a main vector mediating stochastic dispersal events (Cáceres and Soluk 2002, Cohen and Shurin 2003), however few researchers have tried to measure it in a straightforward way (but see Jenkins and Underwood 1998, Brendonck and Riddoch 1999). Adults, eggs or resting stages of aquatic invertebrates sometimes also hitchhike with other animals: e.g. zooplankton with waterfowl (reviewed by Green and Figuerola 2005), fairy shrimps with salamanders (Bohonak and Whiteman 1999) and aquatic mites with flying insects (Bilton et al. 2001).

Despite presumed high dispersal capacity, zooplankton species are sometimes absent from otherwise suitable pools (Jenkins and Buikema 1998, Cáceres and Soluk 2002, Cohen and Shurin 2003). Jenkins and Buikema (1998) suggested that this can be explained by dispersal limitation, or by biological barriers set up by local communities against invaders. Havel and Shurin (2004) proposed that isolation at a scale < 60 m might place few limits on zooplankton dispersal. This view is supported by invisibility experiments in artificial pools by Cohen and Shurin (2003) and by Spencer et al. (2002) who studied rock pools on a spatial scale of 40 × 20 m.

Boileau et al. (1992) argued that the paradox between high dispersal abilities in zooplankton and limited gene flow as presented in many studies

(reviewed by De Meester 1996), could be explained by persistent founder effects. This idea was extended to communities by De Meester et al. (2002) as the Monopolization hypothesis, suggesting that a limited group of colonizing founder species can resist subsequent invaders because of competitive superiority. They propose that the underlying reasons of this competitive advantage are rapid local adaptation, a fast population growth and establishment of a buffering resting propagule bank. Shurin (2000) already showed experimentally that local interactions inhibited settlement of invasive zooplankton species and claimed that dispersal played a minor role in structuring zooplankton communities in the studied ponds.

Small temporary pools have great potential as field laboratories since they are often small and locally numerous providing easy manipulation and statistical power, respectively (Blaustein and Schwartz 2001). They also usually show a gradient in several important environmental variables allowing the study of various ecological processes (Spencer et al. 2002). In this study, we investigate the invertebrate communities in a cluster of 36 temporary freshwater rock pools in South Africa, sampled on four occasions throughout one rainy season. We evaluate the importance of different metacommunity processes influencing invertebrate community structure on a small spatial scale. We also explore whether any spatial community patterns can be attributed to spatial barriers (dispersal limitation) or to local environmental conditions. Furthermore we evaluate the importance of temporary overflows by testing whether connected pools are more similar than isolated ones. Finally we check whether different patterns occur for passive vs active dispersers.

## Material and methods

### Study site

The study site consists of 36 rock pools, situated on a rock shelf on the northwestern plateau at the top of the Korannaberg mountain (28°51'13''S, 27°13'51''E) in the eastern Free State Province of South Africa (Fig. 1). The site comprises an area of approximately 9000 m<sup>2</sup>. The region lies within a predominantly summer rainfall area with an annual precipitation between 600 and 800 mm. The mountain represents an isolated part of the Drakensberg range (Irwin and Irwin 1992) but differs from it in not being basalt capped. It consists of a northwestern and a southeastern plateau, situated at about 1700 m a.s.l. (highest point: 1881 m). It comprises various geological formations. The youngest (Clarence) formation tends to form calcareous concretions from trapped organic matter. Once these concretions are exposed, they weather faster than the

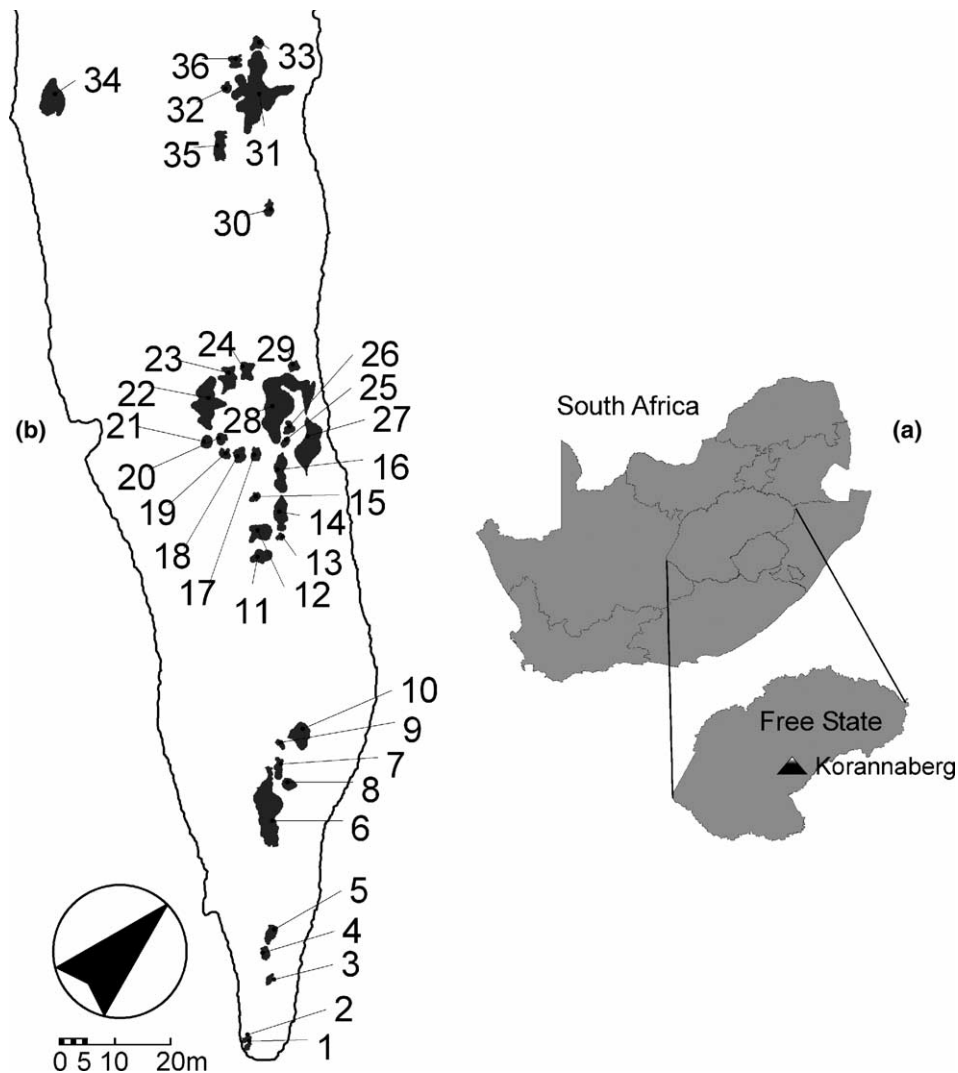


Fig. 1. (a) Location of the Korannaberg mountain in South Africa and (b) the lay out of the different rock pools on the study site.

surrounding sandstone, leaving depressions. Rainwater accumulating in these depressions causes the sandstone quartz to slowly dissolve, resulting in flat bottomed pools with almost vertical sides. Eroded channels occur between ten pool pairs (6–7, 13–14, 15–14, 16–14, 17–18, 18–19, 19–28, 23–24, 27–28, 31–32) which mediate the transport of water between pools when some of these overflow after heavy rains. These relations are mainly asymmetric however exceptionally a temporary symmetric connection can occur between pools 27–28 and 31–32 when both interacting pools are filled. Based on rainfall data and field observations we estimate that these overflow events occur relatively frequent: 8–14 times a year except for a number of deeper pools (e.g. 16 and 31) which do not overflow every year.

### Sampling design

Our study took place during the 1993–94 rainy season following a dry winter and covered a period of 32 weeks (223 days). All pools dried up during winter and filled simultaneously after the first summer rains. In order to integrate seasonal variation in the description of community structure, all pools were sampled at four dates, respectively 12, 37, 96 and 140 days after initial inundation. All zooplankton samples were quantitative and were taken with a funnel-shaped zooplankton net with a maximum diameter of 85 mm. All microhabitats were traversed in order to obtain a representative composite sample for each pool. Sampling time was relative to pool size; therefore sampling effort was comparable in all pools. Samples were fixed first with

neutralized formalin which was replaced with 70% ethanol in the laboratory. All species of which adult individuals were larger than ca 1 mm were counted at a 20× magnification with a dissection microscope. For smaller taxa, six randomly chosen 5 mm rows in a 10×10 cm counting tray were counted at 40× magnification. More rows were counted when a minimum number of 100 individuals was not reached. These counts represented 30% of the total sample. The number of organisms counted was then multiplied by 3.3 to obtain an estimate of the total number of individuals in the sample. With the exception of representatives of the Rotifera, Protoctista, Bryozoa and Collembola, all aquatic invertebrates were included in this study. Anostraca, Spinicaudata, Cladocera, Ostracoda, Mollusca and most copepods were identified down to species level, with the exceptions of *Bryocamptus* sp., Cyclopoida spp., and Harpacticoida spp. Ephemeroptera, Hemiptera, Tardigrada and Diptera were identified to genus level, with the exception of the taxa Tipulidae (family) and Diptera sp. (order). Coleoptera and Odonata were identified to family level. We decided to include informal taxa in our analysis in order to maximise the resolution of identification. For Turbellaria two taxa: A and B were distinguished on the basis of size and epidermis characteristics. Turbellaria A was the smaller of the two species. The taxa Nematoda A and B were distinguished on the basis of size. Nematoda A was the smaller of the two forms. Within aquatic mites (Hydracarina) we distinguished the species *Aquanothrus montanus*, Caeculidae and the informal taxa Prostigmata A and B. A distinction was made between passive and active dispersers in our analyses. Strictly active dispersers do not exist as such species can usually also disperse passively, for instance through connecting channels. In this study all organisms with the potential to disperse actively were indicated as “active dispersers”. Hydrochoric dispersal through channels was hereby regarded as passive dispersal. Problematic aquatic mites were excluded since they can get dispersed passively during the parasitic nymph stage by aquatic insects (Bohonak 1999). Their adult distribution can therefore be ‘biased’ by the habitat preferences of the actively dispersing hosts. The gastropod *Bulinus tropicus* was also excluded. It dominantly is a passive disperser, but can migrate overland during rains (Kerney 1999). A total of 20 passively dispersing taxa and 15 actively dispersing taxa were included in our analyses.

## Environmental variables

Conductivity, pH, water temperature and oxygen content were measured at noon on 16 occasions (5–13, 20, 30, 37, 44, 96, 140 and 223 days after initial

inundation), including the four sampling dates. Missing data were due to the dry state of some pools on some occasions. We initially included both extreme values (minima and maxima) and means in our analysis. However, in practice, only extremes were used because when both variable types were included in our analyses together only the extreme values remained significant, indicating that they may be ecologically more relevant in explaining species occurrence. Correlated environmental variables were not analysed together, avoiding problems of multicollinearity. General habitat and morphometric variables included the sediment content, extent of riparian vegetation and cover by aquatic macrophytes, pool area and maximum depth. The area of each pool was calculated by first drawing each pool to scale and next determining total area with a digital planimeter. Surface readings were LOG transformed prior to analysis. The extent of each of the aquatic macrophyte species (*Isoetes transvaalensis*, *Limosella grandiflora* and *Lindernia conferta*) was rated on the pool area covered. Maximum depth was measured to the nearest 5 mm using a measuring rod. The coverage of the substrate by sediment (Sed) was quantified using a 10 point scale. The riparian influence (Rip) was quantified as the percentage perimeter occupied by vegetation. We used maximum pool depth as an estimator for habitat duration. Predation pressure was estimated as the relative abundance of invertebrate predators (rel ab predators). Two spatial variables were included: pool isolation and connectedness. Pool isolation (Iso) was defined as the average distance to another pool in the cluster (sum of all the nearest edge to edge distances to all the other pools divided by the number of other pools = 35). Connectedness (Con) was quantified as the sum of all overflows arriving at and departing from the pool in question (i.e. number of connecting elements).

## Data analysis

### Redundancy models

All analyses were based on absolute species-abundance data, which were LOG transformed to increase the importance of rare species. Similar results not included in this paper were obtained with presence–absence type of data. In order to assess the importance of spatial context on community structure we used a multivariate approach and applied permutation tests (999 permutations) on redundancy analysis (RDA) models. We opted for RDA rather than canonical correspondence analysis (CCA) since previous detrended canonical correspondence analysis (DCCA) indicated a dominance of linear, rather than unimodal gradients (length of gradients < 0.25). We used a forward selection procedure on the full set of explanatory variables to construct a model for invertebrate community structure. Only significant explaining variables were retained

in the model. Using variation partitioning (Borcard et al. 1992) we compared the amount of variation that was either explained unique or in common by the spatial and environmental variation components. When testing unique effects of space, all environmental variables were used as covariables and vice versa. All RDA analyses were carried out in Canoco for Windows 4.5 (Ter Braak and Šmilauer 1998).

To test whether the relative importance of local versus regional factors differed for organisms with different dispersal strategies, we performed similar tests on actively and passively dispersing species, respectively.

### **Mantel tests**

We used the Bray-Curtis dissimilarity index (Legendre and Legendre 1998) to reconstruct the community dissimilarity matrix  $C_d$ . The spatial configuration of the pools was integrated in a distance matrix  $D$  which was constructed using nearest edge to edge distances between each possible pair of pools. This distance measure was deemed relevant in terms of dispersal pathways. To investigate the effect of connecting channels that occurred between 11 pool couples, we constructed two additional matrices. To check whether connections correspond with more effective dispersal we constructed a corrected distance matrix  $D_c$  where nearest-edge-to-edge distances between connected pools were reduced by assumingly realistic correction factors 2, 4, 5 and 10, which all gave similar results. To test whether connected pools were more similar than unconnected ones, couples of directly and not directly connected pools were respectively given values of 1 and 0 in a connected neighbour matrix  $C_n$  (Cottenie et al. 2003). Finally an environmental distance matrix  $E$  was created using normalised Euclidian distances based on variables with presumed ecological relevance: surface, max depth, min and max pH, max conductivity, min  $O_2$  ( $\text{mg l}^{-1}$ ), vegetation cover, sediment cover and riparian influence. All variables were standardised and surface was LOG transformed. Correlated variables were discarded. The relationships between spatial, environmental and community dissimilarity matrices were analysed using Mantel tests (Mantel 1967). Null model partial Mantel tests (Legendre 2000) were conducted in order to control a third matrix while investigating the relationship between the two others with the freeware Mantel function `mantel.fcn` (J. H. Reynolds and B. Bolker, URL: <http://www.bio.stat.wustl.edu/maillinglists/s-news/200103/msg00154.html>) in S-Plus (Anonymous 1999). Significance of Mantel correlations was computed through permutation (20 000 times). Variance partitioning was not applied on distance matrices since variance in community dissimilarities can not be interpreted the same way

as variance in community composition (Legendre et al. 2005).

Besides whole-community analyses, we have also investigated these relationships separately for active and exclusively passive dispersing species. Results of partial Mantel tests were visualised using a path analysis procedure where partial Mantel coefficients were used as path coefficients (Leduc et al. 1992). Only significant relations were visualised in the diagrams.

### **Diversity patterns**

We investigated the relationship between local diversity and pool isolation using regression models. Besides taxon richness we used the Berger Parker dominance index (Berger and Parker 1970) as a simple measure of heterogeneity.

## **Results**

### **Local vs regional (spatial) factors**

Overall, there was a significant effect of both environment and spatial configuration on invertebrate community structure, with variance partitioning revealing the significant contribution of local ( $\sim 48\%$ ) and regional factors ( $\sim 11\%$ ) to the total variance (Table 1, Fig. 2). The regional (spatial) component significantly explained 11.4% of the variation in the passively dispersing community component ( $p = 0.031$ ;  $p = 0.002$  after correction for environment). In the actively dispersing community component, spatial variables were not ( $p = 0.171$ ) or marginally significant ( $p = 0.047$  after correction for environment) in explaining variation.

### **Spatial patterns in community dissimilarities**

We found strong and highly significant correlations between community dissimilarity and geographical distance ( $D$ ) ( $\sim 40\%$ ) and between community dissimilarity ( $C_d$ ) and environmental distances ( $E$ ) ( $\sim 50\%$ ) (Table 2, Fig. 3a), respectively (Table 2, Fig. 3b). Both correlations were independent of each other since  $E$  and  $D$  were not significantly correlated (Table 2) and correction for  $E$  had very little influence on the level of significance of the relationship between  $C_d$  and  $D$ . The nature of this correlation was typical for the passive dispersers ( $\sim 40\%$ ), even after correction for  $E$ . This was not the case for the actively dispersing community component, where significance of the  $C_d \times D$  correlation was lost after correction for  $E$  (Table 2). Results of the partial Mantel analysis are schematically represented in the form of path diagrams for both active and passive

Table 1. Variance partitioning of the three invertebrate datamatrices (all taxa, passive dispersers, active dispersers) with corresponding p values. Symbols are analogous to Cottenie et al. (2003). [E+S] = total explained variation by all variables in the model, [E] = variation explained by environmental variables, [S] = variation explained by spatial variables, [E−S] = pure environmental variation, [S−E] = pure spatial variation, [E∩S] = variation shared by environmental and spatial variables and 1−[E+S] = unexplained variation.

	All invertebrate taxa		Passive dispersers		Active dispersers	
	Var. explained (%)	p	Var. explained (%)	p	Var. explained (%)	p
[E+S]	56.8	0.001	58.4	0.001	42.6	0.001
[E]	48.4	0.001	49.3	0.001	38.4	0.001
[S]	10.5	0.034	11.4	0.031	4.3	0.171
[E−S]	46.3	0.001	47.1	0.001	38.3	0.001
[S−E]	8.4	0.001	9.1	0.002	4.2	0.047
[EnS]	2.1		2.2		0.001	
1−[E+S]	43.2		41.6		57.4	

dispersers respectively (Fig. 5). Non significant arrows were excluded. The diagrams show that both active and passive dispersers are influenced by environment while space is only important for passive dispersers.

### Spatial patterns in local diversity

A curvilinear relation was found between local taxon richness and pool isolation (Fig. 6a) (polynomial regression: multiple  $r^2=0.21$ ;  $p=0.02$ ). Significant terms in the model included a negative linear ( $p=0.03$ ) and quadratic effect ( $p=0.02$ ). The same relationship was found for the richness of passive dispersers (polynomial regression: multiple  $r^2=0.22$ ;  $p=0.015$ ):

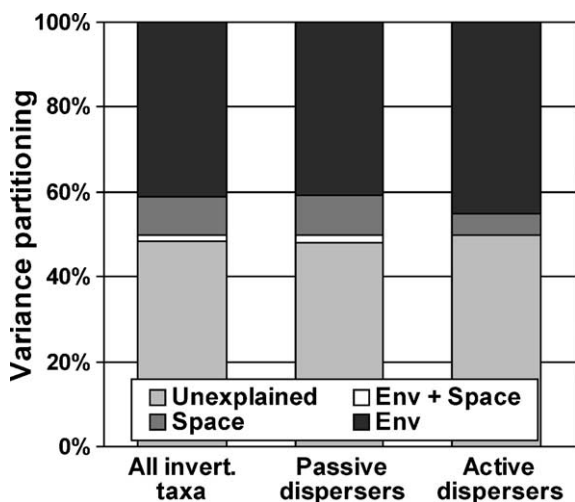


Fig. 2. Variation partitioning (Borcard et al. 1992) of the entire invertebrate datamatrix and of two reduced datamatrices containing passive and active dispersers, respectively (Methods). All three RDA-models were obtained using a forward selection procedure. Four components are distinguished: unexplained variation, pure spatial variance (connectedness and isolation), pure environmental variance and the variance component that is shared by both.

both the linear- ( $p=0.04$ ) and quadratic term ( $p=0.02$ ) were significant. No significant relationship was found between isolation and richness of active dispersers. Berger Parker dominance for the entire community significantly increased with pool isolation (Fig. 6b), (multiple  $r^2=0.18$ ;  $p=0.03$ ). The same pattern emerges for the passive dispersers alone (multiple  $r^2=0.18$ ;  $p=0.009$ ), but not for the actively dispersing community component.

### The importance of connections

Overall, invertebrate communities of connected pools were not more similar than those of unconnected pools (Mantel test,  $r_M = -0.063$ ,  $p=0.06$ ). After correction for environmental differences between interacting pools, this relationship was still not significant (partial Mantel test,  $r_M = -0.06$ ,  $p=0.06$ ). Only for passive dispersers we found a significant effect of connections (Mantel test,  $r_M = -0.070$ ,  $p=0.04$ ), which was marginally significant after correction for environmental differences (partial Mantel test,  $r_M = -0.064$ ,  $p=0.05$ ) (Fig. 4).

Increasing the importance of connections in the distance matrix by downweighing distances between connected pools by different correction factors (2, 4, 5, 10) in a corrected distance matrix  $D_c$ , did not result in a better correlation with the community dissimilarity matrix  $C_d$  (Table 2). The values for  $D_c$  given in Table 2 were calculated with a correction factor of 4. Similar patterns were obtained when applying the other correction factors.

### Discussion

Both local and regional processes played an important role in structuring the invertebrate communities in a cluster of 36 temporary rock pools. Environmental variables explained more variation in community

Table 2. Mantel and partial Mantel correlation coefficients ( $r_M$ ) between spatial distance  $D$ , corrected spatial distance  $D_c$ , environmental distance  $E$  and community dissimilarity  $C_d$  matrices among 36 rock pools. Community dissimilarity matrices were calculated separately for passively and actively dispersing species, respectively.  $p$  values were obtained through permutation (20 000 times). corr. indicates the matrix that was corrected for in partial Mantel tests.

All invertebrates			Passive dispersers			Active dispersers					
Simple Mantel tests			Simple Mantel tests			Simple Mantel tests					
	$r_M$	$p$		$r_M$	$p$		$r_M$	$p$			
$C_d \times D$	0.39	0.0002	$C_d \times D$	0.42	0.0001	$C_d \times D$	0.15	0.0378			
$C_d \times D_c$	0.39	0.0002	$C_d \times D_c$	0.42	0.0002	$C_d \times D_c$	0.15	0.0361			
$C_d \times E$	0.52	0.0003	$C_d \times E$	0.51	0.0003	$C_d \times E$	0.23	0.0141			
$D \times E$	0.15	0.0590									
Partial Mantel tests			Partial Mantel tests			Partial Mantel tests					
	$r_M$	$p$	corr.	$r_M$	$p$	corr.	$r_M$	$p$	corr.		
$C_d \times D$	0.35	0.0002	E	$C_d \times D$	0.38	0.0003	E	$C_d \times D$	0.11	0.0902	E
$C_d \times D_c$	0.35	0.0001	E	$C_d \times D_c$	0.38	0.0001	E	$C_d \times D_c$	0.11	0.0891	E
$C_d \times E$	0.49	0.0001	D	$C_d \times E$	0.48	0.0002	D	$C_d \times E$	0.21	0.0213	D

structure and were more strongly correlated with community dissimilarity than spatial variables (isolation and connectivity), suggesting that local abiotic factors were dominant over regional (spatial) ones. A similar conclusion was drawn by Pinel-Alloul et al. (1995) using a similar approach in lakes and by Cottenie et al. (2003) in connected ponds. As water chemistry data were limited, it is likely that the importance of local factors is still underestimated in our study.

Communities in pools that experience temporary connections through eroded channels were more similar than those in unconnected pools. This is not surprising as high dispersal rates (up to 1000 individuals per overflow in one single rainfall event) were measured in a similar system in Botswana by Hulsmans et al. (2007). In a similar study on highly interconnected permanent ponds, Cottenie et al. (2003) likely showed that direct

connections between water bodies had a homogenising effect on zooplankton community structure. The relationship in our study however only occurred in passive dispersers and was still only marginally significant. This rather weak relationship can be attributed to the fact that, in contrast to the study by Cottenie et al. (2003), overflows are only effective during a short period immediately after heavy rains, resulting in a lower number of dispersing propagules.

Although local factors were dominant, the spatial context can not be overlooked as suggested by the significant positive correlation between nearest edge to edge distances and community dissimilarity. This spatial variable represents the minimum length of dispersal pathways between pools. Havel and Shurin (2004) suggested that distances of less than 60 m should place few limits to zooplankton dispersal. Our results

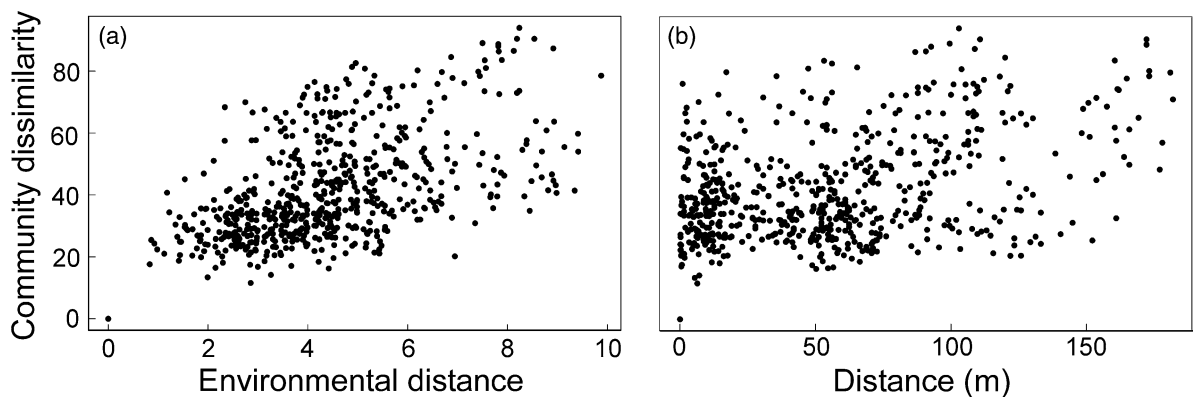


Fig. 3. Relationships between the community dissimilarity matrix  $C_d$  (Bray–Curtis dissimilarities), environmental distance matrix  $E$  (normalized Euclidean distances) and distance matrix  $D$  (nearest edge to edge distance), respectively. Each dot represents the relationship between 2 of the 36 pools and visualizes the relationship between two different distances (environmental distance, spatial distance or community dissimilarity) between the considered pools: (a) =  $C_d \times E$ , (b) =  $C_d \times D$ .

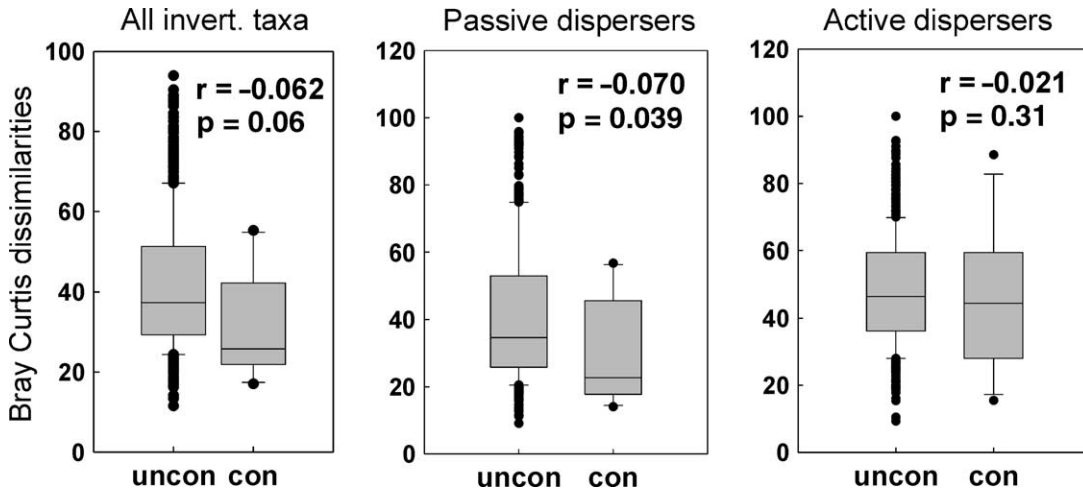


Fig. 4. Boxplots of Bray–Curtis dissimilarities in invertebrate community structure in directly connected (con) and not directly connected (uncon) rock pools. Boxes represent interquartile range; central bar represents the median, dots are outliers ( $> 1.5 \times$  interquartile range);  $r$  = Mantel correlation coefficient and corresponding  $p$  value (20 000 permutations).

on passive dispersers confirm this hypothesis as communities separated by distances of less than 60 m were indeed very similar, while communities got more dissimilar with increasing inter pool-distance (Fig. 3b). This relationship was not significant for actively dispersing taxa where local factors were the main structuring variables. This indifference of most active dispersers to spatial variables was expected due to the

small spatial scale of our study site and since all active dispersers were aquatic insects with flying adult stages that have to re-colonise pools at the beginning of each hydrocycle. The distance to the closest permanent source for recolonisation of the rock pools, is much larger than the spatial dimensions of the studied pool cluster, suggesting that inter-pool distances cannot form spatial barriers.

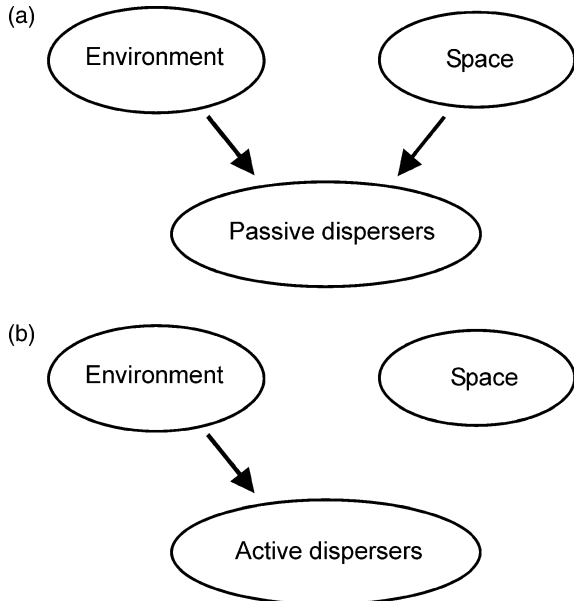


Fig. 5. Path diagrams derived from partial Mantel tests performed on distance matrices, showing the relationships between space, environment and invertebrate communities for (a) passive dispersers and (b) active dispersers. Non significant arrows were excluded.

### Possible explanations for spatial patterns

#### *Spatial-environmental covariation*

Patterns of spatial variation in community structure are explained variably in literature. According to Spencer et al. (2002) nearby communities can be similar because the water bodies they inhabit are more likely to share similar environmental conditions. This could not be confirmed in our study as there was very little overlap in the variation ( $\sim 2\%$ ) commonly explained by spatial and environmental variation (Table 1). Moreover Mantel tests indicated that environmental and spatial distances were not significantly correlated (Table 2). Correction for environmental variation in our spatial analyses also had little or no effect on the results (Table 2).

#### *Physical barriers*

According to Jenkins and Buikema (1998), dissimilarities between pool communities can either be explained by spatial (dispersal limitation) or by biological barriers. Several short-term experimental studies confirmed that most zooplankton species are highly effective dispersers over short distances ( $< 60$  m) and that colonisation rates are species dependent (Cáceres and Soluk 2002, Cohen and Shurin 2004). However there is no consensus about whether dispersal of zooplankton is frequent or not on a



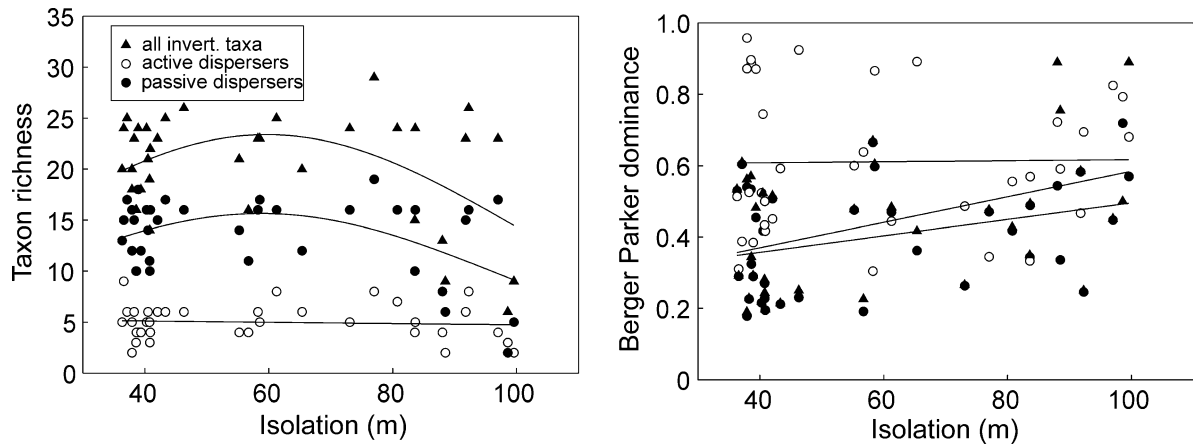


Fig. 6. (a) Local species richness and Berger Parker dominance (b) as a function of pool isolation for different sets of taxa: all invertebrate taxa (triangles), active dispersers (full circles) and passive dispersers (empty circles).

short timescale (De Meester et al. 2002, Bohonak and Jenkins 2003, Louette and De Meester 2005). Our observed spatial pattern of community dissimilarity increasing with spatial isolation intuitively suggests dispersal limitation. However, the combination of the small spatial scale (inter-pool distances ranging from 25 cm up to 168 m) and the ancient geological origin of the studied pools, promoted ample opportunity for dispersal mediated interaction and exchange of species between study pools. Additionally, estimates based on direct measurements of passive dispersal on our study site (wind, overflows and amphibian vectors) confirm that dispersal is frequent on a short timescale (Vanschoenwinkel et al., unpubl.). We therefore argue that all species had the potential to reach every pool on the site during this extensive time period; that inter pool distances are not effective as physical barriers over long time periods and that dispersal limitation alone is for that reason unlikely as an explanatory process.

### Biological barriers

Even when dispersal is most probably not limiting over a time span covering the age of the studied habitat patches, interspecific differences in dispersal abilities can be important during the initial build up of communities, as was proposed by Louette and De Meester (2005) on the basis of field observations in recently dug ponds and as was experimentally shown by Jenkins and Buikema (1998). Furthermore it was suggested that the initial group of colonists affects subsequent community assemblage and ultimately the current community composition through what is called priority effects (Levins and Culver 1971, Blaustein and Margalit 1996). Rapid local adaptation and the establishment of a stock of dormant propagules in the sediment can help initial communities to monopolize resources and to reduce establishment success of late arrivals (De Meester et al. 2002). Although

the Monopolization hypothesis was originally developed for populations, the same principles may well apply for interspecific interactions in a metacommunity context. Higher dissimilarity among and lower richness and higher Berger-Parker dominance in the isolated pools in our study may be indicative of such monopolization effects. Due to low dispersal pressure in isolated pools they are more likely to receive a smaller and less diverse group of fast dispersing initial colonists, which facilitated monopolization of available resources during community assemblage (De Meester et al. 2002) and to some extent freezing the initial spatial community differences.

Local richness was maximized at intermediate levels of isolation among the rock pools in study. This pattern corresponds with predictions of theoretical source-sink models by Mouquet and Loreau (2002) where richness is expected to be maximised at intermediate levels of dispersal. High dispersal rates between nearby pools can explain the high observed similarity among and lower richness in these systems. Temporary overflows can facilitate the mass influx of sufficient individuals or propagules to override the species sorting mechanisms by means of a spatial storage effect (Chesson 2000), resulting in the observed similarities especially among communities of passive dispersers in connected pools. Similarities between nearby pools that are not directly connected can be due to other dispersal vectors. Wind dispersal of dormant resting stages most likely provides the necessary propagule pressure to explain this homogenisation of nearby communities. Vanschoenwinkel et al. (unpubl.) measured the transport of high numbers of invertebrate resting stages on the study site by means of wind action using wind socks and sticky surfaces on the rocky substrate. The intensity of wind dispersal was furthermore related to the proximity of source populations.

## Evaluation of different metacommunity perspectives

Since both patches and species were highly heterogeneous, two main assumptions of the patch dynamics perspective are violated (Kolasa and Romanuk 2005) suggesting that this mechanism cannot satisfactorily explain our observed rockpool metacommunity pattern. Alternatively, the strong link between invertebrate communities and local abiotic conditions in our study and the fact that this relation is largely independent from spatial effects is not in concordance with neutral theory (Hubbell 2001, Chave 2004, McGill et al. 2006) but instead strongly supports a species sorting view (Cottenie 2005, Holyoak et al. 2005).

## General conclusion

Not one of the current theoretical metacommunity perspectives can satisfactorily explain the observed rock pool community patterns. Real metacommunities are therefore probably structured by a mixture of those processes as was also suggested by Leibold and Miller (2004). Although the studied rock pool metacommunity was dependent on the dispersal strategies of the considered species, species sorting definitely was the most important structuring process for both active and passive dispersers. However these processes could not entirely explain the full scope of patterns. When considering passive dispersers, for example, the relative importance of different metacommunity processes apparently changed along the dispersal gradient. Mass effects seemed to override the species sorting mechanism in pools with ample dispersal sources in their proximity. This facilitated community homogenisation through high dispersal and explained observed similarities between nearby communities. At intermediate levels of isolation, the strong link between communities and environment suggests that dispersal is sufficiently high to sort species using the local environment as a filter, but not high enough to maintain populations of species in suboptimal habitats through mass effects. Lastly, lower incoming dispersal in isolated pools may have increased the importance of priority effects and helped initial communities to monopolize resources, resist immigrants and stimulate community differentiation. The curvilinear relation between richness and isolation can likely be explained by the combined action of mass effects and monopolization effects on opposite sides of the dispersal gradient since both mentioned processes can promote competitive exclusion. It is probable that similar processes also operate along dispersal gradients in more complex spatially explicit habitats on larger scales such as ponds, lakes or patchy

terrestrial habitats in fragmented landscapes, where complicating factors are more likely to violate assumptions of theoretical models and distort observed patterns than in the simple environment of a rock pool cluster. As the need to link empirical data with causal mechanisms will be one of the largest challenges in future metacommunity research (Holyoak and Leibold 2005), a demand arises for suitable model systems. In that aspect natural microcosms (Srivastava et al. 2004) such as the freshwater rock pools in this study and so called phytotelmata (pitcher plants, bromeliads, tree holes) may have an important role to fulfil as an intermediate port between theory and the complexity of realistic macro-ecosystems.

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