

## The influence of changing hydroregime on the invertebrate communities of temporary seasonal wetlands

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**Abstract.** Community dynamics in temporary waters are constrained by the hydroregime (depth, timing, duration, frequency, and predictability of water in an aquatic habitat), which in turn is influenced by climatic patterns and anthropogenic use of water in the landscape. Declining rainfall in regions with a Mediterranean climate, such as southwestern Australia, has decreased the depth and duration of water in temporary wetlands, potentially altering the composition of invertebrate communities. We used a long-term data set (6–25 y) to examine temporal changes in hydroregimes and aquatic invertebrate diversity (based on species presence/absence) at 9 seasonal wetlands. The study wetlands maintained distinctly seasonal hydroregimes, despite declining rainfall and the contraction of wetland hydroperiods. Distance-based redundancy analysis (dbRDA) indicated that conductivity,  $\text{NO}_3^- + \text{NO}_2^-$ , and turbidity were the most important factors explaining the changes in invertebrate community composition over time. Allocation of species into 4 trait-based groups based on their resilience to or resistance of drought and their mode of recolonization of a water body upon rewetting revealed that the fauna is dominated by active dispersers. This result suggests that the proximity of source wetlands from which mobile invertebrate species and vertebrate vectors, such as waterbirds, can recolonize seasonal wetlands is an important factor influencing the invertebrate community response to rewetting. Despite the decline in water availability, we found little evidence of a shift to a more arid-adapted fauna. We suggest that the maintenance of a mosaic of wetlands of varying hydroregimes at the whole-landscape scale will be critical to the future persistence of aquatic invertebrate communities in Mediterranean regions where the frequency and intensity of droughts is predicted to increase.

**Key words:** seasonal wetlands, hydroregime, invertebrates, climatic change, resilience, Mediterranean climate.

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The components of a hydroregime, including the predictability, frequency, and duration of water in an aquatic habitat, have a fundamental influence on aquatic community structure and diversity (Brooks 2000, Williams 2006, Vanschoenwinkel et al. 2009). In particular, the duration of water present at a site (the hydroperiod) can directly influence the types of taxa able to occur there by constraining the length of life cycles and altering the relative importance of biotic interactions that structure community

composition (Schneider and Frost 1996, Wissinger 1999, Vanschoenwinkel et al. 2010). Hydroperiod is arguably the 'most influential hydrologic parameter in temporary waters' (Brooks 2000).

Temporary wetlands are water bodies that do not hold water continuously and include wetlands that fill predictably on a seasonal basis and those that fill only after episodic or unpredictable inflows (Williams 2006, Lake 2011). Dynamics in temporary waters are driven by often unpredictable periods of drying that force aquatic biota either to disperse or to use a dormancy strategy (e.g., aestivation or desiccation-resistant eggs) to persist through the disturbance (Williams 1985). These types of adaptations allow the biota of temporary waters to tolerate dry periods, whereas biota from more predictable (perennial) aquatic ecosystems may be more severely affected by occasional droughts (Williams 2006). Therefore, the occurrence of a drying phase should not necessarily be considered 'adverse or catastrophic' for the biota of temporary wetlands (Brock et al. 2003). Invertebrate taxa that persist in temporary wetlands usually do so by reaching a tolerant phase of their development before the wetland dries (Wellborn et al. 1996). Very temporary environments tend to support species with short life cycles, and some of these species rarely occur in more perennial habitats (Wellborn et al. 1996). More mobile invertebrates may disperse across the landscape in wetter years and retract to more reliable habitats when conditions are drier (Wellborn et al. 1996).

Temporary wetlands are significant from a global perspective because, although they may not always be wet, they make up a large proportion of the Earth's freshwaters and support much of its freshwater biodiversity (Williams 2006). Temporary wetlands also play an important role in facilitating the movement of species at a landscape scale (Nicolet et al. 2004). In areas where few perennial water bodies exist, temporary systems have even greater importance in supporting the survival of species and metapopulations (Williams 1985).

Ongoing climatic warming and associated changes in precipitation (IPCC 2007) are a substantial threat to the biodiversity of freshwater ecosystems that is compounded by the effects of changing land use and invasive species (Sala et al. 2000). Climate-driven changes to wetland hydrology have been identified as a key global wetland conservation issue (Roshier et al. 2001, Klein et al. 2005, Waterkeyn et al. 2008) and may have a major impact on shallow wetlands that do not hold water year-round (Carter Johnson et al. 2005, Pyke 2005). Despite its importance, relatively little is known about the effects of supraseasonal drought on

the ecological dynamics of temporary standing waters (Lake 2011).

We expect the biota of temporary waters to have some ability to tolerate drought conditions. However, prolonged droughts may have an adverse effect on the ability of systems to recover. The degree to which systems are affected depends partly on the usual flooding frequency of the wetland (Jenkins and Boulton 2007) and on the prior history of drying in the system (Lake 2011). Climate change is likely to cause an accelerated loss of temporary wetlands because of their dependence on local weather conditions, especially precipitation (Brooks 2000, Serrano and Fahd 2005), and because they are already subject to high rates of development and drainage (Wissinger 1999, Williams et al. 2001).

We investigated the relationships between changes in precipitation, wetland hydroregimes, and invertebrate community composition using a long-term data set (6–25 y) compiled for 9 temporary seasonal wetlands on the Swan Coastal Plain, in southwestern Western Australia. Long-term data sets that allow examination of temporal trends in persistence and stability are rare in freshwater ecology. A major advantage of long-term data sets is the opportunity they provide to interpret changes that include unusual and episodic events and interannual variability. We sought to assess whether a long-term drying trend evident in rainfall records for southwestern Australia has affected wetland hydroregimes and the invertebrate communities they support.

## Methods

### *Site description*

The attributes of long-term (6–25 y) climatic, hydrological, and ecological data sets collected for 9 wetlands on the Swan Coastal Plain (SCP) in the southwest of Western Australia, are given in Table 1. The 9 wetlands are on the Jandakot Groundwater Mound, ~25 km south of the city of Perth (population ≈ 1.7 million) (Fig. 1) and are isolated basin (depressions) water bodies. The wetlands display markedly seasonal hydrographs with maximum depths occurring in late winter–spring and drying in summer or autumn (Fig. 2). They usually are described as seasonal wetlands characterized by a relatively predictable filling and drying regime, and they represent a subset of temporary wetlands.

The wetlands (also called lakes and swamps) range in size from ~3 to 254 ha and are clear (nonturbid), macrophyte-dominated systems, with 1 exception (Shirley Balla Swamp lacks submerged macrophytes). Most wetlands on the Jandakot Groundwater Mound

TABLE 1. Summary of long-term climatic, hydrological, and ecological data sets available for Jandakot Mound wetlands. Climatic data are from the Australian Bureau of Meteorology. Monthly rainfall was recorded at the Perth Airport from 1944 to 2008. Hydrological data are from the Water Information (WIN) database (discrete sample data), and the Hydstra database (time series data), Department of Water, Western Australia. Ecological data are from the Aquatic Ecosystems Research Group, Murdoch University. Depths were recorded approximately monthly to fortnightly at Warton Road Swamp, Shirley Balla Swamp, Lake Banganup, Forrestdale Lake, and Lake Balannup, but some years have missing data.

Wetland	Code	Wetland depth in Australian Height Datum (m AHD)	Water quality	Aquatic invertebrate families (presence/absence)
Thomson's Lake	TL	1952–2008	1996–2008	1989–1990, 1992, 1994, 1996–2008
Lake Kogolup South	KS	1968–2008	1996–2008	1989–1990, 1992, 1994, 1996–2008
Lake Kogolup North	KN	1993–2008	1996–present	1989–1990, 1992, 1994, 1996–2008
Lake Banganup	BA	1963–2008	1996–2008 <sup>a</sup>	1989–1990, 1992, 1994, 1996–2008 <sup>a</sup>
Shirley Balla Swamp	SB	1993–2008	1996–2008	1996–2008
Gibbs Road Swamp	GR	1991–2008	1996–2008	1996–2008
Warton Road Swamp (Harrisdale Swamp)	WR	1999–2008	1996–2008	1996–2008
Forrestdale Lake	FL	1952–2008	2001–2008	2001–2008
Lake Balannup	BL	1973–present	2001–2008	2001–2008

<sup>a</sup> Dry since 2002



FIG. 1. Map of the Jandakot monitoring wetlands showing wetland locations in relation to the coast and the maximum groundwater contours for the Swan Coastal Plain. See Table 1 for wetland codes.

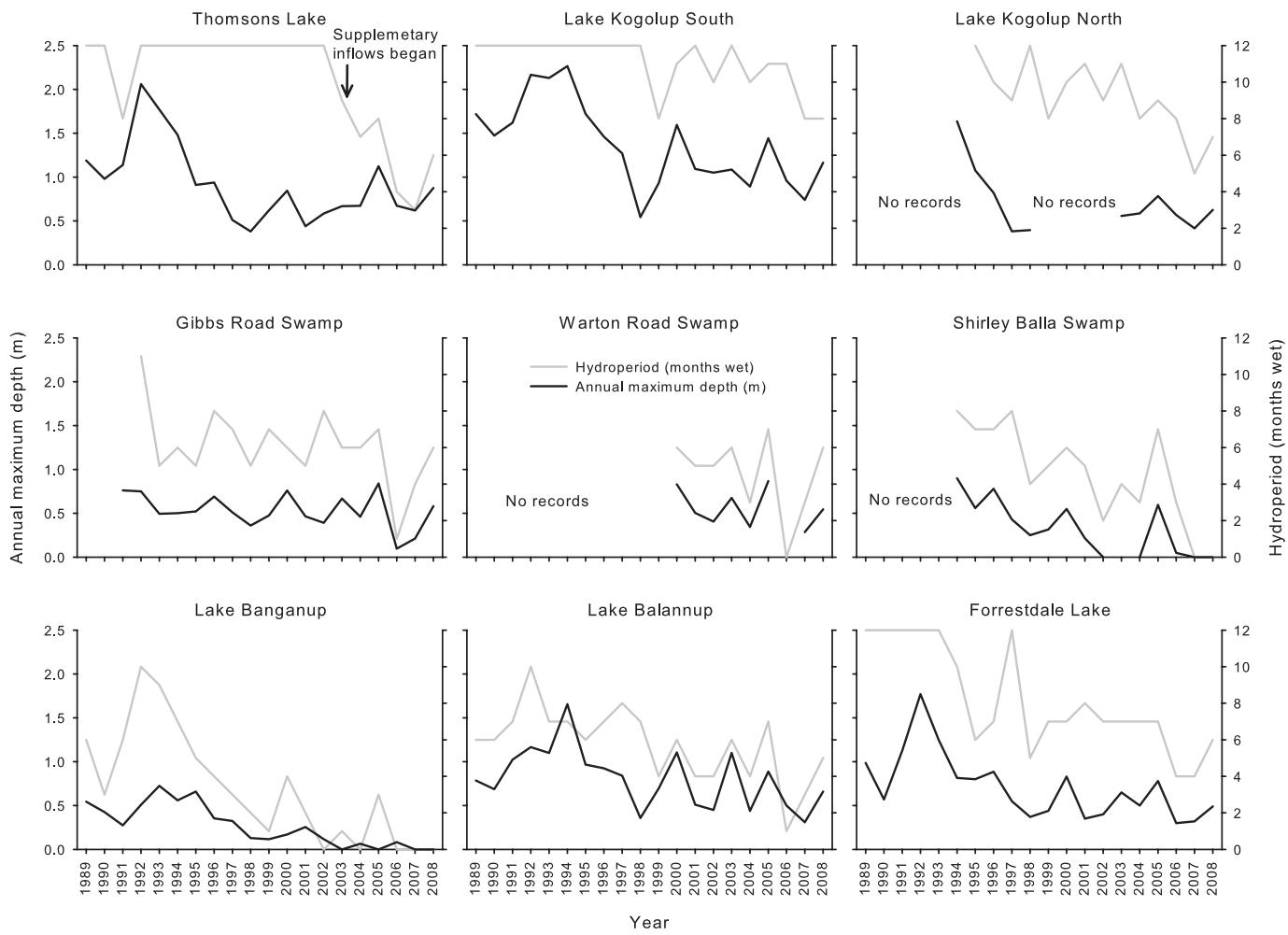


FIG. 2. Hydrographs displaying changes in annual maximum water depths and hydroperiod at the Jandakot monitoring wetlands over time. Note differing lengths of record. Thomson's Lake received supplementary stormwater in winter/spring from 2004 onwards to provide sufficient water for maintenance of annual waterbird breeding (Maher and Davis 2009). Data provided by the Department of Water, Western Australia.

are surface expressions of a shallow, unconfined aquifer that flows from east (inland) to west (coast) (Smith and Hick 2001). They act as flow-through lakes, capturing ground water on the up-gradient side of the regional groundwater flow, and discharging it on the down-gradient side. The depth from which the aquifer contributes water is related to the length (but not the depth) of the water body. Lakes that are short in relation to aquifer thickness receive less groundwater than long lakes (Townley and Turner 1992). Rainfall also makes a significant contribution to the largest water bodies, especially Forrestdale Lake (Dawes et al. 2009).

In the region, rainfall and catchment runoff have the greatest effect on groundwater and wetland depth under natural conditions (Horwitz et al. 2009b). The wetlands are affected by a change in water availability

caused by climatic drying and anthropogenic demands for domestic water supply. Declining rainfall contributes first to aquifer recharge and less to filling wetlands (CSIRO 2009a, b). In a recent hydrogeological investigation of the decline in the aquifer (which has been subject to pumping since 1979), investigators found that continuous extraction has caused a doubling in the seasonal change in the height of the water table (Yesertener 2002). We were unable to obtain data on the volumes of ground water pumped from the Jandakot mound for consumptive use, despite multiple attempts to obtain the information.

#### *Invertebrates and water quality*

Invertebrates are regarded as the most suitable ecological indicators for these ecosystems because the

fish fauna is depauperate (Bunn and Davies 1990) and waterbirds respond to changes in hydrology at much larger landscape scales (Storey et al. 1993). Sampling of aquatic invertebrates has been undertaken at 4 wetlands (Thomson's Lake, Lake Kogolup South, Lake Kogolup North, and Lake Banganup) at almost annual intervals since 1989 (Table 1). The establishment of a state-funded biomonitoring program in 1996, driven by concern over the potential environmental impacts of groundwater extraction for domestic consumption, extended data collection to include 3 additional water bodies (Shirley Balla Swamp, Gibbs Road Swamp, and Warton Road Swamp). At that time, the biomonitoring protocol was simplified (see Papas et al. 1997). An additional 2 wetlands (Forrestdale Lake and Lake Balannup) were added to the monitoring program in 2001.

We used species-level information whenever possible (~25% of taxa), and higher-taxonomic-level identifications when species-level data could not be obtained. The lack of species-level identifications reduced our ability to detect some trends in composition related to life history. However, sufficient information was available to assign most taxa to the trait-based groups recognized by Wiggins et al. (1980; Appendix, available online from: <http://dx.doi.org/10.1899/12-024.1.s1>).

Three wadeable habitats were sampled at each wetland, based on the dominant (assessed by % area or cover) habitats present. These included: open water above bare substrate; submerged macrophytes; emergent macrophytes (predominantly *Typha* sp. or *Bau-meia* sp.); floating macrophytes; and trees, predominantly stands of *Melaleuca raphiophylla* Schauer. Invertebrates were collected from each habitat with a long-handled dip net (250- $\mu\text{m}$  mesh) for a period of 2 min. The net was moved in a zigzag motion from the water surface to the bed over bare substrate and within submerged macrophyte beds. The net was forced vigorously upward from stem bases to the water surface of emergent macrophytes and swept amongst submerged branches in *Melaleuca* stands.

Samples were sorted on site while invertebrates were alive, similar to the protocol used in the national Australian River Assessment System (AusRivAS) program (Turak and Waddell 2001). Each sample was picked for 30 min to obtain a maximum of 200 animals or 10 from each family. Where few invertebrates were present in a sweep, further sweeps were collected and picked for a total time of 30 min. Live-picked animals were preserved in 100% ethanol in the field, followed by transfer to 70% ethanol in the laboratory. Preserved specimens were identified to species where possible, and otherwise to family with

the aid of a stereomicroscope and keys provided by Davis and Christidis (1997). Identifications were confirmed by comparison with specimens in a reference collection held by the Aquatic Ecosystems Research Group at Murdoch University, Perth, Western Australia.

Conductivity, pH, and turbidity were measured in situ at wetland habitats using hand-held meters (conductivity: HI 8733 and 933100, Hanna Instruments, Woonsocket, Rhode Island; pH: HI 8424, Hanna Instruments; turbidity: 2100P, Hach, Loveland, Colorado). Water samples were collected for laboratory analysis of color (gilvin), chlorophyll *a*, and nutrients (total P,  $\text{PO}_4^{3-}$ , total N,  $\text{NH}_4^+$ ,  $\text{NO}_3^- + \text{NO}_2^-$ ). These laboratory-based analyses were done with standard methods (APHA 2005) by personnel at the Marine and Freshwater Research Laboratory (National Association of Testing Authorities accredited) at Murdoch University.

#### Data analyses

We ran analyses with the open-source statistical package R (version 2.13.2; R Development Core Team, Vienna, Austria) and PRIMER (version 6; PRIMER-E, Plymouth, UK) and PERMANOVA+ statistical software (PRIMER-E). Box-Cox transformations were done with an online tool (Wessa 2008).

*Univariate analyses.*—We plotted long-term annual rainfall and autumn–early winter rainfall totals for the Perth Airport rainfall station and annual maximum wetland depths and hydroperiods (mo wet/y) as time series to illustrate the within- and between-year fluctuations in water levels. We calculated hydroperiods from water-level monitoring data. We deemed water present when the recorded depth was  $\geq 1$  cm. We interpolated missing data points by examining rainfall data for relevant years and filling patterns at nearby wetlands.

We used Pearson's product moment or Spearman's rank correlations (*cor* and *cor.test* functions in R) to examine the relationships between total annual rainfall and hydroperiod and community richness and hydroperiod at each wetland. Prior to analysis, we examined data for normality and skewness with histograms, quantile–quantile plots (qqplots), the Shapiro–Wilks normality test, and skewness test (*moments* package for R). We used the Box–Cox family of transformations when necessary.

Wiggins et al. (1980) described 4 groups of invertebrates in temporary ponds in southern Ontario based on their resilience or resistance to drought and their mode of recolonization. These categories have proven useful in a wider range of habitats (e.g.,

Schneider and Frost 1996, Wellborn et al. 1996, Brooks 2000) including standing waters in southern Australia (e.g., Lake et al. 1989). The groups are: 1) Group 1—year-round residents incapable of active dispersal and that avoid drying by aestivating as desiccation-resistant cysts or eggs or by burrowing into wet sediments. Taxa include turbellarians, oligochaetes, cladocerans, copepods, ostracods, and gastropods. 2) Group 2—active dispersers that recruit in spring when water is present and depend on water (or water-dependent vegetation) for oviposition. They must reproduce before the water disappears. These species subsequently survive the dry period as desiccation-resistant eggs and larvae. Taxa include ephemeropterans, coleopterans, dipterans, and mites. 3) Group 3—active dispersers that recruit in summer often by laying eggs in damp or dry sediment after the surface water disappears. They survive the dry period as desiccation-resistant eggs and larvae. Group 3 taxa are often colonizers. Taxa include dipterans, trichopterans, and odonatans. 4) Group 4—Active dispersers and migrants that are dependent on water for egg-laying, but adults spend the dry phase in perennial pools or a series of other temporary pools containing water at different stages (Williams 1985). Many are predators. Taxa include odonatans, hemipterans, and coleopterans.

We used this grouping scheme rather than more complex analyses of life-history traits (*sensu* Robson et al. 2011) because not all taxa could be identified to species and few detailed life-history studies exist for the fauna we studied. We summed total richness of each of the trait groups and plotted the data as stacked columns to assess changes visually over time.

**Multivariate analyses.**—We used the DISTLM routine in PERMANOVA+ to run distance-based Redundancy Analysis (dbRDA), a form of constrained ordination, on the entire invertebrate data set after removing an outlier (only 1 taxon recorded, Lake Banganup 2002) to assess the statistical significance of the relationships between species composition and environmental variables. DISTLM analyzes and models the relationship between the community data set and various predictor variables recorded at the same time, and can produce a dbRDA biplot (Anderson et al. 2008). The environmental variables we used in the modelling were the water-quality variables listed in Table 1.

We accounted for the lack of independence arising from the repeated sampling of the 9 wetlands over time as follows. We used a permutational multivariate analysis of variance (PERMANOVA) with 2 factors (site, time) to identify significant variation in the invertebrate data across the sites or through time.

By including ‘Site’ as a factor in the model, we incorporated the clustering structure inherent through time (i.e., the repeated measures) in the analysis (M. J. Anderson, Massey University, personal communication). A significant result indicated that the factor sites had to be added into the DISTLM analyses to account for the temporal nature of the data set. We created dummy binary variables to code for site and time. We then added these dummy variables to the environmental data file and labeled them with indicators to enable analysis of variables in sets (all site dummy variables were in 1 set, and all time dummy variables in another set). We ran post hoc pairwise comparisons (by site) as part of the PERMANOVA to examine separation between sites based on invertebrate community composition. We adjusted significance levels to account for the multiple comparisons.

When running the dbRDA with the DISTLM routine in PERMANOVA+, we ran analyses conditional on site (forcing its inclusion) to retain the repeated-measures nature of the analysis and to make the environmental variables conditional on known differences among sites. We then ran all of the RDA tests (including sequential tests) on residuals after taking into account the site factor (group of dummy variables). We ran several forms of model fitting, including the Akaike Information Criterion for small groups (AICc) and the Bayesian Information Criterion (BIC) in the DISTLM procedure to assess the most parsimonious model (best fit with least number of variables) (Anderson et al. 2008).

Before analysis, we removed 7 site/time combinations from the environmental data set to exclude site/time combinations for which invertebrate data were not available. A final total of 99 site/time combinations were available for the analysis. We examined environmental variables for normality and skewness with histograms, qqplots, the Shapiro-Wilk normality test, and skewness test (*moments*) and we applied the Box-Cox family of transformations as needed (Wessa 2008). Normality is not required for ordinations, but skewness must be reduced (Legendre and Birks 2012). After transformation, we standardized environmental variables so they could be compared on the same scale with the standardized transformation in the *decostand* function of the *vegan* package in R (Borcard et al. 2011). We also removed 7 site/time combinations from the invertebrate data set to exclude combinations for which environmental data were not available, leaving a total of 99 for the analysis. We distance-transformed presence/absence invertebrate data with the Hellinger transformation in the *decostand* function of *vegan* (Borcard et al. 2011).

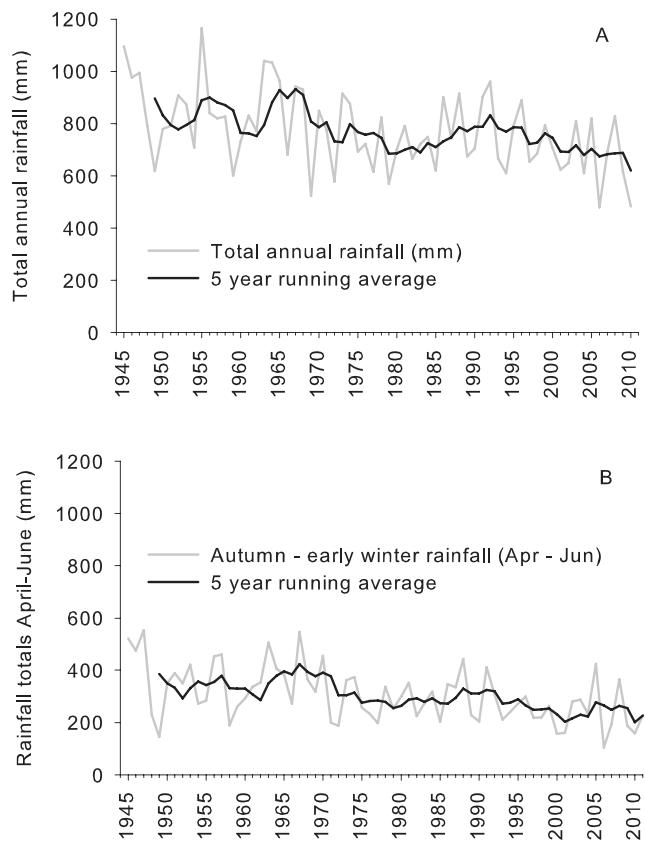


FIG. 3. Totals and 5-y running averages for total annual rainfall (A) and autumn–early winter rainfall totals (April–June) (B) at the Perth Airport rainfall station 1944–2008. Data provided by Australian Bureau of Meteorology.

## Results

### Climate and hydrology

Long-term precipitation records for Perth Airport (the closest long-term station to the Jandakot region) showed a decline in annual totals over time since 1944, but the seasonal pattern of wet winters and dry summers has remained unchanged (Fig. 3A). Annual rainfall ranged from 479.6 to 1164.7 mm/y between 1944 and 2008 (mean =  $781.2 \pm 17.9$  [SE], median = 785.0 mm/y). Late autumn–early winter precipitation totals showed a temporal decline similar to annual totals (Fig. 3B).

Wetland hydrographs revealed a drying trend since the start of records, with annually decreasing maximum water depths and shortening hydroperiods (Fig. 2). Changes were most marked at the shallowest sites, and 2 wetlands (Lake Banganup and Shirley Balla Swamp) rarely contained water in recent years (Fig. 2). Lake Banganup was the most severely affected wetland and was functionally dry in all but 2 y over the last decade (Fig. 2). A temporary increase

TABLE 2. Pearson's product-moment or Spearman's rank correlations between annual maximum depth and hydroperiod (months wet each year) at the Jandakot monitoring wetlands.  $r$  = Pearson's product-moment coefficient,  $\rho$  = Spearman's rank correlation coefficient.

Wetland	df	$p$	$r$ or $\rho$
Thomson's Lake		0.831	$\rho = -0.051$
Lake Kogolup South	13	0.088	$r = 0.456$
Lake Kogolup North	9	0.210	$r = 0.410$
Gibbs Road Swamp	15	0.002	$r = 0.700$
Warton Road Swamp	6	0.003	$r = 0.889$
Shirley Balla Swamp	6	0.005	$r = 0.874$
Lake Banganup	18	0.005	$r = 0.605$
Lake Balannup	18	<0.000	$r = 0.971$
Forrestdale Lake		<0.000	$\rho = 0.820$

in water depths occurred through the early 1990s, with high maximum depths coinciding with a period of high rainfall (Fig. 2, Fig. 3A, B). Maximum depths have decreased since then as rainfall has declined (Fig. 2, Fig. 3A, B), and 5 of the 9 wetlands did not hold water in 2006, the driest year on record (479.6 mm) during the study period. Annual maximum depth was significantly correlated with hydroperiod at 6 wetlands (Table 2). Total annual rainfall was significantly correlated with hydroperiod at only 2 wetlands (Gibbs Road Swamp:  $r = 0.72$ ,  $p < 0.05$ ; Warton Road Swamp:  $r = 0.86$ ,  $p < 0.05$ ), both shallow wetlands on the eastern (inflow) side of the groundwater mound.

### Species composition and environmental factors

Hydroperiod was significantly correlated with invertebrate community richness at only 1 wetland (Lake Kogolup North;  $r = -0.606$ ,  $p = 0.022$ ). No trends were detected in the numbers of taxa belonging to each of the 4 Wiggins faunal groups (Fig. 4). In most years, the fauna was dominated by taxa that actively disperse (groups 2, 3, and 4 combined). Taxa in group 1 (passive dispersers) made up ~1/4 of the taxa in most years. The most common group-1 taxa included ostracods (Cyprididae), cladocerans (Daphniidae and Chydoridae), cyclopoid copepods, and isopods (Amphipodidae). Common group-2 taxa included coleopterans (Dytiscidae and Hydrophilidae), chironomids, and mites (Pionidae). Group-3 taxa (colonists that do not need water for egg laying) were relatively rare. Those recorded included damselflies (Lestidae), mosquitoes (Culicidae), and dragonflies (Libellulidae). Group-2 and group-4 taxa were more common in 1992, a high rainfall year, than at other times.

A DISTLM analysis run in PERMANOVA+ with a forward-selection procedure and the  $R^2$ -selection

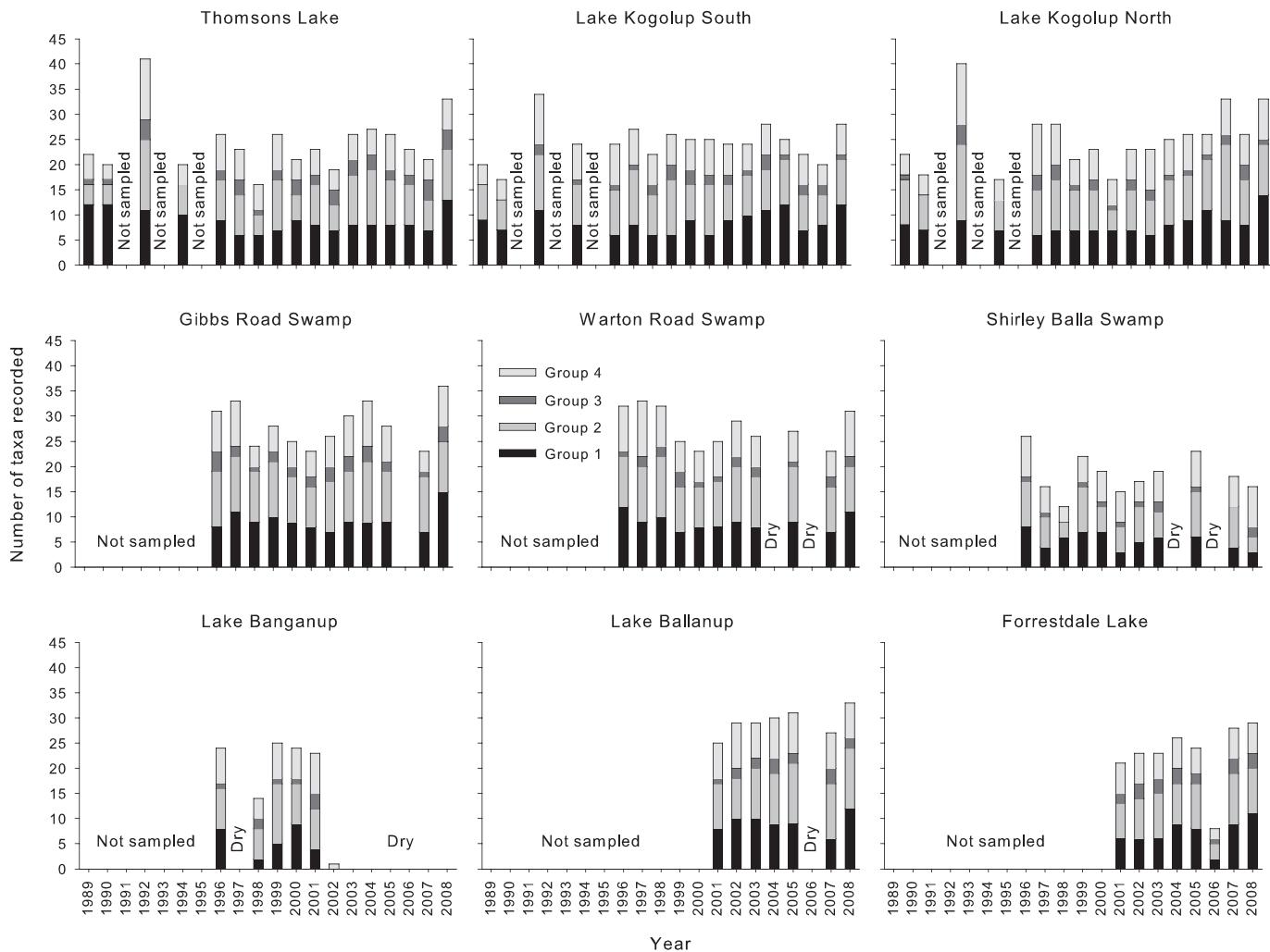


FIG. 4. Numbers of invertebrate taxa collected at Jandakot wetlands over time. Taxa were categorized into groups based on strategies for evading dry periods and recolonizing wetlands (Wiggins et al. 1980). Group 1: stay in pools and avoid dry phase (resistant or burrow into sediment); Group 2: residents, capable of active dispersal, must oviposit on water (or water-dependent vegetation), dormant in dry period; Group 3: similar to group 2, but do not need water for oviposition; Group 4: residents capable of active dispersal, spend dry phase in perennial water.

criteria showed that all the environmental variables and the sites variable together explained 46.22% of the variation in the response data. Including  $>4$  variables in the model that gave nonsignificant results for conditional tests. We reran the DISTLM analysis using different options for model selection. The best procedure for AICc and for BIC selection criteria both generated best models that used the variables site (forced inclusion), conductivity,  $\text{NO}_3^- + \text{NO}_2^-$ , and turbidity. The model chosen was the AICc model ( $\text{AICc} = 625.83$ ,  $R^2 = 0.37025$ ).

The dbRDA plot for this model showed fitted variation from the model only, which is why site effects were so clear (because of forced inclusion of

site; Fig. 5). The fitted variables explained a statistically significant part of the variation in the data set, but other variables not measured in our study also appeared to be contributing to the variation observed.

Higher conductivities were associated with Thomson's and Forrestdale Lakes, and these water bodies were clearly separated from the other fresher-water wetlands (Fig. 5). Higher turbidities and  $\text{NO}_3^- + \text{NO}_2^-$  concentrations were associated with 3 wetlands (Lake Banganup, Shirley Balla Swamp, and Lake Kogolup South), whereas lower turbidities and  $\text{NO}_3^- + \text{NO}_2^-$  concentrations were associated with 4 wetlands (Warton Road Swamp, Gibbs Road Swamp, Lake Kogolup North, and Lake Balannup) (Fig. 5).

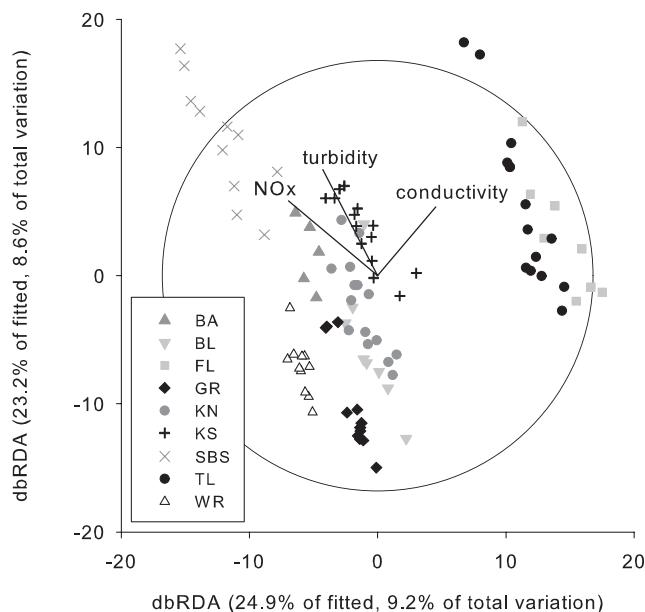


FIG. 5. Distance-based Redundancy Analysis (dbRDA) biplot from Akaike's Information Criterion for small sample sizes model of invertebrate data constrained by all (Box-Cox transformed) environmental variables. Samples are grouped by wetland. Vectors indicate the 4 environmental variables that explained most of the variability in the invertebrate data set.  $\text{NO}_x = \text{NO}_3^- + \text{NO}_2^-$ . See Table 1 for wetland codes and list of environmental variables.

Post hoc pairwise comparisons between sites indicated significant differences (after significance-level adjustment) in invertebrate community composition between some wetlands (Table 3).

TABLE 3. Post hoc pairwise comparisons (from PERMANOVA) of invertebrate community composition between wetlands. Bold indicates a significant difference in community composition between wetlands (after Bonferroni adjustment of significance levels). See Table 1 for site codes.

Wetlands	<i>t</i>	<i>p</i>	Wetlands	<i>t</i>	<i>p</i>
BA, BL	No test		FL, TL	2.2811	0.011
BA, FL	No test		FL, WR	3.011	0.005
BA, GR	1.4899	0.104	<b>GR, KN</b>	<b>2.5345</b>	<b>0.001</b>
BA, KN	1.0569	0.394	GR, KS	1.943	0.006
BA, KS	0.85906	0.618	<b>GR, SB</b>	<b>2.6671</b>	<b>0.001</b>
BA, SBS	1.7501	0.056	<b>GR, TL</b>	<b>3.584</b>	<b>0.001</b>
BA, TL	2.0394	0.02	GR, WR	1.6626	0.021
BA, WR	1.2863	0.185	KN, KS	1.9154	0.012
BL, FL	3.3037	0.003	KN, SBS	2.6832	0.002
BL, GR	2.4454	0.006	<b>KN, TL</b>	<b>3.0786</b>	<b>0.001</b>
BL, KN	3.2265	0.004	<b>KN, WR</b>	<b>2.4208</b>	<b>0.001</b>
BL, KS	2.8254	0.008	KS, SBS	2.0147	0.007
BL, SBS	2.3584	0.009	<b>KS, TL</b>	<b>2.1456</b>	<b>0.001</b>
BL, TL	4.8549	0.002	KS, WR	2.0984	0.004
BL, WR	2.3371	0.013	<b>SBS, TL</b>	<b>3.0937</b>	<b>0.001</b>
FL, GR	4.0834	0.004	SBS, WR	2.5894	0.002
FL, KN	3.0048	0.002	<b>TL, WR</b>	<b>3.5225</b>	<b>0.001</b>

## Discussion

### Have wetland hydroregimes changed over time?

Hydroregimes at the study wetlands showed a drying trend over the period of record, and both depths and durations declined over time. Lake Banganup has remained dry for over a decade. These changes appear to be linked to a decline in water availability that can be attributed to the documented decline in rainfall in southwestern Australia (Bates et al. 2008) and decreasing ground water levels caused by consumptive uses (Yesertener 2002). The timing of wetting in autumn–winter is still predictable, despite less water entering the wetlands at these times.

### Have changes in hydroregimes resulted in changes in invertebrate community composition?

We found no evidence to suggest that changes to wetland hydroregimes have altered invertebrate community composition in spring (the time of maximum water depth) over the study period. For example, 4 of the 5 wetlands that did not fill in the low-rainfall year of 2006 contained invertebrate communities very similar to previous years when the wetlands refilled in 2007. Had documented changes in hydroregime caused a shift to a shorter hydroperiod and more arid-adapted fauna, we would have expected an increase in the proportion of taxa with traits such as desiccation-resistant eggs and short generation times, e.g., Copepoda and Ostracoda (group 1). These types of faunal changes might be driven both by the loss of nonadapted fauna, and over

longer time scales, by the arrival of arid-adapted immigrants from further inland. However, neither an increase in arid-adapted taxa nor a decrease in mesic-adapted taxa (those vulnerable to drying but capable of active dispersal) was evident (Fig. 4). This result suggests that the wetlands are still functioning within a range of natural hydrological variability of which the current fauna are tolerant and that the drying trend to date may not have been long enough to alter patterns of composition at the time of maximum depth in mid-spring (the time that our sampling targeted). In addition, the fluctuations in physico-chemical variables influenced by hydrology (e.g., temperature, pH, dissolved O<sub>2</sub>, salinity) also must have remained within acceptable limits.

Several potential explanations for the apparent resilience of the Jandakot wetland invertebrate fauna can be invoked. Climatically, southwestern Australia is considered to have been more arid in the past, with maximum aridity estimated to have occurred during the Last Glacial Maximum, ~18,000 y before present (De Deckker and Williams 1986). The Australian biota, in general, is considered to have experienced filters of increasing aridity throughout the Quaternary, with precipitation in the present interglacial phase not exceeding previous phases (Morton et al. 2011). Studies reconstructing the palaeoclimate of SCP wetlands during the Holocene have resulted in diverging views, although investigators agree that almost the entire plain would have been submerged during the mid-Holocene when sea levels were 0.5–0.9 m higher than present (Horwitz et al. 2009b). Horwitz et al. (2009a) found that the relatively high occurrence of active dispersers in SCP wetlands could be attributed to invertebrate colonization from cooler southern and warmer northern areas during relatively recent phases of alternating aridity and wetter periods and sea-level fluctuations. It seems likely that the decline in annual precipitation recorded since 1944 has not yet exceeded the severity of past aridification.

Despite reduced periods of inundation, those study wetlands that still fill annually receive their water predictably, in autumn or winter, in contrast with the infrequent and episodic regimes of arid-zone wetlands. Wetland hydroperiods remain >4 to 5 mo long (Fig. 2), providing sufficient time for most invertebrate taxa that occur in temporary wetlands to complete the aquatic phase of their life cycles (Williams 2006), as long as they arrive at the wetland in sufficient time before drying.

The study wetlands are part of a mosaic of perennial and temporary wetlands through the Jandakot region (Balla 1993, Davis et al. 1993) that are potential sources of passive and active dispersers

for recolonization each time they are rewet. The egg bank of temporary wetlands may be long-lived, made up of multiple generations, and unexhausted after a single wetting event (Brock et al. 2003), providing source populations for many resident taxa.

Some investigators have found higher species richness in perennial wetlands than in comparable or nearby temporary systems, but this result may be an artefact of the larger size and greater number of habitats present at perennial wetlands (Wissinger 1999). In contrast, the high variation in species composition over time at temporary wetlands may contribute greatly to its biodiversity (Balla and Davis 1993, Brendonck and Williams 2000, Robson and Clay 2005). This possibility has not been captured by the current data set, which includes only 1 measurement of diversity at each wetland per year at maximum water depth, precluding detection of the effects of hydrological change on intra-annual diversity.

The story told by the data so far may not reveal the effects of longer-term drying. Lake Banganup has now been dry for nearly a decade, so if it were to refill in the future, invertebrate richness is likely to have decreased because of depletion of the egg bank. Frequency of rewetting is critical to community composition because some species that can tolerate short dry periods (e.g., amphipods, isopods, some leeches, some mollusks, and some caddisflies) may not survive in temporary wetlands if dry periods become too long (Wiggins et al. 1980). Despite the long viability of some diapausing eggs, a long-term lack of flooding will deplete the egg bank and reduce its diversity (Hairston and Kearns 2002, Brock et al. 2003). Jenkins and Boulton (2007) found a decline in egg banks after 6 to 20 y of drying in Australian arid-zone wetlands. The numbers of resistant microinvertebrates, particularly cladocerans, declined with time since last inundation. This decline was accompanied by a reduction in the nutrients released from the sediments on the rewetting of long-dry wetlands (Jenkins and Boulton 2007). Recolonization from nearby perennial or more frequently inundated sites by group 2–4 taxa will enable populations to persist through periods of dry years, but persistence is more difficult for taxa that cannot actively disperse.

In temporary seasonal wetlands, nonmobile taxa exhibiting desiccation resistance (group 1 taxa likely to be found in the egg bank), are a relatively important component of the fauna (Fig. 4). Some of the taxa that are unable to disperse actively can be dispersed passively by mobile species, such as waterbirds (Bilton et al. 2001) or other vertebrates (Allen 2007, Waterkeyn et al. 2010), which may account for some of the overlap in invertebrate

composition among sites, despite their apparent lack of mobility. The 3 main methods of zooplankton dispersal are wind, rain, and animals (Allen 2007). In some cases, even larger invertebrates can be important vectors for dispersal of small crustaceans (Beladjal and Mertens 2009). However, water birds are often the most important vectors for many species. The patterns of gene flow in many aquatic invertebrate and plant species can be directly linked to waterbird flyways (Figuerola and Green 2002). Green and Figuerola (2005, p. 149) suggested that “the spatial and temporal scales at which dispersal limitation constrains geographical ranges, species richness and genetic structure of invertebrates depends partly on the density of migratory birds using the area”. Waterbirds may increase in importance as dispersal agents for aquatic plants and invertebrates as more wetlands are lost from the landscape and dispersal for recolonization must occur over greater distances (Green et al. 2008). The extent to which passive dispersal may feature in the recolonization of the study wetlands is not clear. Passive dispersal may be locally patchy and strongly influenced by local landscape features and environmental gradients (Bohonak and Jenkins 2003), and sufficient water must be present in both source and sink wetlands to allow it to occur.

Wetland drying consists of more than a decline in the amount of water available and is associated with other physicochemical changes, such as increased salinity, decreased O<sub>2</sub>, and high light intensities (Williams 1985, Boulton and Brock 1999). These conditions occur regularly in temporary waters, but multiple years of below-average volumes combined with high rates of evapoconcentration over summer can elevate salinities and levels of other variables beyond the tolerance of the original biota. For example, higher turbidities can occur in shallower systems because of an increase in wave-induced sediment resuspension. Accordingly, the main factors explaining variability in the dbRDA (conductivity, NO<sub>3</sub><sup>-</sup>+NO<sub>2</sub><sup>-</sup>, and turbidity; Fig. 5) may all be related to declining wetland water levels. Our results illustrate that some of the variability in the invertebrate composition data can be explained by measured environmental factors, such as depth and water quality, but most remains unexplained. Other significant factors, such as the composition and abundance of vegetation available as habitat and food, biotic interactions (including predator-prey relationships), sources of colonizers, and use by mobile animals (as described earlier), probably play roles in the observed patterns of diversity (Wiggins et al. 1980, Figuerola and Green 2002). Pairwise comparisons of invertebrate

community composition showed significant differences between many pairs of sites, results suggesting that a mosaic of different depths, sizes, and habitat types is important for landscape-level diversity. Relatively small changes in water levels may greatly influence the area of habitat available for invertebrate colonization where the microtopography and associated vegetation of littoral regions are highly heterogeneous. The increase in active dispersers present during the wettest (and deepest) phase of the early 1990s may have been the result of greater habitat availability provided by the inundation of elevated areas of fringing vegetation.

The relationships between hydrology, taxonomic diversity (richness), types of taxa present, and dominant type of recolonization (i.e., dispersal or egg-bank hatching) are summarized in Fig. 6, which depicts 4 scenarios at temporary wetlands under a gradient of drying. Under the high rainfall scenario, wetlands may hold water for several years before drying, taxa with longer life cycles successfully reproduce, and connectivity with wetlands across the wider landscape is good (allowing extensive dispersal). Mobile species (including those from group 4) have enough time to arrive and complete their life cycles. Both active and passive dispersal take place and new propagules are added to sediment egg banks. However, if drying does not occur relatively frequently, some of the taxa that are adapted to a drying phase may no longer be able to occur at the site. Under the average rainfall scenario, the wetland is dominated by taxa from groups 1 and 2, and environmental conditions allow the community to persist by providing favorable conditions for survival and reproduction. Some active and passive dispersal can take place, and the wetland dries regularly, which facilitates the persistence of drought-adapted taxa. After drying, the importance of recolonization from the egg bank increases. Under the low rainfall scenario, the relative importance of group 1 taxa and recolonization from the egg bank increases further, and minimal dispersal can take place because water is not present for long enough. Long-lived taxa are unable to complete their life cycles. Under the scenario of successive dry years, a loss of egg-bank persistence is likely when the dry periods become too long and diapausing eggs start to lose viability (Fig. 6). Currently, in wetlands that have experienced long-term drying, such as Lake Banganup, even when water does enter the system, the wetland does not hold water for long (Fig. 2).

We have interpreted the long-term data available to us as indicating that the invertebrate fauna of Jandakot wetlands appears to have some resilience to

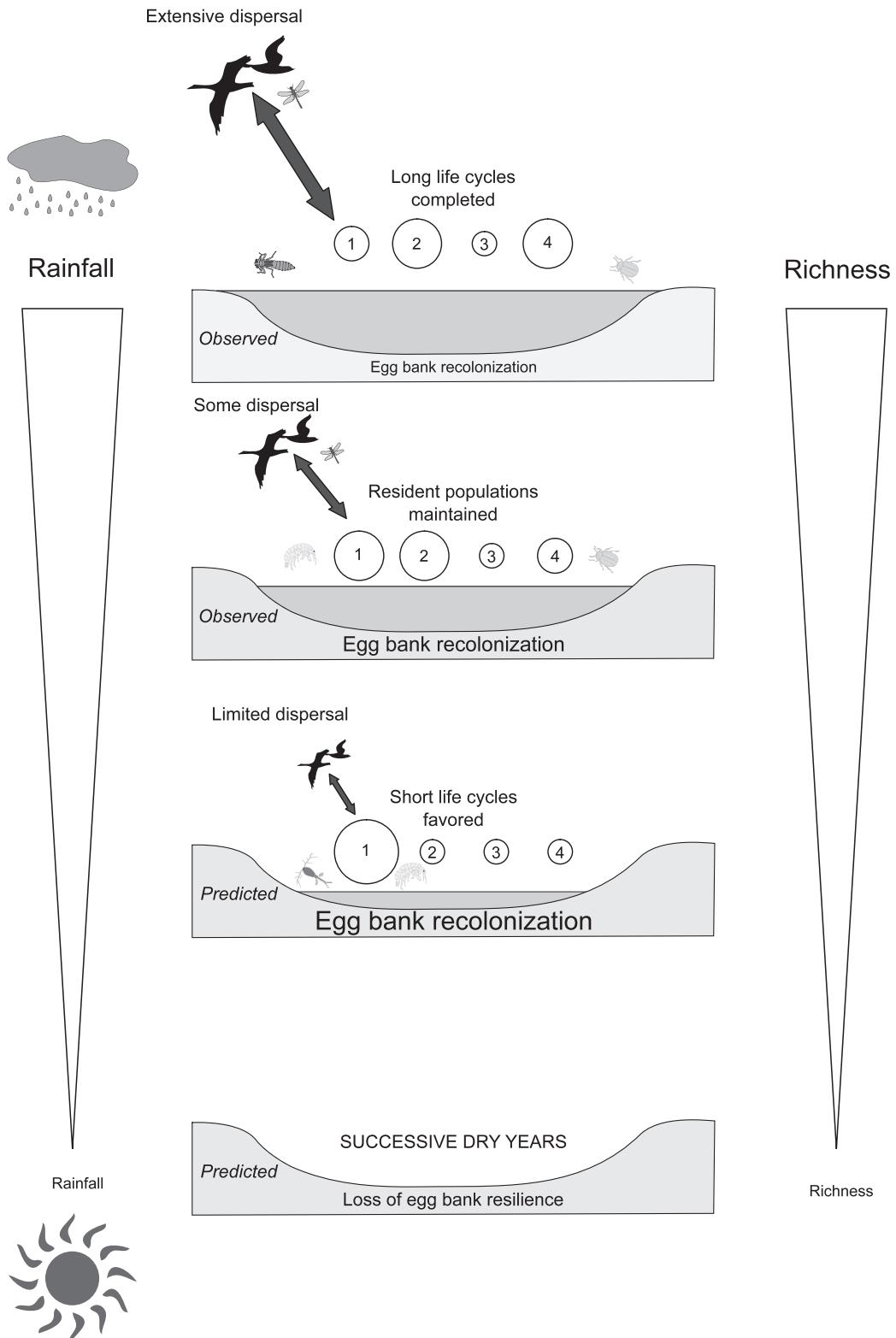


FIG. 6. Conceptual model depicting the relationships between hydrology, taxon richness, relative proportions of the 4 Wiggins et al. (1980) trait-based invertebrate groups and dominant type of recolonization strategy in temporary wetlands under 4 scenarios: high, average, low, and very low rainfall (successive dry years). The 4 trait groups are represented by circles where 1 = group 1, 2 = group 2, 3 = group 3, 4 = group 4 (see text, Fig. 4 for description of groups and Appendix for major taxa).

the current decline in rainfall, but we are aware that, at the landscape level, many wetlands no longer fill annually and some that were perennial in the past have now become seasonal. At the less frequently inundated sites (e.g., Lake Banganup and Shirley Balla Swamp) declines in richness associated with prolonged or supra-seasonal drying probably have already occurred. This loss of wetlands and habitats is likely to continue under a drying climate (Brooks 2000, Serrano and Fahd 2005). Therefore, it is vitally important to consider wetland interdependence when formulating conservation and management strategies (Wissinger 1999) and to take into account the variety of effects that climate change will have on different areas of the landscape (Pyke 2005). A landscape-scale management approach will enable consideration of a range of wetland types and hydroregimes, which will be essential to maintain invertebrate diversity and the persistence of metapopulations.

The long-term data set presented here has enabled us to draw some conclusions regarding the effects of a prolonged decrease in precipitation. We suggest that the usefulness of future data sets will be enhanced by identification of taxa to the level of species, scoring of invertebrate abundances, and a more extensive collection of habitat data, especially the presence and % cover of submerged and emergent aquatic vegetation.

### Conclusions

The tolerance of temporary seasonal wetland ecosystems to prolonged drying is not well understood (Lake 2011), but in the case of the Jandakot wetlands, aquatic invertebrate communities appear to be able to tolerate some level of extended climatic and anthropogenically driven drying. However, we know little about the effect of hydrological change on changes in diversity within an annual wetting and drying cycle or on relative abundance. Once the wetlands cross a hydrological threshold that prevents them from filling in successive years (e.g., Lake Banganup), the ability of invertebrate communities to recover may be diminished (Jenkins and Boulton 2007). The group-1 taxa that commonly make up  $\frac{1}{4}$  of the fauna in the study wetlands rely primarily on resistance traits, such as desiccation-resistant eggs or cysts, but these propagules may decline in viability after extended periods of drying spanning multiple years. The proximity of source wetlands from which mobile invertebrate species and vertebrate vectors, such as waterbirds, can recolonize seasonal wetlands is of critical importance for the persistence of temporary systems in a drying climate. This recolonization

requires the presence of water in both source and sink wetlands. Landscape-level management that aims to conserve a mosaic of wetland types and their various hydroregimes at both local and regional scales will be essential to preserving the diversity of seasonal wetland communities.

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