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Species sorting in space and time—the impact of disturbance regime on community assembly in a temporary pool metacommunity

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Abstract. Ecosystems generally are not stable over long periods of time and are subject to disturbances of different frequencies and intensities. As a result, natural communities usually are not in equilibrium, and temporal snapshots can show different stages of community assembly. Nonequilibrium is especially common in temporary aquatic systems where desiccation continuously resets the development of communities and hydroperiod is an important determinant of species richness and community structure. We investigated effects of disturbance regime on community assembly of aquatic invertebrates in a cluster of 36 temporary rock pools in central South Africa. Pools were assigned to 4 categories based on their long-term disturbance regime and were sampled 4 times during 1 inundation. Disturbance modulated the relative importance of deterministic and stochastic processes driving community assembly and reduced both α and β diversity. Premature desiccation truncated community development. Initial communities were dominated by resident large branchiopods (fairy shrimp and clam shrimp). Arrival of flying colonists, including many predators, caused a drastic change in community composition and initiated a new successional phase dominated by cladocerans. For residents, the link between local environment and community structure was strongest early during inundation and decreased during community assembly. For flying colonists, variation in arrival time and habitat selection led to a better match between communities and environment later during inundation. We conclude that the combination of colonization–extinction dynamics and niche partitioning in space and time determines metacommunity structure in this extreme type of aquatic habitat.

Key words: community assembly, disturbance, succession, species replacement, temporal niche segregation, temporary pools, hydroperiod, hydroregime, large branchiopods.

Recent studies support the dominance of species-sorting processes (Leibold et al. 2004) as a main structuring agent in lentic freshwater communities (Cottenie 2005, Vanschoenwinkel et al. 2007, Waterkeyn et al. 2008). Local environmental conditions act as a filter, and dispersal acts as fuel (Cottenie and De Meester 2004). However, many freshwater invertebrates have dormant life stages, so recolonization of the habitat after disturbance events relies on recruitment from the regional species pool and from the local dormant species pool in the sediment. The presence of a reserve of dormant species and genotypes in situ has important consequences for the assembly of communities because it allows dispersal in space (Figuerola and Green 2002, Panov et al. 2004, Vanschoenwinkel et al. 2008) and in time (Warner and Chesson 1985, Mergeay et al. 2007). Local environmental conditions, including those that serve as hatching cues (Brendonck and De Meester 2003), determine whether dispersal is translated into species establishment. Despite significant interest in

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the importance of local and regional processes in shaping communities, surprisingly little attention has been devoted to the relative importance of these processes during community assembly and during different phases of succession.

Temporary aquatic habitats are characterized by drastic disturbance in the form of a recurring dry phase (Wellborn et al. 1996, Williams 2006). These habitats provide a convenient model system in which to study ecological and evolutionary processes in a simplified setting outside the laboratory because of their relatively small size, local abundance, and simple physicochemical environment. Recent development of accurate hydrological models for rock pools (Hulsmans et al. 2008, Vanschoenwinkel et al. 2009) has enabled researchers to reconstruct the inundation history (hydroregime) of temporary pools from historical climate data. These models provide an opportunity to link present communities to the long-term disturbance history of their respective habitats.

Temporary pond communities typically undergo changes during inundations. Depending on the hydroperiod and the study system, 2 or 3 successional phases usually can be distinguished (Lake et al. 1989, Boix et al. 2004). Lahr et al. (1999) distinguished 4 phases in a Sahelian rain pool. In general, communities are dominated initially by resident species recruited from the dormant propagule bank (temporal dispersal), and this phase is followed by a period of increasing importance of flying colonists (spatial dispersal) (Jocqué et al. 2007). Dispersal in both space and time contributes to community assembly in habitats with dormant propagule banks and provides the fuel for species-sorting processes. Local environmental conditions, including hatching cues (Brendonck and De Meester 2003), determine whether dispersal is translated into species establishment.

In previous research, we developed a hydrological model to assess the impact of hydroregime on community structure (Vanschoenwinkel et al. 2009) and evaluated the importance of different metacommunity paradigms (Vanschoenwinkel et al. 2007). Based on an integrated community data set, we concluded that species sorting was the dominant community structuring agent. In the present study, we expanded on these findings by integrating temporal community dynamics. We studied community assembly in a set of 36 temporary rock pools that differed in their long-term disturbance regime and sampled invertebrate communities 4 times during 1 inundation. First, we investigated the effect of disturbance on community assembly and local diversity patterns. We hypothesized that disturbance, by truncating community assembly, would act as a life-history-selective filter and reduce α diversity. Chase (2007) suggested that deterministic niche-based processes would be more important under harsh conditions. Therefore, we hypothesized that among-pool variation in community composition (β diversity) would decrease with increasing disturbance.

Next, we focused on the pools that remained inundated during the study period and evaluated the relative importance of niche-based processes during community assembly by quantifying the link between local environmental conditions and community composition at different moments during an inundation. We made a distinction between 2 main groups of temporary pool inhabitants with contrasting life-history and dispersal strategies. The 1st group consists of resident species that hatch from dormant life stages (resting eggs, cryptobiotic life stages) and are dependent on vectors (wind, water, animals) to disperse to other pools. The 2nd group is made up of actively dispersing flying colonists, which do not possess dormant life stages and must recolonize the pools with inundation. We expected the match between community composition of residents and local environment to decrease during inundations because of stochastic factors and source–sink dynamics caused by passive dispersers carried to pools via overflowing water. We expected variation in dispersal capacity, arrival time, and longer generation times of flying colonists to lead to a time lag and a better match between community composition and local environmental conditions later during inundations.

Last, we focused on the subset of pools that remained wet throughout the season to explore possible successional phases and to test the hypothesis that changes in predation regime during long inundations would cause temporal niche segregation and replacement of predation-sensitive by predation-tolerant taxa later during inundations (predicted by Spencer et al. 1999).

Methods

Study site

Our study site consisted of a cluster of 36 temporary rock pools (area: 0.6–50 m^2) at the summit of the Korannaberg Mountain (Free State Province, South Africa; lat 28°51′13″S, long 27°13′51″E). Pools usually fill at the start of the rainy season (October–November), periodically hold water during the season, and dry during the winter months (June–August). The largest pools can hold water >1 y, but these events are exceptional. A more detailed description of the study site, its geology, and the invertebrate communities can be found in Vanschoenwinkel et al. (2007, 2008).

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TABLE 1. Overview of differences in disturbance regime (E = ephemeral, S = short-lived, M = medium long-lived, L = long-lived pools) based on long-term hydrological variation (85 y).

	Hydroperiod (d)			Desiccation frequency (no. of dryings/y)		
Disturbance regime	Median	Mean	SD	Median	Mean	SD
E (n = 6)	5	8	8	15	16	3
S (n = 8)	7	16	25	12	12	3
M (n = 12)	8	28	49	8	8	3
L (n = 10)	13	57	95	6	6	3

Disturbance regime

We reconstructed disturbance regimes via a hydrological model and long-term (85 y; 1920–2004) meteorological data (Vanschoenwinkel et al. 2009). We used model-generated estimates of mean hydroperiod, mean number of inundations/y, and their standard deviations (SDs) as measures of hydrological variation. We used hierarchical cluster analysis to categorize pools based on disturbance regime (PRIMER, version 5; Primer-E, Plymouth, UK). We constructed a similarity matrix based on normalized Euclidean distances and used standardized values of hydroperiod, number of inundations/y, and their respective SDs. We used Unweighted Pair Group Method with Arithmetic Mean (UPGMA; Sneath and Sokal 1973) as the linkage rule. Trees based on 1 or any combination of these 4 hydrological variables were consistent and divided pools among 4 clusters (disturbance regimes): ephemeral (E), short-lived (S), medium long-lived (M), and long-lived (L) pools (Table 1). E and S pools are shallower, more ephemeral pools characterized by more frequent and shorter inundations. M and L pools have larger basins and can be filled to various extents depending on the amount of rainfall. These pools experience, on average, longer inundations and are characterized by much more variation in hydroperiod. A detailed overview of hydrological variation in each disturbance category is given in Table 1.

Sampling design

We sampled during the 1993–1994 rainy season over a period of 32 wk (223 d). All pools had dried during the previous winter and filled simultaneously after the first summer rains on 2 October 1993. We sampled all pools on 14 October and 8 November 1993, and 6 January and 19 February 1994 (12, 37, 96, and 140 d after filling).

Evaporative water loss caused the water level in the pools to decrease gradually between day 12 and day 37 and eventually led to desiccation of E and S pools. E pools were dry by day 37, and S pools were dry by day 96. Heavy showers (120 mm) on 14 December (day 73) reflooded E and increased water levels in S, M, and L pools before the day 96 sampling. Spells of precipitation compensated for evaporation and kept pools inundated until day 140.

Unless pools were dry, we sampled invertebrate communities quantitatively with a funnel-shaped net (64-μm mesh) with a maximum diameter of 85 mm. We traversed all microhabitats to obtain a representative composite sample for each pool. Sampling time was proportional to pool size, so sampling effort was comparable in all pools. We fixed samples with neutralized formalin, which was replaced with 70% ethanol in the laboratory. We counted all species with adults >~1 mm at 20× magnification under a dissection microscope. For smaller taxa, we counted individuals in 6 randomly chosen 5-mm rows in a 10 × 10-cm counting tray at 40× magnification. We counted individuals in more rows when a minimum number of 100 individuals was not reached. These counts represented 30% of the total sample. We multiplied the number of organisms counted by 3.3 to estimate the number of individuals in the sample.

We included all aquatic invertebrates except representatives of the Rotifera, Protoctista, Bryozoa, and Collembola in our study. We identified Anostraca, Spinicaudata, Cladocera, Ostracoda, Mollusca, and most Copepoda to species. We identified *Bryocamptus* sp., Cyclopoida spp., and Harpacticoida spp., Ephemeroptera, Hemiptera, Tardigrada, and Diptera to genus except Tipulidae (family) and Diptera sp. (order). We identified Coleoptera and Odonata to family level. We included informal taxa in our analysis to maximize the resolution of identification. We distinguished 2 taxa of Turbellaria (A and B) on the basis of size and epidermis characteristics (Turbellaria A was smaller). We distinguished Nematoda A and B on the basis of size (Nematoda A was smaller). Within aquatic mites (Hydracarina), we distinguished *Aquanothrus montanus*, Caeculidae, and informal taxa Prostigmata A and B.

We measured O_2 (mg/L), conductivity (μS/cm), and pH on each sampling date with WTW meters (conductivity meter 330i, O_2 meter 315i, pH meter 340; WTW, Weilheim, Germany). We measured water level with a graduated rod at the deepest point in each pool. We used a geographical information system interface (ArcGIS 8.1; ESRI, Redlands, California) to quantify pool area and vegetation cover (%) from a detailed map. We estimated sediment content visually on a 10-point scale.

Data analysis

Data analysis consisted of 2 main parts. First, we investigated the effect of disturbance regime on community assembly and diversity patterns (including all pools; $n = 36$). Second, we used a subset of pools that remained wet during the season (longest-lived M and L pools; $n = 22$) to investigate temporal community dynamics. We tested 3 predictions.

Prediction 1: disturbance truncates community assembly and reduces α and β diversity.—We used a repeated measures analysis of variance (ANOVA) to investigate differences in taxon richness (α diversity) in pools with contrasting disturbance regimes at different sampling times. The sequential nature of the data (measurements taken more closely in time are more strongly correlated) can result in inefficient analyses by traditional forms of ANOVA (Little et al. 1998). Therefore, we used a general linear mixed model (Proc MIXED in SAS version 9.1; SAS Institute, Cary, North Carolina) with an unstructured covariance selected based on Akaike's Information Criterion (AIC; Burnham and Anderson 1998). We used ANOVA to quantify the overall effect of disturbance regime on α diversity by testing for differences in cumulative taxon richness among pools with different disturbance regimes over the whole inundation.

We used the similarity index of Raup and Crick (1979) as a measure of β diversity (Lepori and Malmqvist 2009) because it is robust to differences in local species richness among sites (Van Calster et al. 2007). This index uses the number of shared species as a measure of association and estimates the probability that communities are associated rather than randomly drawn from the regional species pool. We obtained a dissimilarity index (RCD) by subtracting from unity. We tested differences in β diversity (pairwise RCD) among pools with different disturbance regimes with nonparametric Kruskal–Wallis tests because error distributions were not normal. We used ANOVA (Statistica 8.0; StatSoft, Inc., Tulsa, Oklahoma) to test for differences in community dissimilarity at different sampling times because errors were normally distributed. We did parallel analyses with the more conventional Bray–Curtis and Jaccard's indices, which revealed similar patterns and are not presented here. We used a correspondence analysis (CA) biplot to visualize temporal variation in community composition during inundations in pools with different disturbance regimes (CANOCO for Windows, version 4.5; Microcomputer Power, Ithaca, New York).

Prediction 2: life history and dispersal strategy determine efficiency of species sorting during community assembly.—We used a variation partitioning procedure (Borcard et al. 1992, Peres-Neto et al. 2006) to quantify the link between local environmental conditions and community composition during inundations. For each sampling date, we used redundancy analysis (RDA) based on abundance data to determine the amount of variation in community structure that was either uniquely or commonly explained by environmental and spatial variables. We included only significant variables identified with a forward-selection procedure in the RDA models (CANOCO for Windows). We used RDA rather than canonical correspondence analysis (CCA) because detrended canonical correspondence analysis (DCCA) indicated linear gradients. We inferred significance from Monte Carlo permutation tests (999 permutations). We did adjusted variation partitioning with the software VARCANV (Peres-Neto et al. 2006) to correct for biases associated with sample size and to compare differences between variation components. VARCANV cannot account for empty observations, so this analysis was limited to the pools ($n = 22$) that remained inundated throughout the study period.

A detailed study of spatial community patterns was not the goal of our study, but we did want to consider potential effects of connectivity and incoming passive dispersers during the inundation on community composition. Vanschoenwinkel et al. (2008) measured high dispersal rates via water connections and found that incoming dispersal via wind decreased with increasing pool isolation in this system. Therefore, we included connectivity (the number of hydrological connections) and isolation (average distance to other pools) explicitly in our analyses as spatial variables. To account for nearby sources, we included the number of pools within a 5-, 10-, and 20-m radius as dummy variables. Last, we used principal coordinates analysis (PCO; metric multidimensional scaling) based on an Euclidean distance matrix of interpool distances to include important spatial gradients as spatial variables in our RDA models. We included axes characterized by positive eigenvalues as spatial variables. The PrCoord function in CANOCO calculates the full solution of a PCO. PrCoord stores its output (sample scores on individual axes), which forms the basis for a distanced-based RDA (db-RDA) (Legendre and Anderson 1999). We included the environmental variables O_2 (mg/L), conductivity (μS/cm), pH, maximum depth, surface area, maximum volume, vegetation cover (%), plant species richness, sediment content, relative abundance of predators, and basic hydrological variables (mean and SD hydroperiod, mean and SD inundation frequency, median hydroperiod, maximum hydroperiod) related to the disturbance regime of the pools (Vanschoenwinkel et al. 2009).

We specifically distinguished 2 main groups of taxa based on their life histories and dispersal mode. The 1st group consisted of passively dispersed resident species that hatch from dormant life stages (resting eggs, cryptobiotic life stages) and included Crustacea, Turbellaria, Tardigrada, and Nematoda. The 2nd group consisted of actively dispersing flying colonists that recolonize pools at the beginning of each inundation. This group consisted exclusively of aquatic insects. We distinguished a total of 20 passively (residents) and 15 actively (flying colonists) dispersing taxa. The gastropod *Bulinus tropicus*, Oribatidae, Caeculidae, and Prostigmata were excluded from this analysis because of their complex dispersal modes.

Prediction 3: Changes in predation regime drive species replacement and temporal niche segregation.—We plotted temporal abundance patterns of the most important taxonomic groups (large branchiopods, Cladocera, Cyclopoida, Calanoida, Turbellaria) and actively colonizing predators (Hemiptera, Coleoptera, Odonata) to assess whether community assembly in temporary pools involved replacement of taxa (species replacement) or groups through time and whether this replacement was associated with changes in the abundance of predatory taxa. The taxon 'large branchiopods' refers to fairy shrimp (Anostraca), clam shrimp (Spinicaudata, Laevicaudata, Cyclestherida), and tadpole shrimp (Notostraca), primitive crustaceans that typically occur early during inundations and are restricted to temporary aquatic habitats. This life-history pattern is in contrast with that of the water fleas (Cladocera), which are more predation-tolerant, smaller members of the class of the Branchiopoda and usually peak in abundance later during inundations (Jocqué et al. 2010). In our study pools, large branchiopods are represented by 3 species: the fairy shrimps, *Branchipodopsis drakensbergensis* and *Branchipodopsis* sp., and the clam shrimp, *Leptestheria striatoconcha*.

Results

Prediction 1: disturbance truncates community assembly and reduces α and β diversity

Disturbance significantly reduced α diversity (cumulative taxon richness) ($F = 12.42$, $p < 0.001$). Taxon richness was significantly lower in E pools than in M and L pools (Tukey Honestly Significant Difference [HSD], $p < 0.05$; Fig. 1A). However, taxon richness did not differ among pools with different disturbance regimes within sampling dates ($F = 2.12$, $p = 0.12$; Fig. 1B). Disturbance also reduced β diversity ($H = 37.6$, $p < 0.01$). RCD did not differ between E and S pools and was significantly lower in E than in M and L pools (Fig. 2A), a result indicating that disturbed communities were more similar than undisturbed communities. Moreover, RCD was significantly lower after 97 and 140 d than after 12 or 37 d of inundation ($F = 22.4$, $p < 0.001$; Fig. 2B).

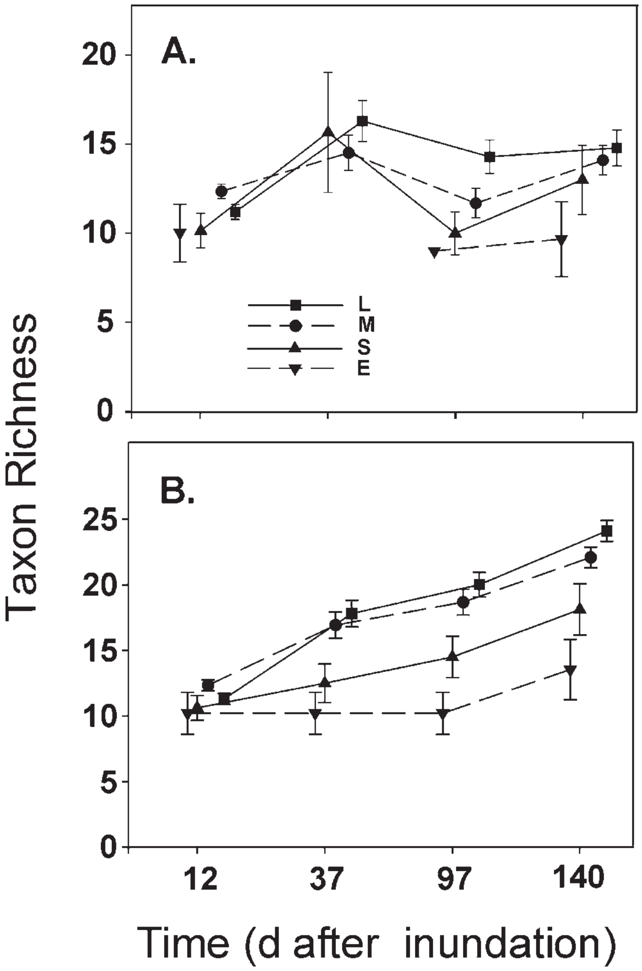

FIG. 1. Mean (±1 SE) taxon richness (A) and cumulative taxon richness (B) in pools with different disturbance regimes (E = ephemeral, S = short-lived, M = medium long-lived, L = long-lived pools).

Community temporal trajectories visualized in the CA biplot indicated that communities were similar in all pools 12 and 37 d after filling (t1 and t2, respectively; Fig. 3). E pools clustered slightly apart from S, M, and L pools. Community composition in E, S, M, and L pools followed more or less the same trajectory until E pools dried.

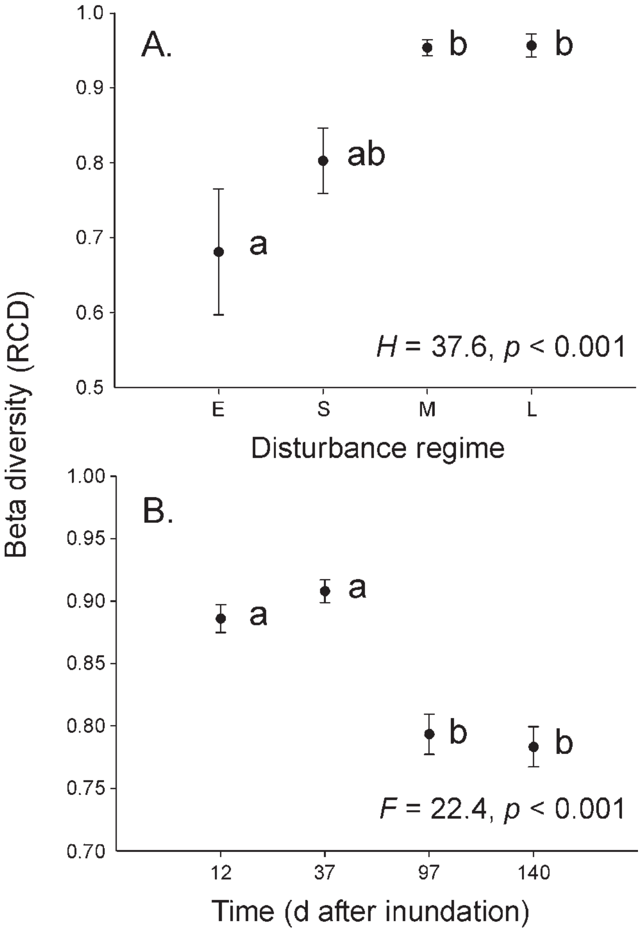

FIG. 2. Mean (±1 SE) β diversity (Raup and Crick Index of Dissimilarity [RCD]) in pools with different disturbance regimes (A) and on different sampling dates during community assembly (B). The results of the Kruskal–Wallis test (among disturbance regimes) and analysis of variance (among sampling dates) are indicated on the graphs. Points with different letters are significantly different ($\alpha < 0.05$).

Prediction 2: life history and dispersal strategy determine efficiency of species sorting during community assembly

Resident species and flying colonists showed contrasting temporal dynamics (repeated measures ANOVA; $F_{\mathrm{col}} = 7.65$, $r^2_{\mathrm{col}} = 0.39$; $F_{\mathrm{res}} = 3.61$, $r^2_{\mathrm{res}} = 0.17$). Time ($p = 0.008$), life-history–dispersal mode ($p = 0.0001$), and their interaction ($p = 0.01$) significantly affected temporal variation in taxon richness (Fig. 4A). Taxon richness of flying colonists increased significantly between days 12 and 37 (Tukey HSD, $p < 0.05$) and remained high over time. Taxon richness of residents also increased significantly between days 12 and 37 (Tukey HSD, $p < 0.05$), but then decreased. Dispersal mode ($p < 0.001$) significantly affected relative abundance of resident species, but neither time nor the time × dispersal mode interaction effects were significant (repeated measures ANOVA, $F = 2.60$, $r^2 = 0.18$; Fig. 4B). Relative abundance of resident species tended to be correlated with water levels, whereas relative abundance of flying colonists was highest when water levels were low, but these relationships were not statistically significant (Spearman $r = 0.80$, $p = 0.2$).

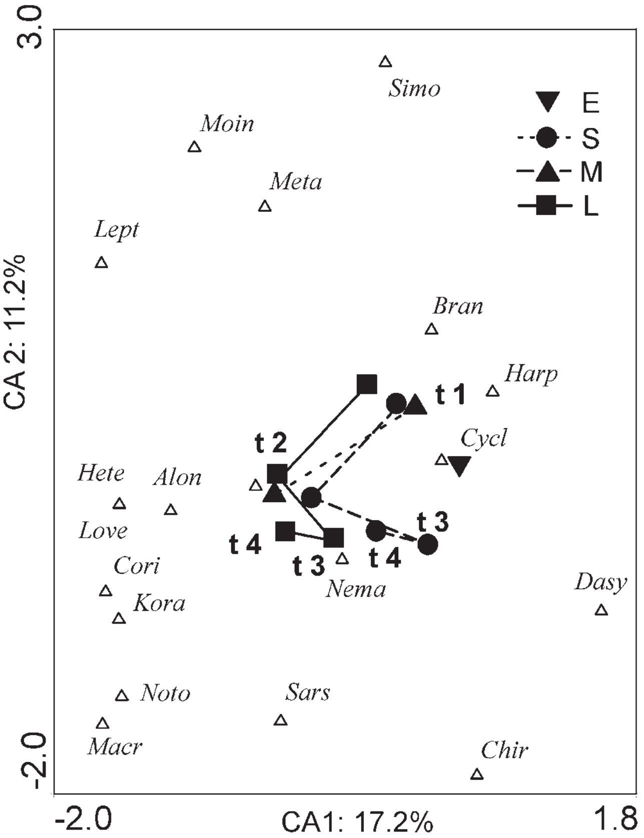

FIG. 3. Correspondence analysis (CA) biplot illustrating the relationships among communities in pools with different disturbance regimes (E = ephemeral, S = short-lived, M = medium long-lived, L = long-lived pools) at different phases of community assembly during 1 inundation (time since inundation: t1 = 12 d, t2 = 37 d, t3 = 97 d, t4 = 140 d). Only taxa for which >10% of variation is captured are presented. *Alon* = *Alona costata*, *Bran* = *Branchipodopsis* spp., *Chir* = Chironomidae, *Cori* = Corixidae, *Cycl* = Cyclopoida, *Dasy* = *Dasyhelea* sp., *Harp* = Harpacticoida, *Hete* = *Heterocypris incongruens*, *Kora* = *Korannacythere devriesi*, *Lept* = *Leptestheria striatoconcha*, *Love* = *Lovenula falcifera*, *Macr* = *Macrothrix propinqua*, *Meta* = *Metadiaptomus transvaalensis*, *Moin* = *Moina micrura*, *Nema* = Nematoda, *Noto* = Notonectidae, *Sars* = *Sarscypridopsis gregaria*, *Simo* = *Simocephalus vetulus*. Variation explained by each axis is given after the axis title.

For residents, variation partitioning revealed stronger links between local environmental conditions and the structure of early communities (12 d) than of late

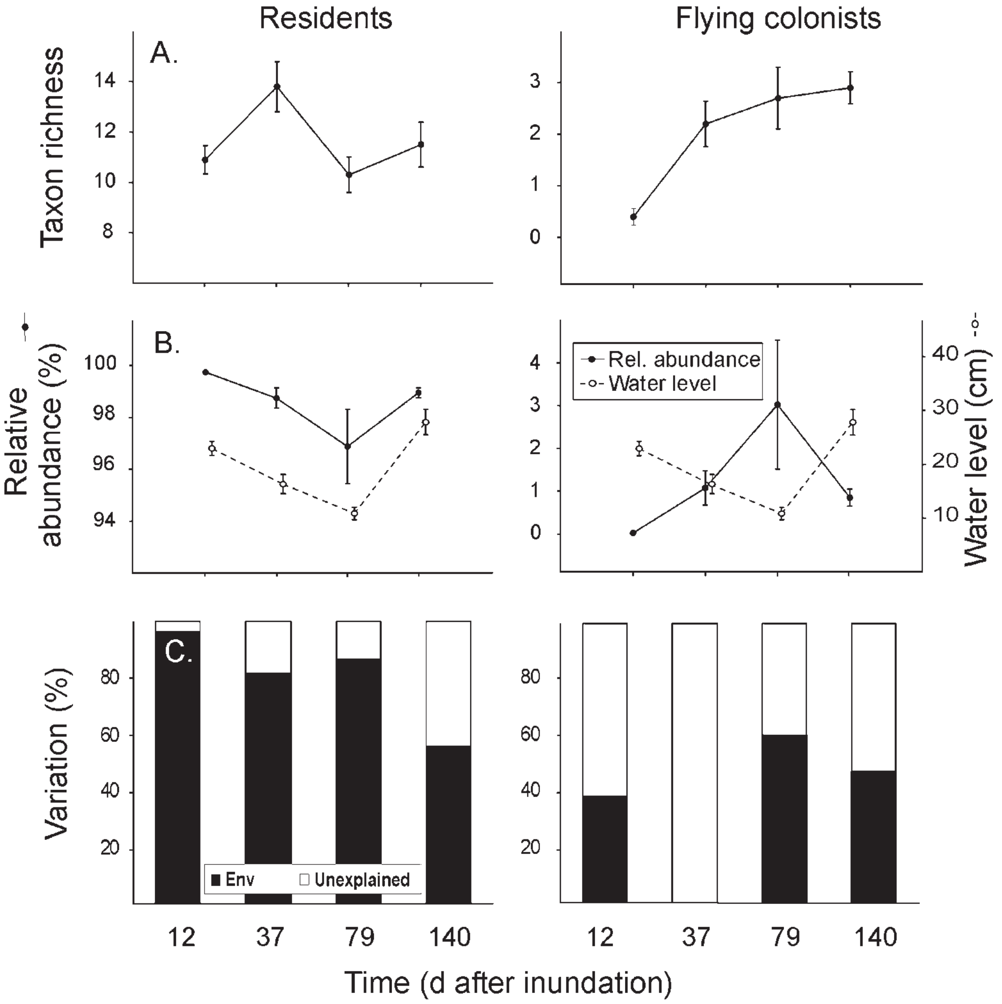

FIG. 4. Mean (±1 SE) taxon richness (A), relative abundance (B), and % variation explained by environmental (env) variables (C) of resident and flying colonist taxa on 4 sampling days in pools that remained flooded throughout the inundation period. Spatial variables did not explain significant amounts of variation.

communities (140 d) (Table 2). For flying colonists, local environmental conditions and community structure were less clearly linked. Local environmental conditions explained none of the variation in community structure on day 37 (Fig. 4C), but explained 60% of the variation on day 79, when water levels were lowest. Low water levels concentrate biota and might have caused stronger species sorting among flying colonists by day 79 (Fig. 4B, C). We did not detect any significant effects of spatial variables on community composition (Appendix).

Prediction 3: Changes in predation regime drive species replacement and temporal niche segregation

Early communities were dominated by large branchiopods (Anostraca and Spinicaudata) (Fig. 5A), cyclopoid copepods (Fig. 5B), and Turbellaria (Fig. 5C). Calanoid copepods peaked on day 37 (Fig. 5D). Predator communities shifted from Turbellaria to predatory insects that actively colonized the pools (Odonata, Hemiptera, and Coleoptera) (Fig. 5E). The decline in the abundance of large branchiopods coincided with an increase in abundance of predatory insects. Cladoceran abundances peaked later in the season, after the disappearance of large branchiopods (Fig. 5F), replacing the latter as the dominant filter feeders.

Discussion

Over 4 sampling periods covering an entire wet season, cumulative taxon richness was lowest in the most ephemeral rock pools. This result supports the accepted concept of lower diversity in habitats experiencing more severe disturbance regimes (Ther-

TABLE 2. Variance partitioning of invertebrate data matrices on 4 sampling days in pools that remained flooded throughout the inundation period. Analyses were performed separately for residents and flying colonists. [E] = variation explained by environmental variables, [S] = variation explained by spatial variables. Because spatial effects were not significant, other variance components: [E – S] = pure environmental variation, [S – E] = pure spatial variation, [E ∩ S] = variation shared by environmental and spatial variables, are not given. – indicates no significantly contributing variables were identified using forward selection.

	T1 (12 d)		T2 (37 d)		T3 (97 d)		T4 (140 d)	
Variable	%	*p*	%	*p*	%	*p*	%	*p*
Resident species								
[E]	92	0.001	75	0.002	79	0.006	45	0.004
[S]	17	0.21	–	–	0	0.37	0	0.47
Flying colonists								
[E]	38	0.01	–	–	60	0.05	50	0.009
[S]	56	0.09	0	0.26	–	–	24	0.15

riault and Kolosa 2001, Urban 2004, Serrano and Fahd 2005). Community snapshots, on the other hand, did not reveal differences within sampling periods in local taxon richness in pools with different disturbance regimes. This result underlines the need to consider seasonal variation in diversity assessments of temporary aquatic habitats. Disturbance reduced β diversity (Fig. 2A). Frequent disturbance can result in strict selection of a limited number of tolerant species and strong deterministic processes that lead to low β diversity among disturbed patches (Chase 2007, Lepori and Malmqvist 2009). In less-disturbed patches, less physical disruption and, in the case in temporary pools, longer growing periods can increase the importance of stochastic processes (birth, death, extinction) and lead to higher β diversity.

Duration and timing of inundations are fundamental structuring agents in temporary aquatic habitats (Schneider and Frost 1996). Drying can truncate the development of certain groups, whereas longer hydroperiods might permit species to avoid competition via temporal niche segregation within inundations. The successional phases and species replacement observed during inundations in our study are indicative of such processes. First, temporal variation in abundances of different taxa (Fig. 5A–F) support a 2-phase succession pattern, which is characteristic of relatively short-lived temporary waters lasting several months or less (Jocqué et al. 2007). Second, high similarities (Figs 2B, 3) and comparable taxon richness (Fig. 1A, B) among communities with different disturbance regimes early in the inundation cycle suggest truncation of community development by desiccation.

Initial communities were dominated by organisms, such as large branchiopods, cyclopoid copepods, and turbellarians, that entered the active community via in situ dispersal from the dormant propagule bank. The strong link between local environment and initial community structure of resident species emerging from the dormant propagule banks suggests highly efficient species-sorting processes early in the inundation. The presence of dormant propagules that reflect long-term assemblages of established species (as a consequence of species sorting) and species-specific responses to hatching cues (demonstrated for many freshwater invertebrates; reviewed in Brendonck and De Meester 2003) might be important mechanisms explaining this initial pattern.

The 2nd successional phase was characterized by the appearance of actively dispersing flying insects and replacement of large branchiopods by smaller cladocerans as dominant filter feeders. Variable levels of predation by incoming predators, such as Hemiptera and Coleoptera (Binckley and Resetarits 2005), could reduce the importance of the abiotic environment as the dominant ecological filter for resident prey. However, predation did not emerge as a significant predictor in our RDA models. Thus, the poorer match between resident taxa and local environmental conditions in the 2nd than in the initial phase was more probably a consequence of the increasing importance of stochastic processes (recruitment, mortality, extinction, colonization) later during inundations.

The link between local environmental conditions and assemblages was weaker for flying colonists than for residents, particularly early during inundation (Fig. 4C). Flying colonists in our study generally lack the ability to survive dry phases in situ. As a result, they migrate to permanent ponds in the region during the dry season and recolonize the pool cluster after the first rains. The small spatial scale of the pool cluster probably does not pose any dispersal barrier for organisms capable of flight. Flying adults can move constantly among pools and select optimal

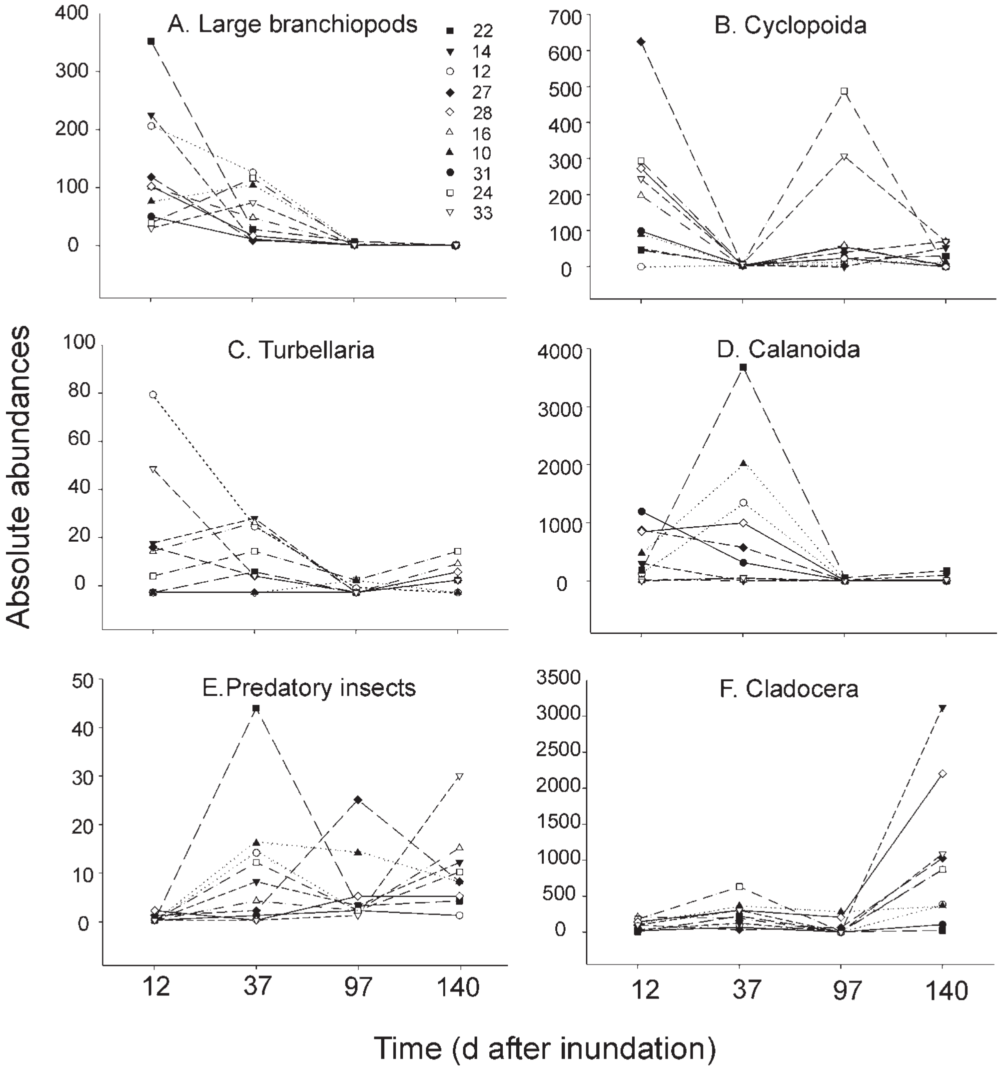

FIG. 5. Absolute abundances of large branchiopods (A), Cyclopoida (B), Turbellaria (C), Calanoida (D), predatory insects (E), and Cladocera (F) on 4 sampling days in pools that remained flooded throughout the inundation period. For clarity, only dynamics of the 12 most long-lived pools are presented. Pool numbers and corresponding symbols are given in the key to symbols in panel A.

feeding and breeding grounds. Thus, the match between flying colonists and local conditions is updated constantly and potentially results in a good community–environment match. The better match between abiotic environment and community structure and increased richness of flying colonists later in the season probably were the result of variation in arrival time and the fact that these organisms need more time to develop populations than do resident zooplankton, which hatch soon after inundation (Jocqué et al. 2007) and reproduce quickly.

Maximum pool depth emerged as the most important variable explaining community patterns of flying colonists. Deeper basins are most likely to hold water long enough to allow successful reproduction. Shallow, zooplankton-rich pools might provide excellent feeding conditions for adult Hemiptera and Coleoptera, but might not hold water long enough for their nymphs/larvae to mature to flying adults able to escape the habitat when conditions deteriorate.

In general, we did not find indications that passive dispersal strongly affected community assembly because no unique effects of pool connectivity or isolation emerged from our analysis. Reasons for this apparent discrepancy with the results of a previous study (which did report spatial effects explaining community structure; Vanschoenwinkel et al. 2007) probably lie in the more restricted data set in the present study (only the 22 pools that were wet throughout the season were analyzed).

Large branchiopods are highly specialized taxa characterized by early hatching, fast growth, and a generalist diet. Fairy shrimp are strong competitors and can effectively filter rotifers and crustacean larval stages from the water (Sarma and Nandini 2002). However, because of their size, large branchiopods are particularly vulnerable to vertebrate (Bohonak and Whiteman 1999) and invertebrate predation (Brendonck et al. 2002). Our results indicate that the arrival of flying predators might have ended the competitive advantage of large branchiopods and tipped the balance in favor of cladocerans. In effect, the temporal variability in predation regime and the difference in predation sensitivity led to temporal niche segregation between the 2 groups. Sensitivity to predation also is generally accepted as an explanation for the absence of large branchiopods from permanent waters (Kerfoot and Lynch 1987). Fryer (1986) suggested that large branchiopods are specialized to use enemy-free space optimally, but this view might be too simplistic (Brendonck et al. 2002). Specialist predators, such as Turbellaria, also form resting eggs and enter the community soon after inundation together with the large branchiopods (Fig. 5A, C). Their later decline coincides with the disappearance of large branchiopods, on which they prey (De Roeck et al. 2007). This timing might reflect exhaustion of their main food source and could indicate a strong predator–prey bond between groups (Blaustein and Dumont 1990).

The question whether communities converge or diverge through time is fundamental to an understanding of community assembly. β diversity decreased in pools that remained inundated throughout the season. Steady arrival and population development of flying colonists probably explain the general homogenization of communities later during inundations (Fig. 2B). Less-efficient species sorting, as observed for residents later in the season, might indicate the increased importance of stochastic (birth, death, colonization, and extinction) relative to niche-based deterministic processes (Samuels and Drake 1997, Chase 2003).

Vector-mediated dispersal was not limiting at our study site (Vanschoenwinkel et al. 2008), and the rock-pool metacommunity was structured mainly by species-sorting processes (Vanschoenwinkel et al. 2007). Species-sorting processes in patches with dormant propagule banks might operate in both space and time. Thus, temporal heterogeneity in biotic and abiotic conditions in combination with efficient in situ dispersal in time from the dormant propagule bank might lead to efficient within-patch species sorting during and among different inundations.

Conclusions

We conclude that community (re)assembly in temporary aquatic habitats is predominantly driven by disturbance regime. Disturbance reduced both α and β diversity by acting as a life-history-based selective filter modulating the relative strength of deterministic and stochastic processes (Lepori and Malmqvist 2009). Compared to the relatively stable environments of permanent ponds and lakes, invertebrate communities in temporary aquatic habitats rely on constant recolonization from the regional and dormant species pool. Thus, community structure and local richness patterns in the often extreme environment of these habitats depend on whether local extinctions are compensated by efficient dispersal in time and space.

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APPENDIX. Environmental and spatial variables retained via forward-selection procedures in redundancy analysis models explaining community structure on 4 sampling dates during the period of inundation. Axes represent species scores along dominant spatial axes obtained using principal coordinate analysis (PCO). – indicates no significantly contributing variables were identified using forward selection.

	Residents		Flying colonists	
Sampling period	Environmental	Spatial	Environmental	Spatial
T1	O_2 Surface area Maximum depth Median duration of inundations	Axes 3, 5	Sediment content	Axes 1, 2, 4, 6 Isolation
T2	Surface area Median duration of inundations	–	–	Axis 5
T3	Inundation frequency Conductivity Water temperature	Axis 5	Maximum depth Water temperature	–
T4	Vegetation cover	Axis 5 Connectivity	Maximum depth Vegetation richness	Axes 3, 5