

# Community structure in temporary freshwater pools: disentangling the effects of habitat size and hydroregime

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## SUMMARY

1. Hydroregime (duration, frequency and predictability of the aquatic phase) is a key feature of temporary aquatic habitats that not only moulds community structure and diversity (species sorting) but also life history characteristics of the inhabitants (natural selection). However, since hydroregime is a complex multidimensional entity that cannot be estimated from short term observations, morphometric variables are commonly used as proxies for hydroregime, making it impossible to separate effects of habitat size and hydroregime on biota.

2. We have used a simple hydrological model, validated with recent (average  $r^2 = 96\%$ ) and historic water level observations (average  $r^2 = 81\%$ ), to accurately reconstruct hydroregime based on historical rainfall and evaporation data in a cluster of 36 temporary rock pools in central South Africa.

3. Using the model output, we demonstrated that both hydroregime and habitat size had unique and shared effects on temporary pool biota and that these effects depended on the dispersal modes of the taxa. Model-generated hydrological data explained more variation in community patterns than short-term observations of hydroperiod. Hydroregime was more important for passive dispersers than for active dispersers that can migrate when pools dry up. Basin morphometry was a relatively poor predictor of pool hydroregime. We concluded that simple modelling may greatly improve the resolution of studies linking hydroregime to biological variables.

4. An accurate account of hydrological variation provides a firm foundation to understand community and population structure and dynamics in temporary aquatic habitats. Since many of these habitats have been destroyed or degraded in recent decades, our findings and tools may contribute to the development of reliable conservation guidelines.

*Keywords:* ecohydrology, hydrological modelling, hydroregime, temporary pools, variation partitioning

## Introduction

The hydrological gradient is fundamental to our understanding of temporary aquatic habitats (Wellborn, Skelly & Werner, 1996; Blaustein & Schwartz, 2001; Urban, 2004), which range from

microhabitats in leaf axils and pitcher plants to the macrohabitats of temporary ponds and rivers (Williams, 2006). Studies of ecological and evolutionary processes along this gradient, however, suffer from the fact that hydrological variation is a relatively complex entity that is not straightforward to measure.

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The contribution of different hydrological variables to stability (hydroperiod, desiccation frequency) and predictability (inter- and intra-seasonal variation in inundations) of a temporary aquatic habitat can be defined as the hydroregime (see also Hulsmans *et al.*, 2008). Hydroregime is one of the key selective agents in temporary waters known to facilitate local adaptation of populations (Hamer & Appleton, 1991; Simovich & Hathaway, 1997; Johansson & Suhling, 2004) and evolution of specialised taxa (Williams, 2006). In general, temporary pool inhabitants have developed two main strategies (sometimes subdivided into four: Wiggins, Mackay & Smith, 1980) to persist in this peculiar habitat: either to survive desiccation *in situ* via resistant life stages, or to actively migrate elsewhere when the water disappears (Williams, 2006). As a result, dispersal mode is expected to influence the way organisms experience hydroregime.

It is commonly agreed that to understand patterns in (meta) community structure and diversity (Wellborn *et al.*, 1996; Urban, 2004) and in life history variation (Stoks & Mcpeek, 2006), the long-term hydrological variation of the habitat should be taken into account. However, for logistic reasons very few studies (Pajunen & Pajunen, 2003; Brooks, 2004; Bauder, 2005) have monitored temporary pool hydroregime for 10 years or more. As the hydrology of temporary aquatic habitats is generally quite unpredictable (Williams, 2006; Hulsmans *et al.*, 2008), long-term observations are required to cover inter- and intra-annual variation in the number (inundation frequency) and duration (hydroperiod) of inundations. Instead, most studies have used rough estimates of permanence based on scattered visual inspections of water presence (Fischer *et al.*, 2000; Andrushchyshyn, Magnusson & Williams, 2003; Eitam *et al.*, 2004a) or have used basin depth (Jocqué *et al.*, 2006) or surface area to volume ratio as indirect estimators (Marcus & Weeks, 1997). As a result it is usually impossible to separate effects of habitat size and hydroregime on water quality and biota. While detailed long-term hydrological information of temporary aquatic habitats is not often available, regional rainfall and evaporation data are usually easy to obtain, providing opportunities for hydrological modelling. Models have been developed to reconstruct hydrological variation in vernal pools in California (Pyke, 2004), seasonal forest pools (Brooks & Hayashi, 2002; Brooks, 2005) and other types of temporary wetlands (Mitsch,

Straskraba & Jørgensen, 1988; Giraud *et al.*, 1997). In general, these models were developed for a limited number of pools or wetland types and included extensive parameterisation, mostly related to surface water-ground water interactions (Pyke, 2004). Furthermore, most of these models have tried to explain short term water level fluctuations rather than reconstruct long-term hydrological variation.

In this study, we apply a simple bucket model, validated using recent and historical water level measurements and making use of basic rainfall and evaporation data as inputs, to reconstruct long-term hydrological variation (85 years) of 36 temporary rock pools. The model output allows us to accurately quantify the hydroregime of each pool. We investigate collinearity between habitat size and hydroregime and verify whether morphometrical variables provide reliable information about hydroregime. Furthermore, we assess the unique and shared effects of habitat size and hydroregime on invertebrate community structure using a multivariate approach. Here a distinction was made between passive and active dispersers in order to investigate the role of dispersal mode. Finally, we discuss the general implications of the model and associated tools to uncouple habitat size from hydroregime for the study of biological patterns and processes along hydrological gradients and for the conservation management of the threatened temporary pool habitat and its biota.

## Methods

### Study site

The study site consists of a series of 36 rock pools situated on a sandstone rock shelf (7400 m<sup>2</sup>) on the north-western plateau of the Korannaberg mountain (28°51'13"S; 27°13'51"E) located in the eastern part of the Free State Province (South Africa). The geometry of the pools on the rock shelf is shown in Fig. 1. Pools are geologically derived from calcareous concretions that originated from trapped organic matter. Upon exposure, these concretions weather faster than the surrounding sandstone, leaving a depression with a flat ellipsoid shaped bottom and nearly vertical sides within the impermeable bedrock. Rainfall is mainly limited to the wet season (October–April). The high annual evaporation of 1100–1500 mm deviates

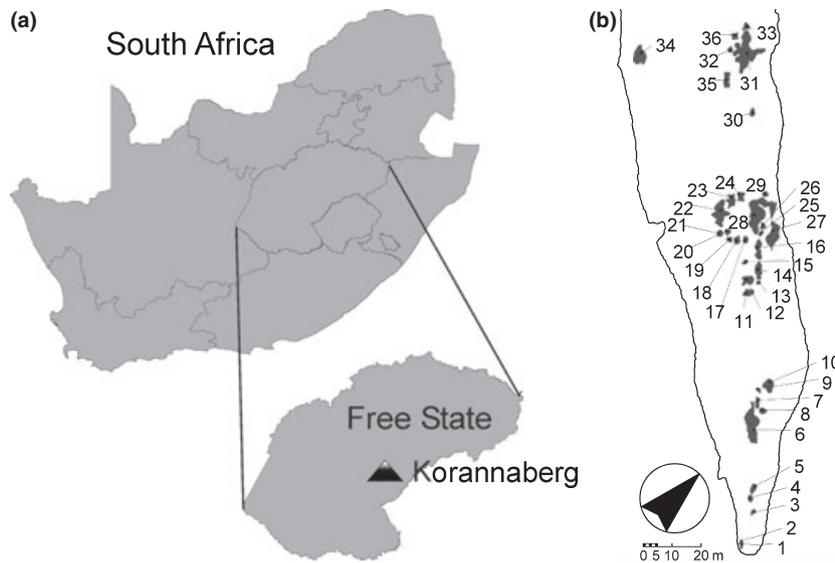


Fig. 1 Study site. (a) Location of Korannaberg Mountain in South Africa. (b) lay out of the 36 rock pools.

considerably from the mean annual precipitation of 450–700 mm, resulting in aquatic systems being mostly of a temporary nature. The combination of temperature, evaporation and rainfall results in a net water loss in this semi-arid area.

#### Field measurements

The water level ( $d$ ) of all 36 pools was measured on a daily basis from 7 October to 25 November 2005 between 8 and 9 AM at the deepest point in each pool. Water level was measured using a calibrated rod (accuracy: 5 mm). The maximum depth of each pool basin ( $d_{\max}$ ) was integrated in the model as the upper filling limit. Water level, rather than pool volume was modelled. This was a valid simplification considering the bucket shape (vertical sides) of the pool basins. The area of each pool was calculated by drawing each pool to scale using a 50 cm  $\times$  50 cm grid and calculating the total area with a digital planimeter. Rainfall was the only contributor of water, evaporation the only loss. To calibrate the model, daily rainfall measurements were made at the site using a standard rain gauge situated at the centre of the pool cluster for the whole study period. Aquatic vegetation in the study pools is usually scarce or absent, hence no explicit transpiration term was included in the model. However, since evaporation rates were calibrated separately for each pool, any effects of vegetation are compensated for.

Maximum depth of the pool basin ( $d_{\max}$ ) was used as an upper limit for pool filling in the model. The amount of overflowing water ( $O$ ) is not explicitly quantified. Occasionally, when pools overflow, water can flow from one pool to another. However, this potential inflow of water was not taken into account in the current model as this would require additional parameterisation and complicate the model. Field observations suggest that such overflow events do not occur very frequently (only for six of the 36 studied pools) and that the volume of transported water is usually very small and negligible compared to the volume of water already present in the receiving basin.

#### Model calibration

Two pool specific parameters ( $R$  and  $C$ ) were used to calibrate the model. The catchment factor ( $R$ ) accounts for pool specific catchment size and was expressed as the amount of water level gained (in mm) for every 1 mm of rain:

$$R = \frac{\Delta d}{\Delta P}$$

with  $\Delta d$  = water level gained after a shower (mm);  $\Delta P$  = amount of rainfall during that specific shower (mm).

This parameter is best calculated when a pool is completely dry and receives a measured amount of

precipitation, causing the pool to partially fill up but not to overflow.  $R$  was first estimated on 19 October 2005 after 25 mm of rain. A second assessment of  $R$  on 11 November 2005 after 4.5 mm of rain revealed few or no differences.

The pool specific evaporation factor ( $C$ ) was calculated to account for differences in evaporation rates related to pool location on the site. Pool location may have differential effects on evaporation through variable levels of, for example, shade, wind exposure, macrophyte cover, sediment type and thickness, compared to conditions at the other pools and compared to local conditions at the weather station. In the model,  $C$  has a standard value of 1. This value can be  $>1$  when evaporation rates for the target pool are on average higher and  $<1$  when lower than at the weather station.

Pool specific evaporation rate is then calculated as:

$$E = \frac{E_{\text{ClassApan}}}{A_{\text{ClassApan}}} \times A_{\text{pool}} \times C$$

with  $E$  = evaporation ( $\text{mm day}^{-1}$ );  $E_{\text{ClassApan}}$  = Class A pan evaporation ( $\text{mm day}^{-1}$ ) measured at the weather station;  $A_{\text{pool}}$  = pool area;  $A_{\text{ClassApan}}$  = standard surface area of a Class A evaporation pan;  $C$  = pool specific evaporation factor.

Model accuracy ( $r^2$  of Pearson correlations between model predicted and observed water levels) was calculated for all possible values of  $C$  within the range of 0–10 (steps of 0.1) in order to fine-tune the model. For each pool the  $C$ -value corresponding with a maximum  $r^2$  between predicted and observed water levels was selected.

#### General water balance model

Parameters were integrated in a general water balance model:

$$\Delta d = (\Delta P \times R) - E\Delta t - O + \epsilon \quad (1)$$

with  $\Delta d$  = change in water level (mm) during a time period  $\Delta t$ ;  $\Delta P$  = amount of rainfall (mm) received during  $\Delta t$ ;  $E$  = pool specific evaporation rate (mm);  $R$  = pool specific catchment factor;  $O$  = overflow water lost from the basin when  $d > d_{\text{max}}$  (mm);  $\epsilon$  = error term.

The basic formula (1) was modified to eqn (2) to generate a daily estimate for each pool's water level. At the start of an inundation,  $d_{t-1}$  equals zero.

$$d_t = d_{t-1} + (P \times R) - E_m - O + \epsilon \quad (2)$$

with  $d_t$  = water level at day  $t$  (mm);  $d_{t-1}$  = water level at day  $t-1$  (mm);  $P$  = cumulative rainfall on day  $t$  (mm);  $R$  = pool specific catchment factor;  $E_m$  = average daily pool specific evaporation ( $\text{mm day}^{-1}$ ) in month  $m$ ;  $O$  = overflow water lost from the basin when  $d_t > d_{\text{max}}$  (mm);  $\epsilon$  = error term.

#### Reconstruction of hydroregime

Making use of model eqn 2, we reconstructed long-term hydrological variation (85 years; from 1920 to 2004) of the 36 study pools. Simulations were based on daily rainfall data from the nearest weather station at Excelsior (18 km from the study site; 28°56'S; 27°03'E) and on average monthly evaporation data from the weather station at Clocolan (32 km from the study site; 28°55'S; 27°34'E). Rainfall measurements from October to November 2005 at the study site confirmed that local rainfall patterns were virtually identical to those measured in Excelsior. Evaporation data (Penman Monteith) were acquired from the Clocolan weather station because it is situated on a similar altitude as the Korannaberg pools. As evaporation data were not available for the entire 85-year period, we calculated average daily evaporation (in mm) for each month, based on 14 years (daily from 1992 to 2004) of available evaporation measurements (Penman Monteith method) (Allen *et al.*, 1998). Both the commonly used class A pan and Penman Monteith evaporation measurements can be used to run the model, taking into account that Penman Monteith is usually 30% lower than class A evaporation (Hess, 1996; Enciso & Wiedenfeld, 2005). Penman Monteith evaporation data were converted to their class A pan equivalent. A standard class A pan has a standard surface area of 1.14 m<sup>2</sup>, which was used as a reference when correcting  $E$  for pool area (see above). Rainfall data were not available for several months in 1921 (February; May–July), 1924 (July), 1928 (May, September), 1937 (August), 1943 (May), 1991 (August) and 2003 (January). As most missing data were from summer months (May–September), when there is virtually no rainfall, and since missing data were diluted in the extended 85 years reconstruction, their impact on the output of our model is likely to be negligible.

Using pool area, max depth, the calibration parameters ( $R$  and  $C$ ) and meteorological data as inputs, the model reconstructs a daily time series of pool water level. From the generated water level series the model calculates four hydrological variables with a one day resolution: mean inundation length (mean hydroperiod), the standard deviation of inundation length (SD hydroperiod), average number of inundations per year (inund freq) and the standard deviation of the number of inundations per year (SD inund freq). The combination of these variables will henceforth be referred to as the hydroregime. Water levels of the 36 studied pools as observed in the field from 7 October to 25 November 2005 were plotted against model generated water levels. The proposed water balance model was implemented in Microsoft Excel and is available from the corresponding author upon request.

#### *Model validation*

For each pool a Pearson correlation coefficient  $r$  with corresponding  $P$ -value was calculated between observed and modelled water levels during 50 consecutive days of water level observations (7 October to 25 November 2005).  $r^2$  was used as a measure for model accuracy. Calibration (parameterisation) and model validation making use of the same series of observed water levels may artificially improve the fit of the model during that specific time period. To correct for this and to verify the ability of the model to predict depth series during periods other than those used for parameterisation, the 2005 dataset was divided into a training dataset (first 25 water level observations; 7–31 October) for parameterisation and a testing dataset (second 25 water level observations; 1–25 November) for validation. Furthermore, to check whether the model performed equally well during historic inundations, an additional validation was performed making use of available water level measurements in all 36 study pools from four scattered dates in the 1993–94 rainy season (7–14 October, 1, 8, 15 November; 1 January; 19 February; 15 May). Again, for each pool, an  $r^2$  was calculated based on Pearson correlations between modelled and observed water levels (testing dataset) and used as a measure of model accuracy.

#### *Collinearity of morphometry and hydrology*

To investigate the feasibility of using habitat size variables (area, max depth) as reliable predictors of hydroregime, we assessed the overlapping variation between hydrological and habitat size variables and calculated correlations between these two groups of variables. Principal components analysis (PCA) was performed to reduce the dimensions of the dataset and to visualise relationships.

#### *Community structure analyses*

Sampling of invertebrate communities took place in the 1993–94 rainy season following a dry winter during which all pools dried up. Pools filled simultaneously after the first summer rains. To integrate seasonal variation in the description of the invertebrate community structure, all pools were sampled on four occasions after 12, 37, 96 and 140 days of filling respectively. All 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 so that sampling effort was comparable in all pools. Samples were fixed with neutralised formalin and this was replaced with 70% ethanol in the laboratory. All species of which adult individuals were larger than about 1 mm were counted under a dissection microscope at 20 $\times$  magnification. For smaller taxa, six randomly chosen 5 mm rows in a 10  $\times$  10 cm counting tray were counted at 40 $\times$  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 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 (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. Exclusively active dispersers do not exist as such species can usually also disperse passively, for instance through connecting channels. In this study all organisms with adult life stages capable of flight were defined as active dispersers. Hydrochoric dispersal through channels was 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 is usually a passive disperser, but can migrate overland during rains. A total of 20 passively dispersing taxa and 15 actively dispersing taxa were included in our analyses.

To verify whether species-poor assemblages were nested subsets of species-rich assemblages we tested for nestedness in a presence-absence matrix including all invertebrate taxa in the studied pools using the program BINMATNEST (Rodriguez-Girones & Santamaria, 2006). The program generates three *P*-values corresponding with three different null models. All three models resulted in the same probability values in our analyses.

To investigate unique and shared effects of pool hydroregime and habitat size on abundances and taxon richness of pool invertebrates, we used a multivariate approach and applied variation partitioning (Borcard, Legendre & Drapeau, 1992) on redundancy (RDA) models (999 Monte Carlo permutations). Habitat size variables included 'area' and 'max depth'. Absolute abundances of different taxa were log(10) transformed prior to RDA to increase the importance of rare compared to abundant taxa. Taxon richness was not transformed. RDA was used rather than CCA since previous detrended canonical correlation analysis (DCCA) indicated a dominance of linear, rather than unimodal gradients (length of

gradients <3). Four variation components are distinguished: pure habitat size variation (hydrological variables used as covariables), pure hydrological variation (habitat size variables used as covariables), variation explained in common by habitat size and hydroregime and unexplained variation. RDA models were constructed using the Canoco software package (Ter Braak & Šmilauer, 1998). To determine whether model-generated hydrological variables better explain community structure and richness than information from short term observations, we compare these results with results obtained by repeating the analysis using only hydroperiod (observed length of inundations during the sample season) as a predictor variable.

To test whether the relative importance of hydroregime and habitat size differed for organisms with different dispersal strategies, all analyses were also performed for datasets containing only actively or passively dispersing taxa respectively. Note that the impacts of hydroregime and habitat size on taxon richness were also analysed in Statistica 8.0 (Statsoft 2007) using multiple regression analysis; as the results were identical to those from the RDA we only include the RDA results.

## Results

### Model validation

Model generated values for water level fitted the observed water level series in the 36 pools during four

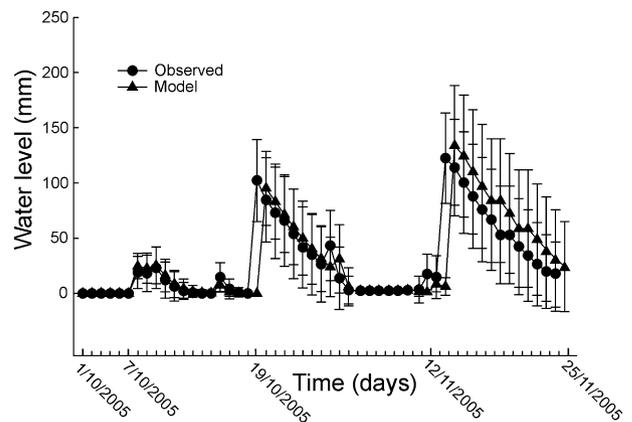


Fig. 2 Plot of observed (circle) and model reconstructed (triangle) water levels for the 36 rock pools during four inundations in the 2005 rainy season. Plot = average water level over all 36 pools, Error bar = standard deviation.

**Table 1** Basic habitat size (max depth and area) and model calibration parameters *R* (catchment factor) and *C* (evaporation factor) of the 36 Korannaberg rock pools and summary statistics of hydroregime variables (hydroperiod and inundation frequency) modelled over a period of 85 years (1920–2004) including median, mean and standard deviation (SD). The three rightmost columns contain the  $r^2$  and corresponding *P*-values from Pearson correlations between model generated and observed water levels during (a) 25 consecutive days in 2005 (testing dataset), (b) the entire observation period of 50 days in 2005 and (c) eight scattered historic water level measurements in 1993–94 respectively

Pool	Max depth (mm)	Surface (m <sup>2</sup> )	<i>R</i>	<i>C</i>	Hydroperiod (days)			Inundation frequency (inundations/year)			Model versus obs 05 ( <i>n</i> = 25)		Model versus obs 05 ( <i>n</i> = 50)		Model versus obs 93–94 ( <i>n</i> = 8)		
					Median	Mean	SD	Median	Mean	SD	$r^2$	<i>P</i>	$r^2$	<i>P</i>	$r^2$	<i>P</i>	
1	150	0.46	2.4	3.3	5	15	25	12	12	3	0.99	****	0.98	****	0.95	****	
2	55	0.39	7.8	7.5	6	8	6	17	17	3	0.82	****	0.81	****	0.77	**	
3	240	0.79	2.8	2.2	5	17	32	12	11	4	0.95	****	0.96	****	0.95	****	
4	240	4.92	5.2	1.5	4	9	12	15	15	3	0.99	****	0.91	****	0.99	****	
5	275	6.82	5	0.46	6	15	24	12	12	3	0.96	****	0.95	****	0.97	****	
6	370	50	7.2	0.06	10	33	53	7	7	3	0.92	****	0.91	****	0.74	**	
7	310	11.35	4.4	0.18	8	28	50	8	8	3	0.98	****	0.93	****	0.83	**	
8	310	4.18	4.4	0.49	8	32	56	8	8	3	0.99	****	0.98	****	0.75	**	
9	170	1.32	4	1.6	7	17	25	11	11	3	0.99	****	0.98	****	0.85	**	
10	270	16.5	4	0.08	13	69	120	11	11	3	0.96	****	0.92	****	0.61	*	
11	255	6.84	5.6	0.3	9	27	43	11	11	3	0.91	****	0.91	****	0.85	**	
12	340	14.8	4.8	0.13	11	53	93	5	5	3	0.95	****	0.94	****	0.73	**	
13	55	1.06	6.7	1.9	8	10	9	13	16	3	0.94	****	0.91	****	0.57	*	
14	320	17.3	5.2	0.09	14	80	141	4	4	3	0.90	****	0.92	****	0.58	*	
15	100	2.52	4.4	0.75	10	16	18	12	12	3	0.98	****	0.98	****	0.65	*	
16	230	20.6	5.6	0.09	12	42	65	6	6	3	0.95	****	0.94	****	0.67	*	
17	230	4.65	3.6	0.36	8	30	51	8	8	3	0.98	****	0.96	****	0.74	**	
18	240	4.68	3.6	0.37	8	30	52	8	8	3	0.99	****	0.97	****	0.65	*	
19	45	2.79	3.3	0.49	8	11	11	14	14	3	0.83	****	0.70	****	0.77	**	
20	210	3.12	2.4	0.49	7	26	48	9	9	4	0.98	****	0.95	****	0.83	**	
21	280	3.76	4.8	1.4	3	6	9	16	17	4	0.99	****	0.99	****	0.99	****	
22	370	34.2	4.4	0.05	9	41	75	6	7	3	0.98	****	0.93	****	0.91	**	
23	210	13.5	3.6	0.12	8	25	43	6	7	3	0.98	****	0.93	****	0.94	**	
24	180	14.75	5.2	0.14	11	25	36	9	9	3	0.97	****	0.96	****	0.85	*	
25	220	2.12	3.2	0.85	7	26	47	9	9	4	0.99	****	0.97	****	0.98	****	
26	257	4.56	3.2	0.34	8	31	58	8	8	3	0.99	****	0.98	****	0.93	**	
27	340	28.1	6.4	0.42	13	46	72	5	6	3	0.95	****	0.93	****	0.7	n.s.	
28	380	65.9	8	0.03	20	101	172	3	3	2	0.95	****	0.92	****	0.7	n.s.	
29	182	2.96	3.6	0.63	8	24	40	9	9	3	0.99	****	0.97	****	0.95	**	
30	182	8.04	3.4	0.24	5	12	19	13	13	3	0.94	****	0.87	****	0.88	**	
31	260	63.2	6.4	0.03	16	60	96	4	5	2	0.98	****	0.95	****	0.65	n.s.	
32	220	3.84	3.2	0.42	7	26	46	9	9	4	0.99	****	0.98	****	0.91	**	
33	190	8.12	3.2	0.14	12	52	86	5	5	3	0.97	****	0.95	****	0.71	n.s.	
34	160	23	4.8	0.08	10	21	29	11	10	3	0.93	****	0.89	****	0.85	*	
35	180	13.25	4.8	0.21	9	20	29	11	10	3	0.99	****	0.95	****	0.93	**	
36	150	6.74	4	1	2	3	3	16	17	4	0.99	****	0.85	****	0.98	****	
											<b>Avg</b>	<b>0.96</b>		<b>0.93</b>		<b>0.81</b>	
											<b>SD</b>	<b>0.04</b>		<b>0.06</b>		<b>0.13</b>	

*P*-values: \* $<0.05$ ; \*\* $<0.01$ ; \*\*\* $<0.001$ ; \*\*\*\* $<0.0001$ ; \*\*\*\*\* $<0.00001$ ; n.s., non significant.

inundations in the 2005 rainy season with an average  $r^2$  of  $93 \pm 6\%$  (Fig. 2, Table 1). All correlations were highly significant ( $P < 0.00001$ ). Only during the fourth inundation, when pools were almost completely filled, was water level overestimated by

1–2 cm. Splitting the dataset into training and testing datasets only slightly affected model accuracy as model generated values fitted the observed series in the testing dataset with an average  $r^2$  of  $96 \pm 4\%$ . All correlations between modelled and observed water

levels were highly significant ( $P < 0.00001$ , Table 1). Historic water level observations in the 36 study pools during 1993–94 were fitted with an average  $r^2$  of  $81 \pm 13\%$ . For all but four pools this correlation was significant or highly significant (Table 1).

#### Reconstructed hydroregime

Average predicted hydroperiod in the 36 study pools varied between 3 and 101 days. Predicted inundation frequency ranged from 3 to 17 inundations per year (Table 1). Variation in predicted hydroperiod was high, with standard deviations ranging from 3 days for small shallow pools up to 171 days for large deep pools, resulting in significant correlations between 'SD hydroperiod', 'max depth' and pool area respectively (Table 2). Variation in number of inundations was relatively low with standard deviations ranging from two to four inundations per year.

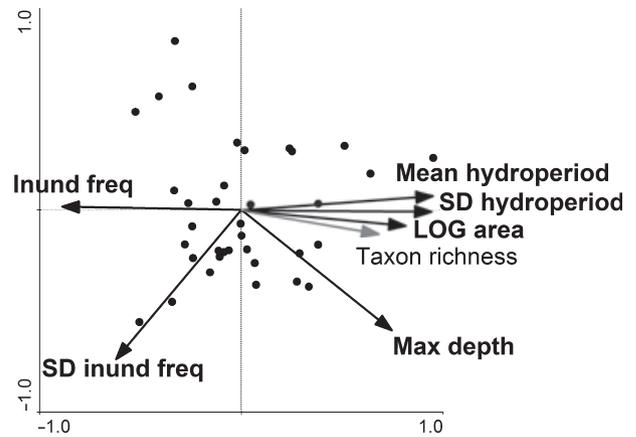
#### Collinearity of morphometry and hydroregime

The general collinearity between hydroregime and habitat size is visualised in a PCA biplot (Fig. 3) in which 84.9% of the variation in morphometrical and hydrological variables among pools is captured by the first two PCA axes. All correlations between morphometrical and hydrological variables were

**Table 2** Pearson correlations ( $r$ ) between habitat size variables and simulated hydroregime variables (all variables were log transformed except max depth, inund freq and SD inund freq)

	$r$	$P$
Area $\times$ max depth	0.65	***
Area $\times$ hydroperiod	0.61	***
Area $\times$ SD hydroperiod	0.58	***
Area $\times$ inund freq	-0.64	***
Area $\times$ SD inund freq	-0.44	**
Max depth $\times$ hydroperiod	0.39	****
Max depth $\times$ SD hydroperiod	0.48	****
Max depth $\times$ inund freq	0.42	****
Max depth $\times$ SD inund freq	0.01	n.s.
Hydroperiod $\times$ SD hydroperiod	0.97	****
Hydroperiod $\times$ inund freq	0.84	****
Hydroperiod $\times$ SD inund freq	0.33	****
Inund freq $\times$ SD inund freq	0.27	***
Inund freq $\times$ SD hydroperiod	0.33	****
SD hydroperiod $\times$ SD inund freq	0.27	***

Significance is indicated as follows: n.s., non-significant; \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ; \*\*\*\* $P < 0.0001$ .



**Fig. 3** Biplot based on a PCA (first two axes explaining 84.9% of total variation) illustrating the relationships between hydroregime (mean hydroperiod, SD hydroperiod, inund freq and SD inund freq) and morphometrical variables (log area; max depth) for the 36 studied pools. Taxon richness is plotted as a supplementary variable.

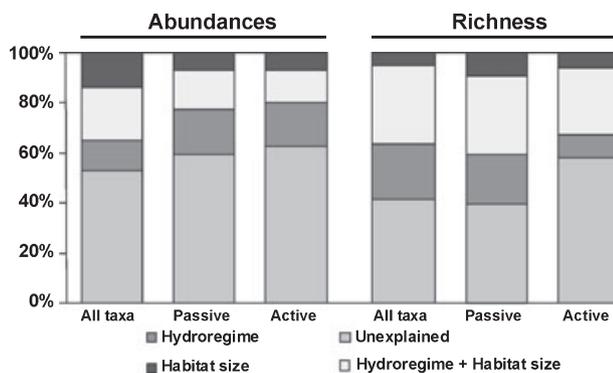
explicitly tested and corresponding  $P$ -values are given in Table 2. Hydrological variables were, in general, strongly correlated with one another except for the variable 'SD inundation frequency', which was only weakly correlated with the other hydrological variables. The morphometrical variable 'log area' was significantly correlated to the commonly used hydroregime variables 'hydroperiod' ( $r = 0.61$ ) and 'inundation frequency' ( $r = 0.64$ ). 'Max depth' on the other hand was only weakly correlated to 'hydroperiod' ( $r = 0.39$ ) and 'inundation frequency' ( $r = 0.41$ ).

#### Invertebrate community structure

Overall we found significant effects of both habitat size and hydroregime on invertebrate community structure, with variation partitioning revealing significant contributions of both morphometric (abundances: 24%, richness: 36%) and hydrological variables (abundances: 37%, richness: 54%) in explaining variation in the invertebrate data matrices (Table 3, Fig. 4). Together, habitat size and hydroregime explained a substantial amount of the total variation in invertebrate communities (abundances: 47%, richness: 59%). A relatively large amount of variation in community structure consists of variation that is explained in common by hydroregime and habitat size variables: 15% (abundances) and 31% (richness). Both habitat size and hydroregime also

**Table 3** Variation partitioning (%) on RDA (redundancy analysis) models of invertebrate data matrices (all taxa, passive dispersers, active dispersers) based on of absolute abundance and taxon richness respectively, with corresponding *P*-values. [Hs + H] = total explained variation by all variables in the model. [Hs] = variation explained by habitat size variables. [H] = variation explained by hydrological variables. [Hs - H] = pure habitat size variation. [H] = pure hydrological variation. [Hs ∩ H] = variation shared by habitat size and hydrological variables and 1 - [Hs + H] = unexplained variation. (a) Results obtained after inclusion of hydrological variation reconstructed by means of the model. (b) Results obtained after including observed hydroperiod during the sampling season as hydrological variable

	All invertebrate taxa				Passive dispersers				Active dispersers			
	Abs. abund.		Richness		Abs. abund.		Richness		Abs. abund.		Richness	
	RDA	<i>P</i>	RDA	<i>P</i>	RDA	<i>P</i>	RDA	<i>P</i>	RDA	<i>P</i>	RDA	<i>P</i>
(a)												
[Hs + H]	47	0.001	58.7	0.001	40.7	0.001	60.4	0.001	37.3	0.001	42.1	0.007
[Hs]	23.9	0.001	36.3	0.004	22.8	0.001	40.4	0.002	19.9	0.001	32.9	0.004
[H]	37.1	0.001	53.6	0.001	33.6	0.001	51.2	0.001	30.3	0.001	36.3	0.003
[Hs - H]	9.1	0.004	5.1	0.18	7.1	0.048	9.2	0.049	7	0.096	5.9	0.27
[H - Hs]	22.3	0.005	22.4	0.009	17.9	0.002	20	0.015	17.4	0.017	9.2	0.35
[Hs ∩ H]	14.8		31.2		15.7		31.2		12.9		27	
1 - [Hs + H]	53		41.3		59.3		39.6		62.7		57.9	
(b)												
[Hs + H]	28.7	0.001	41	0.001	28.3	0.001	46	0.001	22.4	0.001	32.9	0.003
[Hs]	23.9	0.001	36.3	0.004	22.8	0.002	40.4	0.001	19.9	0.001	32.9	0.004
[H]	17	0.001	32.3	0.002	19	0.001	34.4	0.001	8.1	0.02	11	0.04
[Hs - H]	11	0.007	8.9	0.11	9.2	0.01	7	0.14	14.3	0.007	22.3	0.006
[H - Hs]	4	0.03	4.9	0.11	5	0.03	5.6	0.07	2.6	0.36	0	0.95
[Hs ∩ H]	13		27.4		14		33.4		5.6		10.6	
1 - [Hs + H]	71.3		59		71.7		59.8		77.6		70.4	



**Fig. 4** Variation partitioning (Borcard *et al.*, 1992) of invertebrate data matrices containing absolute abundances and taxon richness respectively. Analyses were performed on matrices containing all invertebrate taxa as well as on reduced data matrices containing either passive or active dispersers. All six RDA models were obtained using a forward selection procedure. Four components are distinguished: pure hydroregime variation, pure habitat size variation, unexplained variation and the variation component that is shared by both.

explained unique variation in absolute abundances (9 and 22% respectively). Hydroregime, but not habitat size, accounted for unique variation in local taxon richness (22%) (Table 3, Fig. 4).

Compared to variation partitioning results obtained with model-generated hydrological variables (Table 3a), use of only observed hydroperiod during the sample period as a predictor of hydroregime resulted in lower percentages of variation explained in absolute abundances (17% versus 37%) and richness (32% versus 54%) (Table 3b). In general, large deep pools with long hydroperiods and a low inundation frequency were characterised by higher taxon richness, while small shallow pools which experience short hydroperiods, a high inundation frequency and a high variation in inundation frequency were characterised by a lower richness (Table 3, Fig. 3). The presence-absence data matrix was significantly nested, independent of the null model used ( $P < 0.00001$ ).

#### Impact of dispersal mode

Habitat size (c. 20%) and hydroregime (c. 30%) explained a comparable amount of variation in passive and active disperser abundances (Table 3a). In the passively dispersing community component, however, hydroregime explained significantly more variation in taxon richness than in the actively

dispersing community component (51% versus 36%; after correction for habitat size: 20% versus 9%) while effects of habitat size were comparable for passive and active dispersers (33% versus 40%; after correction for habitat size: 5.9% versus 9.2%).

## Discussion

### *Model performance*

Making use of a simple water balance model and long term (85 years) climate data we reconstructed hydrological variation in 36 temporary rock pools. Overall, the good fit (c. 93%) and highly significant correlation coefficients between model-generated and observed water levels in the pools over 50 days in 2005 indicate the accuracy of our model in reconstructing daily water level series. Water level was slightly overestimated during one of four inundation cycles in 2005 after the most intense rains. This probably results from the fact that pool basin sides are slightly wider at the top leading to a slight violation of our bucket model assumption when pools are filled completely. Two validations of the model during time periods not used for parameterisation demonstrated that the model is not only able to reconstruct, but also to predict historical hydrological variation based on historic rainfall and evaporation records and using a limited series of observed water levels for parameterisation. The somewhat weaker correlations in 1993–94 ( $r^2$ :  $81 \pm 13\%$ ) compared to 2005 (average  $r^2$ :  $96 \pm 4\%$ ) probably result from lower statistical power due to the limited number of observations per pool ( $n = 8$ ) in the former time period.

### *Reconstruction of hydroregime*

Our simulations indicated large variation in hydroperiod, especially in deeper pools. Pools with large basins can be filled to a variable extent resulting in a wide range of possible hydroperiods depending on amount of rainfall. The small basin depth of shallow pools, on the other hand, constrains the maximum number of days a pool can retain water without additional precipitation. There was not much variation in the number of inundations per year (inundation frequency), suggesting that this variable is relatively predictable.

### *Invertebrate community structure*

Several researchers have argued that hydroregime (usually only hydroperiod is considered) is the most important community-structuring factor in temporary pools and wetlands (Schneider & Frost, 1996; Theriault & Kolasa, 2001; Jenkins, Grissom & Miller, 2003). This point is supported by our study because habitat size and hydroregime together explained roughly half of the observed variation in invertebrate community structure (abundances 47%, local richness 59%). As in our study, most studies have also revealed a positive relationship between various estimates of permanence and richness (Spencer *et al.*, 1999; Eitam, Norena & Blaustein, 2004b; but see Schneider, 1999; Eitam *et al.*, 2004a). RDA models based on reconstructed hydrological variation were twice as successful ( $r^2$  was roughly two times higher) in explaining variation in community structure and richness compared to models based on hydroperiod observations. This indicates that reconstructing hydrological variation may be superior to short-term observations of water presence in explaining community patterns.

Hydroregime and habitat size variables were significantly correlated. Others have also observed that water bodies with larger surface areas are usually deeper and experience longer hydroperiods and fewer inundations per year than smaller ones (e.g. Spencer *et al.*, 1999; Wissinger *et al.*, 1999). Although some studies have corrected for this overlapping variation (Wissinger *et al.*, 1999; Eitam *et al.*, 2004a) it is often not taken into account. Further studies have used habitat size variables, such as maximum depth or surface to volume ratio, as indexes of the duration of inundations (hydroperiod or permanence) and used this to interpret community patterns or life history evolution (e.g. Marcus & Weeks, 1997; Jocqué, Riddoch & Brendonck, 2007). We argue that it may be dangerous to use such predictors because, as was shown in this study, habitat size and hydroregime explain both shared and unique variation in community structure, indicating that their individual effects on biota can be different. Larger pools, which usually provide better homing beacons for flying colonists, may also provide more microhabitats (March & Bass, 1995) and reduce the chance of local extinction by supporting larger populations and providing more stable physicochemical conditions than smaller pools

(Kiflawi, Eitam & Blaustein, 2003). Longer average hydroperiods, in turn, also facilitate the establishment of organisms with a more diverse array of life history strategies (Wissinger *et al.*, 1999) and can also enhance biotic interactions (Schneider & Frost, 1996). In contrast, desiccation frequency (corresponding to inundation frequency) may reset community assembly and is therefore sometimes used as a measure of disturbance (Therriault & Kolasa, 2001). The correlation between maximum depth and average hydroperiod in our study was relatively weak ( $r = 0.39$ ), as was also shown by Brooks & Hayashi (2002) in forest pools in North America. This emphasises the need for cautious use of morphometrical variables to estimate pool permanence. The observed overlap between hydroregime and morphometry indicates that without correction (e.g. using partial CCA/RDA and variation partitioning) any observed community patterns cannot unequivocally be attributed to either of these sets of variables. In addition, as a substantial amount of variation in community structure (abundance 12% and local richness 22%) was explained uniquely by hydrological variables, this component is missed when relying solely on predictors based on habitat size.

We expect that the error incurred by using indirect measures of permanence will be even larger in more complex temporary water types where variable groundwater interactions can distort collinearity between morphometry and pool hydrology. In such cases, variation partitioning can provide a solution, enabling researchers to distinguish unique from commonly explained variation (Borcard *et al.*, 1992). Only through modelling or long-term monitoring these effects of habitat size can be statistically uncoupled from effects of hydroregime.

#### *Impact of dispersal mode*

Besides the commonly accepted paradigm of random dispersal followed by non-random, site-specific mortality (species sorting; Leibold *et al.*, 2004), habitat selection (e.g. by actively dispersing aquatic insects) provides an alternative community structuring mechanism (Binckley & Resetarits, 2005). We found clear effects of dispersal mode on the response of invertebrate communities to habitat size and hydroregime. As was demonstrated by variation partitioning, hydroregime was more important for the local richness of

passive than for active dispersers, while no clear differences were found in the amount explained of variation in abundance. In temporary aquatic habitats, passively dispersing organisms are, in general, permanent pool inhabitants that survive desiccation *in situ* (Panov & Cáceres, 2007). As a result, they are exposed to continuous selection pressures imposed by the hydroregime of the habitat, which continuously moulds the community. Conversely, the ability to actively migrate offers species the chance to rapidly colonise after inundation and exploit resources, often without having to face the consequences of desiccation. As a result, catastrophic events such as a succession of very short inundations will have more severe consequences for the coexistence of passively dispersing permanent pool inhabitants (e.g. through exclusion of species with longer aquatic life cycles), than for the local richness of active dispersers that are able to rapidly recolonise habitats. Differences between passive and active dispersers are, however, not always clear and exceptions have to be made for those taxa that, for example, lay their eggs during the dry phase, and hence do not possess reliable cues about the next inundation (Wiggins *et al.*, 1980). Because many temporary pool organisms produce dormant life stages, current communities may not only reflect the conditions (e.g. hydroperiod) of the present inundation but also the success of species recruiting propagules to the propagule bank during previous inundations (storage effect; Warner & Chesson, 1985). This may explain why average hydroperiod and desiccation frequency and their variation were more relevant in explaining community structure ( $r^2 = 34\%$  versus  $19\%$ ) and richness ( $r^2 = 51\%$  versus  $34\%$ ) of these taxa than hydrological snapshots (hydroperiod of the inundation during which communities were sampled).

#### *Conservation implications*

Although caution is needed when generalising patterns observed in individual systems, some degree of generalisation is a prerequisite for the development of reliable guidelines for the conservation management of temporary aquatic habitats. This is particularly relevant because many temporary aquatic habitats worldwide have been destroyed or degraded in recent decades (King, Simovich & Brusca, 1996; Davies & Day, 1998; Eder & Hödl, 2002). Previous research has

confirmed that bigger pools tend to persist for longer and contain more species. Our study has shown that habitat size and hydroregime not only have mutual but also unique effects on community structure and diversity. This indicates that in order to conserve diversity it will be necessary to protect habitats of different sizes and permanence classes (when not clearly correlated). Nested subset patterns of invertebrate taxon richness, as also found by Baber *et al.* (2004), support the idea of a higher conservation value of large, more permanent systems. This, however, does not mean that small pools are expendable as they often contain exclusive taxa (Williams *et al.*, 2004; De Meester *et al.*, 2005) and may fulfil a crucial function as stepping stones between larger pools, helping to maintain metacommunity and metapopulation dynamics and stability (Leibold *et al.*, 2004). Quantification of long-term hydrological variation based on simple modelling may greatly improve the resolution of studies that aim to explain community and population patterns along hydrological gradients. Thus, the current model and the tools we used to uncouple effects of habitat size from hydroregime may help to develop reliable conservation measures for threatened temporary pool habitats and their biota.

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