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Key Points:

- The Murray-Darling Basin, which covers one million square kilometers, was developed to support irrigated agriculture from the early 1900s
- The secondary salinization that followed became a major concern, and mitigation strategies have since reduced salinity levels
- Evidence from long-term monitoring of macroinvertebrates suggests that salinity mitigation has been effective in reversing past impacts

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Long-Term Monitoring of Macroinvertebrate Communities Over 2,300 km of the Murray River Reveals Ecological Signs of Salinity Mitigation Against a Backdrop of Climate Variability

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Abstract We investigated the ecological effects of salinity mitigation strategies in the Murray-Darling Basin (MDB) using macroinvertebrate data collected over 2,300 km of the Murray River between 1980 and 2012. The MDB covers $1 \times 10^6 \text{ km}^2$ and includes both temperate and semiarid climate zones. It was extensively developed to support irrigated agriculture in the early to mid-1900s, and the secondary salinization that followed has become a major concern. During 1975–1985 daily salinity levels, measured as electrical conductivity above the Murray River off-take points for South Australia's major urban water supplies, were above $800 \mu\text{S/cm}$ for 40% of the time, necessitating mitigation strategies that have reduced the average salinity by about $150 \mu\text{S/cm}$ since monitoring began. The MDB has also experienced several major floods and droughts during this time, and surface temperatures in the MDB have increased by 0.8°C since 1910, mostly in the last 50 years. We hypothesized that (1) taxa richness would increase in response to floods; (2) community structure would shift toward tolerant, opportunistic taxa in response to warming; and (3) geographical ranges of species would change in response to shifting stream isotherms and reducing salinity. Our hypotheses were supported, although increases in water temperature appeared to be due principally to the 1997–2009 Millennium drought. Importantly, against a backdrop of significant climate variability, we believe we have distinguished a change in community structure along a salinity gradient and that changes over the 33 years can in part be attributed to mitigation strategies.

Plain Language Summary Groundwater in the Murray-Darling Basin is naturally salty as a result of the low rainfall and high evaporation that has concentrated salt borne by the rain over tens of thousands of years. The introduction and expansion of irrigated agriculture since the early 1900s rose water tables over large areas and increased the discharge of saline groundwater into the Murray River. The increasing salinity in the lower Murray River raised environmental and public health concerns in the 1970s, and a program of salinity mitigation was implemented. Using long-term data, we have documented changes occurring along 2,300 km of the Murray River over a 33-year period. Aquatic macroinvertebrates—which includes insects, crustaceans, mussels, snails, and worms that spend all or part of their life in water—have increased or decreased in abundance in response to natural factors such as floods and droughts and also to changes brought about by the construction of weirs and the side effects of agriculture on the pH and salinity of river water. Importantly, there are ecological signs that salinity mitigation strategies have been effective in reversing past impacts.

1. Introduction

Secondary salinization of rivers has in the past led to the collapse of irrigated agricultural systems and the civilizations that depended on them (Jacobsen & Adams, 1958; Pillsbury, 1981), and even with today's scientific and technological proficiency it presents a global and growing threat to agricultural production and aquatic ecosystems (Cañedo-Argüelles et al., 2013; Pillsbury, 1981). This is especially the case in inland arid and semiarid regions where large amounts of salt are concentrated in soils and subsequently leached into rivers through rising water tables caused by irrigation (Cañedo-Argüelles et al., 2013; Smedema & Shiati, 2002). More than half of the world's large river systems are either moderately or severely affected by dams built primarily to support irrigated agriculture (Nilsson et al., 2005), and irrigation has been reported to be responsible for the salinization of rivers such as the Amu Darya and Syr Darya in Central Asia, the Breede

River in South Africa, the Ebro River in Spain, the Great Menderes River in Turkey, and the Colorado River in the United States (Cañedo-Argüelles et al., 2013; Pillsbury, 1981). Some countries are now investing hundreds of millions of dollars to mitigate and control the salinity of rivers (Murray-Darling Basin Authority, MDBA, 2015; Pillsbury, 1981). Australia is one such example, where the Murray River, one of the large river systems identified by Nilsson et al. (2005) as severely impacted, has been the focus of a salinity mitigation program for over 30 years (MDBMC, 2015; Schrobback et al., 2008).

Development throughout the Murray-Darling Basin (MDB) in the twentieth century saw widespread environmental degradation of its rivers and wetlands from regulation for transport, irrigated agriculture, and hydroelectricity generation, and the growth of cities and towns. In the 1920s and 30s, 14 weirs, 13 with locks, were constructed along the Murray River to aid navigation and irrigation, and to provide reliable water supplies to towns, and the first stage of the Hume Dam was completed in 1936 (present capacity 3,040 GL). In the lower reaches of the Murray River below the confluence with the Darling River most of the weir pools of each storage extend to the storage upstream, making the river more like a series of lakes, particularly when river flows are low. Irrigation, originally conceived in the late nineteenth century as a means of reducing climatic risk and encouraging closer settlement of the hinterland, expanded rapidly throughout the MDB for 60 years until about 1980 (Musgrave, 2008). Dam construction also continued through this period to meet the needs of irrigators and the need for hydroelectricity generation to secure the nation's power supply, despite warnings about the economics of irrigation and hydropower and the failure of closer settlement schemes (Cruse, 2008; Musgrave, 2008). The MDB is now referred to as Australia's food bowl, accounting for one third of the national food supply, and while irrigated agriculture occupies less than 2% of the MDB's 1×10^6 km² (14% of Australia's land surface), it accounts for 40% of the MDB's agricultural output and about two thirds of Australia's total agricultural water use (Australian Bureau of Statistics, 2008).

The ensuing environmental problems now known to be associated with irrigation and dams (Nilsson et al., 2005) were compounded by two factors in the MDB. First, the extreme variability in rainfall and inflows requires that storages be more than twice the size of the world's average, or six times the size of the European average, to achieve the same level of supply security (Musgrave, 2008; Smith, 1998); a corollary being that the disruption to the natural flow regime is likely to be greater in Australia (McMahon & Finlayson, 1995; Musgrave, 2008). The long-term annual inflow to the MDB is a modest 31,600 GL, with a range of 6,700 to 117,900 GL (Water Act 2007 - Basin Plan, 2012). Regulation has reduced the natural average annual flow at the mouth of the Murray River by 62%, from 12,498 to 4,712 GL (Maheshwari et al., 1995). The natural spring flood pulse has been virtually eliminated, and the timing of the seasonal peak flow has shifted at Albury, below the Hume Dam, from winter-spring to summer-autumn, with little change evident further downstream in the timing of peak flows (Maheshwari et al., 1995). Second, in common with many semiarid areas of the world, groundwater in the MDB is highly saline. Rain-borne salt has accumulated in sediments over tens of thousands of years of relative aridity (Evans et al., 1990; Herczeg et al., 2001), and by raising the water table irrigation and tree clearing have contributed to the salinization of large areas of land and the export of salt to rivers (Macumber, 1990). A time series analysis of chloride measurements for the Murray River, taken between 1938 and 1981 at the town of Morgan, upstream of the Murray River off-take points for South Australia's major urban water supplies, revealed that chloride levels were seasonal, with higher mean levels occurring between March and May when flows were lower, and that mean levels had increased exponentially by 0.97% per annum after adjusting for flow (Cunningham & Morton, 1983), or 51% over the 43-year period. Between 1975 and 1985 daily salinity levels, measured as electrical conductivity (EC), exceeded the World Health Organization's guideline for human consumption of 800 μ S/cm for 40% of the time at Morgan (Blackmore et al., 2000). Salinity levels have remained above 800 μ S/cm for prolonged periods during times of drought and low flow. Daily salinity levels were above 800 μ S/cm at Morgan for 31 months between January 1965 and June 1968 (a period of drought and low flow), with levels peaking at 1,400 μ S/cm in February 1968. In the early 1980s, during a low flow period, salinity at Morgan was above 800 μ S/cm for 18 consecutive months, with a peak of 1,400 μ S/cm in July 1982 (MDBMC, 2015).

Urban development created another set of problems for the MDB's rivers. The population of the MDB grew to two million, and urban sewerage and storm water drainage, which was contributing almost half of the nutrient load to the MDB's rivers during dry periods, was implicated as the main cause of algal blooms, one of the worst stretching over 1,000 km of the Darling River in 1991 (Smith, 1998).

From the 1980s and particularly in the 1990s the growing realization of the unsustainability of current practices led to ongoing policy reforms and initiatives to halt the growth in water diversions in the MDB, provide for environmental flows, and address the issues of rising salinity levels and algal blooms. Guided by the National Strategy for Ecologically Sustainable Development (McKay, 2008), a cap was placed on diversions for consumptive uses in the MDB in 1995, limiting diversions to the 1993–1994 level, and in 1997 water entitlements began to be converted from volumetric entitlements to share entitlements of the consumptive pool (McKay, 2008) to enable adaptive management of the resource into the future (Pagan, 2008). In 2002 the MDBMC established The Living Murray Initiative, and in 2004 The Living Murray Program began recovering water for environmental flows, as well as building management structures to enable flooding of wetlands and lakes (MDBA, 2016; MDBC, 2007). The Living Murray and other programs have so far recovered about 74% of the target of 2,750 GL annually (MDBA, 2017b), to achieve the long-term sustainable diversion limit of 10,870 GL/year (Water Act 2007 - Basin Plan, 2012). The MDBMC also initiated the Salinity and Drainage Strategy in 1988 to reduce salinity through a program of lowering groundwater levels and constructing a salt interception scheme in some irrigation districts, which to date has reduced salt loads by 400,000 t/year and achieved an average reduction in EC of 150 $\mu\text{S}/\text{cm}$ at Morgan (MDBMC, 2015). In 1994 the MDBMC developed The Algal Management Strategy for the Murray-Darling Basin to reduce nutrient pollution in the MDB's rivers (MDBMC, 1994). Biomonitoring programs were established during this period to evaluate the effects of control measures, according to the requirements of the Murray-Darling Basin Agreement and the Basin Plan (Water Act 2007 - Basin Plan, 2012). One of the longest running programs is the River Murray Water Quality Monitoring Program (WQMP), which started in 1980, spans 2,300 km of the Murray River, and includes both water quality and macroinvertebrate monitoring (Lawrence & Paterson, 2005). While there are other long-term (Daufresne et al., 2007; Flourey et al., 2013; Fruget et al., 2015; Jackson & Füreder, 2006) and large-river-scale (Angradi et al., 2009) macroinvertebrate monitoring programs that have been reported in the literature, this is to the best of our knowledge the longest running, large-river-scale monitoring program reported thus far.

Since monitoring started, there have been several major flooding events and intense drought periods that have impacted on flows in the Murray River. Most notable are the flood events in 1993 and 2010–2011 that caused widespread flooding along the river (MDBA, 2017a), the drought of 1982–1983 that contributed to the closure of the Murray mouth for the first time in recorded history (MDBA, 2017a), and the Millennium drought from 1997 to 2009, in which southeastern Australia experienced the most persistent rainfall deficit on record (CSIRO, 2012; MDBA, 2017a). In addition, surface temperatures in the MDB have increased by 0.8 °C since 1910 (Timbal et al., 2015), with the greatest increase in the last 50 years, and there is evidence of a drying trend that may be attributable to climate change (CSIRO, 2012; Neave et al., 2015). Indicative calculations for lowland streams by Isaak and Rieman (2013) suggest that a long-term warming rate of 0.1–0.2 °C/decade could produce a shift in stream isotherms of 1.3–25 km/decade, though the shift is likely to be much greater during times of drought (Mosley, 2015). The effects of restoration efforts on macroinvertebrate assemblages must therefore be assessed against a backdrop of a variable and changing climate.

Aquatic macroinvertebrates have been extensively studied in the field and laboratory, and the body of literature that now exists enables some predictions to be made with regard to how macroinvertebrate communities are structured along rivers, and how they would respond to changes in water quality, episodic floods and droughts, and gradual warming. The river continuum concept (Vannote et al., 1980) predicts that the structure and function of macroinvertebrate communities conform to continuous gradients in width, depth, and velocity of a river, as well as the type and location of bioenergetic inputs. Further, the continuous gradient in community structure can be disrupted or reset through regulation by dams (the serial discontinuity concept of Ward & Stanford, 1983), inputs from tributaries, or anthropogenic disturbances such as nutrient enrichment, organic pollution, and changes in land use (Vannote et al., 1980). Numerous studies have reported the effects on macroinvertebrate communities of anthropogenic disturbances such as pollution, land use and riparian alteration, and associated changes in water quality (Chessman, 1995; Chessman, 2003; Horrigan et al., 2005; Kefford et al., 2006, 2011; Quinn et al., 1997; Reynoldson et al., 1997; Rutherford & Kefford, 2005). Increasingly long-term biological monitoring programs using macroinvertebrates have been valuable for detecting long- and short-term patterns in the ecological health of rivers and identifying drivers of change (Bradley & Ormerod, 2001; Daufresne et al., 2007; Jackson & Füreder, 2006; Vaughan & Ormerod, 2012), including changes due to drought/flood disturbances and directional trends in

macroinvertebrate communities that may be associated with global warming (Chessman, 2009; Daufresne et al., 2007; Floury et al., 2013; Fruget et al., 2001). Two of these studies (Daufresne et al., 2007; Fruget et al., 2001) indicate that the effects of hydroclimatic factors are generally consistent with the intermediate disturbance hypothesis (Connell, 1978), in that species richness is low during steady conditions of low flow and high temperature but increases during periods of flood as space is opened for colonization by less competitive individuals (Townsend & Scarsbrook, 1997). Extreme hydroclimatic events consistently produce shifts in community structure, including patterns of appearance/disappearance of some taxa that may be consistent with latitudinal/altitudinal shifts in geographic range due to climate change and a shift toward eurytolerant and invasive taxa with gradual warming (Daufresne et al., 2007). There is also some evidence that community structures do not recover following these hydroclimatic events and that their sensitivity to such events might decrease over time (Daufresne et al., 2007). Where interventions have been made to improve water quality, long-term studies generally indicate that the effects were secondary to those of gradual warming (Daufresne et al., 2007; Fruget et al., 2001, 2015). The general consistency of these findings suggests that similar patterns will be observed in the macroinvertebrate communities of the Murray River.

Several studies have specifically addressed the effects of salinity on aquatic macroinvertebrates, many in an Australian context, but only community level predictions can be made at this point in time. Kefford et al. (2006) measured the acute salinity tolerance of 110 macroinvertebrate taxa collected from the southern MDB, and Kefford et al. (2004) found that acute tolerance is a reasonable reflection of the maximum field distribution (the maximum salinity at which a taxon is recorded in the field), but these measures provide no indication of changes in species abundance that sometimes occur at low salinities (Rutherford & Kefford, 2005). Schäfer et al. (2011) developed a salinity index (SPEAR_{sal}) based on a database of the physiological sensitivities to salinity of macroinvertebrate taxa from southeast Australia, but while it may be useful for signaling changes due to salinity the index only predicts that sensitive taxa are replaced by tolerant taxa as salinity increases. Species response curves would be more useful for making predictions regarding changes in salinity. Horrigan et al. (2005) developed salinity sensitivity scores (for selected families) from samples taken across Queensland streams and made predictions about the probability of occurrence of those families with increasing salinity based on taxon-specific response curves. However, we note that for taxa that were generally absent from the more saline waters in the lower reaches of the Murray River during the 1980s, such as the freshwater yabby *Cherax destructor* (Parastacidae) and some caddisflies (*Hydroptila* spp.), their predictions were conflicting for samples taken from edge and riffle habitats. Furthermore, without more information on the particular genera or species observed in Horrigan's study, it is difficult to generalize their results to those from the Murray River WQMP. At the community level, Kefford et al. (2011) found that species richness appears to peak at an EC between 300 and 490 $\mu\text{S}/\text{cm}$ in samples from across southeast Australia and that there was a statistically significant decline at <99 and $>1,500$ $\mu\text{S}/\text{cm}$. Overall, it is reasonable to predict that community composition will have changed with reducing salinity in the lower Murray River (below the junction with the Darling River) and that species richness may have increased.

The aim of the present study is to describe and explain the spatiotemporal patterns in macroinvertebrate communities of the Murray River, and more specifically to assess the evidence for ecological signs of improvements in salinity. We expect that the macroinvertebrate communities will exhibit a spatial trend in response to environmental gradients in water quality, temperature, and flow and that this pattern will change over time in response to floods, gradual warming, and improvements in water quality. More specifically, we hypothesize that (1) the number of taxa will increase in response to floods, in accordance with the intermediate disturbance hypothesis, (2) the community will exhibit a shift toward tolerant, opportunistic taxa in response to warming, and (3) geographical ranges of species will change over time in response to shifting stream isotherms (due principally to drought) and reducing salinity.

2. Methods

2.1. Study Sites

The Murray River rises near Mount Kosciuszko at an elevation of 1,430 m, draining the western side of the Australian Alps, and flows 2,500 km to the Southern Ocean, near Goolwa in South Australia. The Murray River flows through four geomorphologically distinct tracts that may be identified as the Headwaters, Riverine, Mallee, and Lower Murray tracts, the detailed characteristics of which have been described

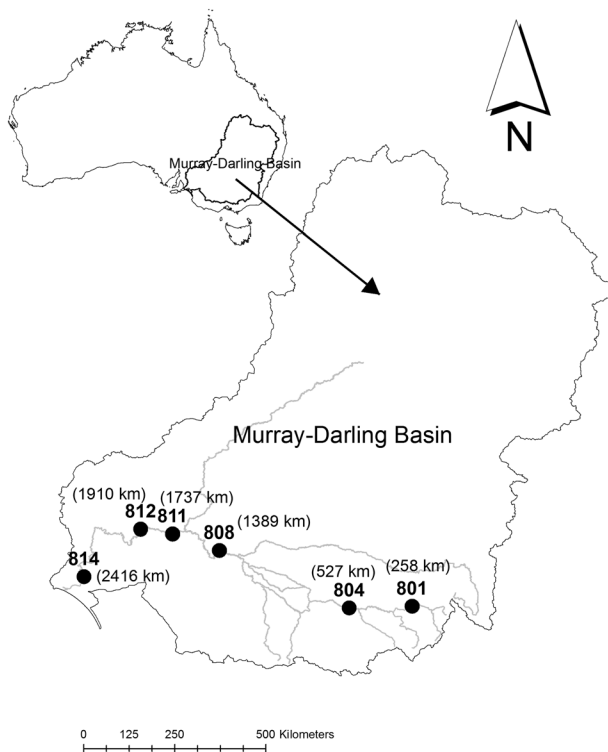


Figure 1. Map of the Water Quality Monitoring Program sites, with site numbers and distances from source (in parentheses).

elsewhere (Eastburn, 1990; Thoms et al., 2000). In the headwaters it is a swift flowing river upstream of the Hume Dam, at an elevation of 150 m and about 300 km from its source. Below Hume Dam the Murray flows westward in a shallow channel across the riverine plains, then through a deeper channel that cuts through the red and brown clays of the semiarid Mallee Zone. At Morgan the river turns south and travels the final 315 km, passing through the Lower Murray tract and Lake Alexandrina before discharging into the Southern Ocean. Annual flow in the Murray River is highly variable, with an *average* of around 11,000 GL, and a range of between 2,500 GL in a dry year and 40,000 GL in a wet year. Six sites were selected along the Murray River from Jingellic in the montane region of the catchment to Woods Point near the Murray River mouth, covering a distance of over 2,300 river kilometers (Figure 1). Site 801 lies within the Headwaters tract; Site 804 in the Riverine tract; Sites 808, 811, and 812 in the Mallee tract; and Site 814 is in the Lower Murray. Each site was located close to existing MDBA water quality monitoring sites to allow a comparison between water quality data and biological data (Bennison et al., 1989). Mean annual rainfall in the alpine headwaters is approximately 2,000 mm and the monitoring sites span a range of climates from temperate conditions in the upper catchment, with mean annual rainfall of 810 mm at the first site in Jingellic, through to a semiarid zone in the midreaches, with annual rainfall of approximately 260 mm, and a return to more temperate conditions toward the Murray River mouth, with mean annual rainfall of approximately 400 mm.

2.2. Macroinvertebrate Monitoring

Macroinvertebrates were collected using artificial substrate samplers (ASSs) in winter (May–June) and summer (October–December; Bennison et al., 1989). The data set used in this manuscript covers the period 1980 through to 2012 (Paul et al., 2018). The ASSs (Bennison et al., 1989) were constructed from a section of black plastic *Gutterguard* (mesh size 10 mm), 180 mm high and 240 mm in diameter containing one and a quarter new, commercially available polypropylene, leno weave onion bags (total area $1,000 \times 420 \text{ mm} = 0.42 \text{ m}^2$) as substratum. The *Gutterguard* was formed into a basket; onion bags were placed inside with a clean river rock or half brick for ballast and fastened with nylon cord top and bottom. Ten ASSs were placed on the substrate within the photic zone at each site and retrieved after a 6-week colonization period. About five ASSs were retrieved for each year/season/site combination. Samples were sieved through a 250- μm mesh sieve, then animals were removed and preserved in 70% ethanol. Samples were sorted and identified to the lowest taxonomic level possible (typically genus or species) and counted. Exceptions to this were (1) Nematoda and Nemertea were identified to phylum; (2) Oligochaeta and Hirudinea were identified to class; and (3) Acarina were identified to order. The current database includes 543 taxa, but due to changes in taxonomy over time these had to be grouped according to the 388 taxa known prior to 1985 (Bennison et al., 1989). Prior to analysis, this set of 388 taxa was reduced to 105 taxa (mostly genera and families) that were regularly collected (>10% of samples from any site).

2.3. Environmental Variables

Water quality data were obtained from the MDBA's WQMP (see Lawrence & Paterson, 2005; Paul et al., 2018). The WQMP includes weekly measurements of pH, turbidity, EC, water temperature, total Kjeldahl nitrogen (TKN), and total phosphorus (TP). All water quality variables were measured using standard methods (see Mackay et al., 1988).

Flow, or data used to calculate flow, is measured either continuously or instantaneously at a network of 140 gauging stations throughout the Murray River system (MDBA, 2012). Daily flow data were obtained from the nearest upstream gauging station for the present analysis.

Daily meteorological measurements of air temperature and rainfall in proximity to the water quality monitoring sites were obtained from the Bureau of Meteorology (2012).

All observations were averaged over 12 weeks for two seasonal periods referred to as winter and summer, where the midpoint of each period coincided with the date of deployment of the ASSs used to monitor the macroinvertebrate communities.

2.4. Data Analysis

2.4.1. Modeling the Spatiotemporal Patterns in the Environmental Variables

The objective of this part of the analysis was to describe the spatiotemporal patterns in the environmental variables. Both space (distance from source) and time were entered into models as continuous variables. Modeling the spatial component as a function of distance from source, rather than as a function of site (a categorical variable), will produce a more general and parsimonious description of the data. The *mgcv* package in R (R Development Core Team, 2013; Wood, 2006) was used to fit generalized additive models (GAMs). The flexibility of GAMs makes them suited to the task of extracting the important features of the data without the need for complex parametric models (Wood, 2006). An identity link function was used in all models except for the rainfall model, which used a log link, and error distributions were Gaussian, or in the case of right-skewed distributions, inverse Gaussian or Gamma. Space-time plots for each variable were examined as part of an exploratory analysis, and diagnostics within *mgcv* were used to check the adequacy of the error distribution and link function used in each of the models.

2.4.2. Modeling the Abundance and Richness of the Macroinvertebrate Community as a Function of Space, Time, and the Environmental Variables

GAMs were also used to model the richness and total abundance of the community as a function of space and time, then as a function of the environmental variables with space and/or time included to account for any remaining systematic patterns. For both richness and abundance, a negative binomial error distribution and log link was used. Abundance and richness are defined as the average number of individuals per ASS retrieved and the number of taxa for each year/season/site combination, respectively, using the reduced set of 105 taxa. The environmental variables included pH, turbidity, EC, TKN, TP, water temperature, air temperature, rainfall, and flow. Current velocity is more important in structuring communities than is volumetric flow, but velocity data were not available. The normalized flow at each site, achieved by mean centering and scaling by the standard deviation, was therefore used to approximate the temporal effects of velocity on macroinvertebrate communities.

2.4.3. Modeling the Macroinvertebrate Community Structure as a Function of Space, Time, and the Environmental Variables

An exploratory principal coordinates (PCOs) analysis was done using the *cmdscale* function in the *vegan* R package (Oksanen et al., 2013). PCOs were computed from a between sample Bray-Curtis dissimilarity matrix of the fourth root transformed multivariate species abundance data, with a correction for negative eigenvalues (Legendre & Anderson, 1999). A fourth-root transformation of the abundance data was done to emphasize the contribution of less abundant taxa before calculating Bray-Curtis dissimilarity coefficients (Clarke, Gorley, et al., 2014; Clarke, Tweedley, & Valesini, 2014). The PCO scores represent the state of the community at a point in time and space, and systematic patterns in the community data will usually be revealed in the first few PCO axes, where each nontrivial PCO axis reflects an underlying ecological gradient (Faith et al., 1987; Gauch, 1982; Gauch et al., 1977; Legendre & Legendre, 2012; ter Braak & Prentice, 1988). Diagnostic tools were used to help identify the number of potentially nontrivial PCO axes (Paul & Anderson, 2013); these included the broken-stick method (Frontier, 1976), bootstrapped eigenvalue-eigenvector method (Jackson, 1993), and the holistic and conditional random permutation methods (Paul & Anderson, 2013). These tools can only serve as a guide to the number of ecological meaningful PCO axes. It is well known that ordinations produce three kinds of axes (Gauch, 1982; Gauch et al., 1977)—structure axes, spurious polynomial axes, and noise axes—and while these diagnostic tools can help to focus attention on a few potentially important axes, further examination of patterns in space-time plots of individual PCO scores is required in choosing those axes thought to contain ecological meaningful information.

Distance-based redundancy analysis (dbRDA) was used to model the community data as a function of space and time, as well as the environmental variables, using the *capscale* function in the *vegan* R package (Oksanen et al., 2013). The multivariate species data, expressed as a set of PCOs (as discussed above), were modeled first as a function of space and time (Legendre & Anderson, 1999; Paul & Anderson, 2013), then as a function of the environmental variables, with space and time included to account for the remaining systematic variation. This enabled an assessment of the percentage of the variation explained by the

environmental variables and the percentage explained by space and time after partialling out the environmental component. Permutation tests for the regression coefficients were based on 999 permutations of residuals under a reduced model (Anderson & Legendre, 1999). The assumption of exchangeability, which underpins the permutation tests used in dbRDA, was checked by plotting the residuals versus fitted values for the first few PCO axes. In dbRDA the fitted PCO axes are usually subjected to an eigenvalue decomposition to produce a constrained ordination diagram, but it is sometimes preferable to plot the individual fitted and observed PCO values in space-time plots in order to visualize the trajectories and the level of agreement between the observed and fitted values (Paul & Anderson, 2013); it is also preferable with large data sets for which 2-D ordination diagrams appear cluttered. Spearman correlations between each PCO axis and the environmental variables are provided with the space-time plots to assist with the interpretation of the underlying ecological gradients.

With regard to interpretation of the variance explained by ordination axes, Økland (1999) notes that 30–70% of the total inertia is due to polynomial distortion axes that arise from lack-of-fit of the data to the species response model implicit in any eigenvector ordination method; that is, the eigenvalue-to-total-inertia ratio underestimates the compositional variation in structure axes. He recommends that interpretation of ordination analyses be based on relative values of explained variation for different sets of explanatory variables, rather than on absolute values of the fraction of variance explained by a particular set of variables. For this reason, we have also provided the variation explained by environmental variables as a percentage of the variation accounted for by space and time.

2.4.4. Modeling Taxa Response Curves Along Ordination Axes

Shade plots produced with PRIMER v7 software (Clarke & Gorley, 2015) were used to visualize the patterns in *coherent groups* of taxa over the first four PCO axes of the macroinvertebrate analysis (Clarke, Tweedley, & Valesini, 2014). At its simplest, a shade plot is a data matrix in which entries are represented by a linear gray scale from white (the taxon is absent) to black (the maximum data value in the matrix). For this purpose, those taxa that were present in fewer than 10 of the 269 samples were eliminated because they were considered to have insufficient occurrences to be capable of providing meaningful patterns. The fourth-root transformed abundances were averaged in groups of 16–17 samples at a time, within 16 slices of variable width taken along each of the PCO axes (the x axes). Note that it is important to average over approximately constant numbers of samples, especially for strongly transformed abundances, if species accumulation artifacts are to be avoided. Taxa are ordered within the shade plots to reveal the role they play in determining the ecological gradients represented by the PCO axes. The idea here is that the structure among samples, which determines the PCO axes, is inherently driven by the structure among species—namely, their intercorrelations. On the y axis of the shade plot, the taxa are therefore grouped using *coherent species* analysis (Somerfield & Clarke, 2013), which uses Type 3 Similarity Profile (SIMPROF) tests to identify groups of taxa with statistically different responses among groups, over all samples, and statistically indistinguishable (coherent) patterns within each group. The ordering of these groups and the taxa within each group is then optimized using the method of Clarke, Gorley, et al. (2014). As suggested by Somerfield and Clarke (2013), we investigated the effect that different significance levels (0.1%, 0.5%, and 5%) for the Type 3 SIMPROF tests have on the number of coherent groups identified. A significance level of 0.5%, was deemed to produce a reasonably stable set of 30 groups. The lower significance level of 0.1% produced no groups, which would suggest this was an overly stringent criterion given the obvious structure among samples, as indicated by PCO analysis. The higher significance level (5%) produced more singletons. Further, on changing the significance level from 0.5% to 5% 26 of the 30 groups remained the same, with the four remaining groups (groups D, K, T, and AC) being split into two or three groups of one or more taxa.

In keeping with the aim of data reduction, the (generalized) mean abundance for coherent groups of taxa were then modeled as a function of the PCO axes. Modeling species response curves along individual ordination axes using generalized linear or additive models has been done previously (Lepš & Šmilauer, 2003; ter Braak, 1985; ter Braak & Šmilauer, 2002), but here we model coherent group average abundances as a function of the first four PCO axes in a multiple regression, rather than separately for each axis. In effect, this is analogous to the principal component solution of the factor model (Johnson & Wichern, 2002), where a few (nontrivial) principal components are taken to represent the latent common factors in a factor analysis. The response curve models used the generalized mean (to exponent $\frac{1}{4}$) of the taxa abundances for each coherent group, and the contributions of the first four PCOs were quantified using the deviance explained

by the individual smooth (PCO) terms and overall explained deviance, as well as the null deviance as a measure of the total variation (corrected for the mean) in the generalized mean abundance. The latter two statistics were used to rank the coherent groups in order of importance, while the explained deviance for individual terms was used as a measure of the *loading* of each PCO on the coherent group abundances, analogous to the estimated factor loadings in a factor analysis (Johnson & Wichern, 2002). GAMs with a log link and negative binomial error distribution were used for all coherent groups. As suggested by Oksanen and Minchin (2002) for modeling species distribution curves, a maximum effective degrees of freedom of 6 was used in all GAMs (by setting the basis dimension). This, however, is only an upper limit that is used to improve computational efficiency. The actual degrees of freedom, which was generally much lower, is controlled by the degree of penalization selected during fitting by generalized cross validation (Wood, 2006). Residual diagnostics within mgcv were used to check the adequacy of the error distribution and link function, as well as the choice of basis dimension, for each of the models.

2.4.5. Counterfactual Analysis to Elucidate How Environmental Changes Have Influenced Groups of Taxa

To predict the change in coherent group abundances that would occur under new environmental conditions, the PCO multiple regression model was first used to predict the PCO scores resulting from a change in the environmental variables, then the response curve models were used to predict abundances of coherent groups of taxa. This enabled analysis of counterfactual questions such as, *What would the macroinvertebrate community have been had the water temperature not warmed, or salinity mitigation strategies not been implemented?* See Pearl (2000, 2014) for further information on counterfactual analysis. Until a more complete causal model is developed, this analysis accounts only for the direct effects of environmental variables. It does not, for example, account for the indirect effect of temperature on macroinvertebrates that is mediated by water quality.

3. Results

3.1. Spatiotemporal Patterns in the Environmental Variables

All of the environmental variables, except rainfall, displayed a seasonal pattern. The fitted GAMs in Figure 2 were deseasonalized to highlight the longer-term patterns, though it is important to note that seasonal variation can be as ecologically important as long-term trends in means. All environmental variables except rainfall and ambient air temperature exhibited statistically significant distance-by-time interactions at the 0.05 significance level; that is, the spatial pattern varied over time.

Rainfall was highest in the upper catchment and lowest within the midreaches, with an increase again toward the Murray mouth (Figure 2f). The spatial pattern in ambient air temperature was the opposite, with higher temperatures in the midreaches and lower temperatures at either end of the river (Figure 2g). Rainfall was depressed and air temperature elevated during the droughts of 1982–83 and 1997–2009, whereas the reverse pattern occurred in the mid-1990s and 2010s, corresponding to floods in the Murray River.

The water quality variables—EC, turbidity, TKN, TP, water temperature, and pH—generally displayed an increasing trend downstream (Figures 2a–2d). Longitudinal patterns in flow were less clear except that highest flow rates were experienced at the lower end of the river system (Figure 2e). The magnitude of the spatial trends varied over time. EC declined in the mid-Murray sites from an average of about 400 to 200 $\mu\text{S}/\text{cm}$ (Sites 808–812, Figure 2b) and remained low at about 40 $\mu\text{S}/\text{cm}$ at the upper sites, 801 and 804. EC at Site 814 decreased from 800 to 400 $\mu\text{S}/\text{cm}$ and was particularly higher than at other sites during periods of drought in the early 1980s and mid-2000s. Turbidity was highly variable in the middle and lower reaches of the Murray River (Figure 2b), particularly in the sites downstream of the Darling River and Lake Victoria (Sites 811–814) but exhibited a gradual decline over the study period from an average of 60 to 40 NTU. Turbidity was generally less than 10 NTU at Site 801. TKN averages ranged between 0.2 and 0.8 mg N/L, and TP between 0.02 and 0.15 mg P/L. TKN and TP showed similar temporal trends to turbidity (graphs not shown). The pH at Site 801 diverged from other sites in the early 1980s (Figure 2a), decreasing from about 7.3 in the early 1980s to 6.6 in 2005. The water temperature (Figure 2d) increased by about 2.5 °C over the 33-year period at Site 801, while at Site 804 it increased by 2.0 °C, and at all other sites it increased by an average of 0.8 °C. Most of the increase in water temperature occurred during the drought of 1997–2009.

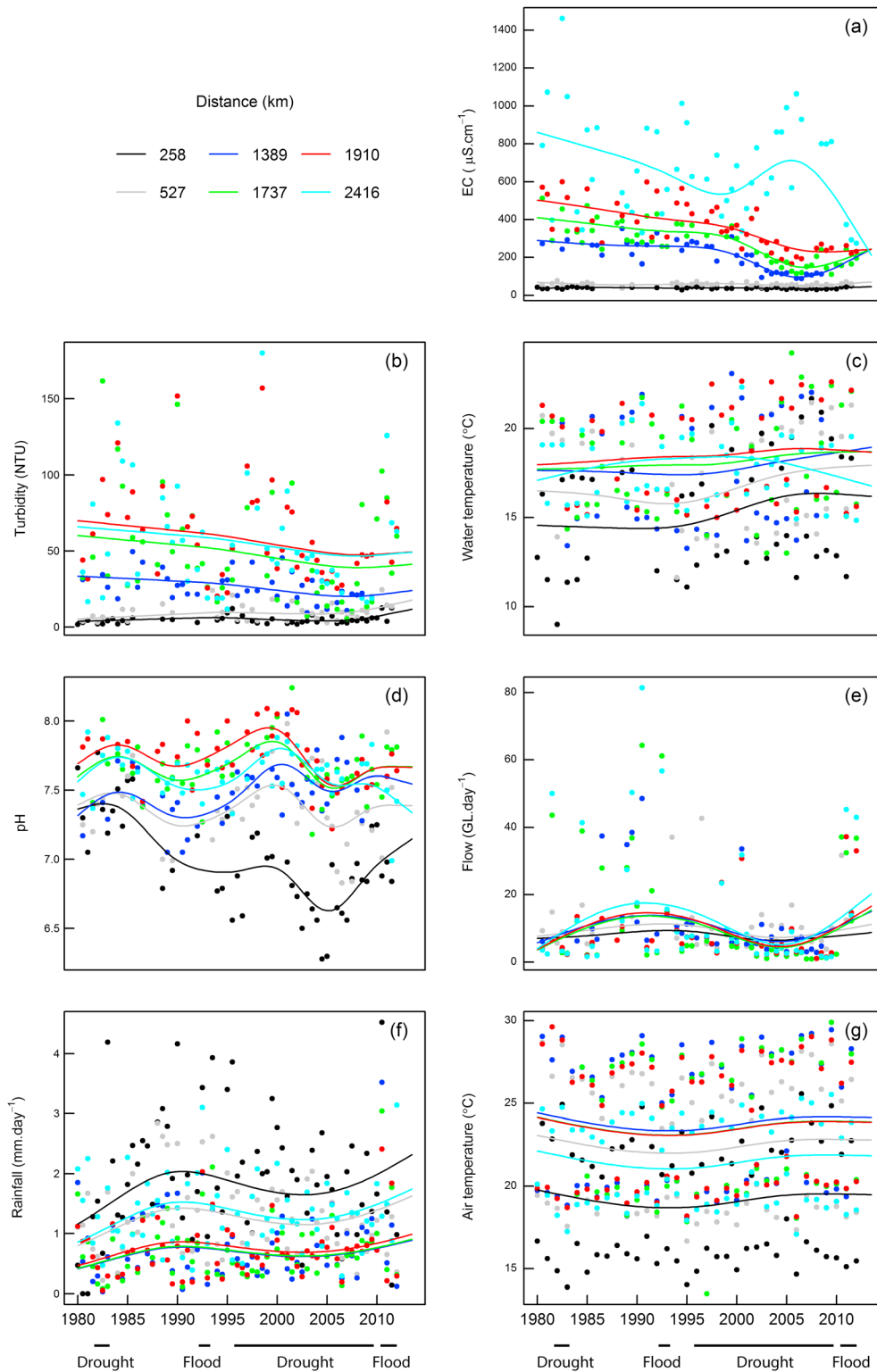


Figure 2. Space-time plots of environmental variables: (a) electrical conductivity (EC), (b) turbidity, (c) water temperature, (d) pH, (e) flow, (f) rainfall, and (g) air temperature. Lines represent the deseasonalized component of the fitted generalized additive models, to highlight the longer-term patterns. Color indicates site distance from source (km). Sites 808, 811, and 812 at distances 1,389, 1,737, and 1,910 km are located within the semiarid region. Periods of drought and flood are indicated with horizontal lines beneath the time axis.

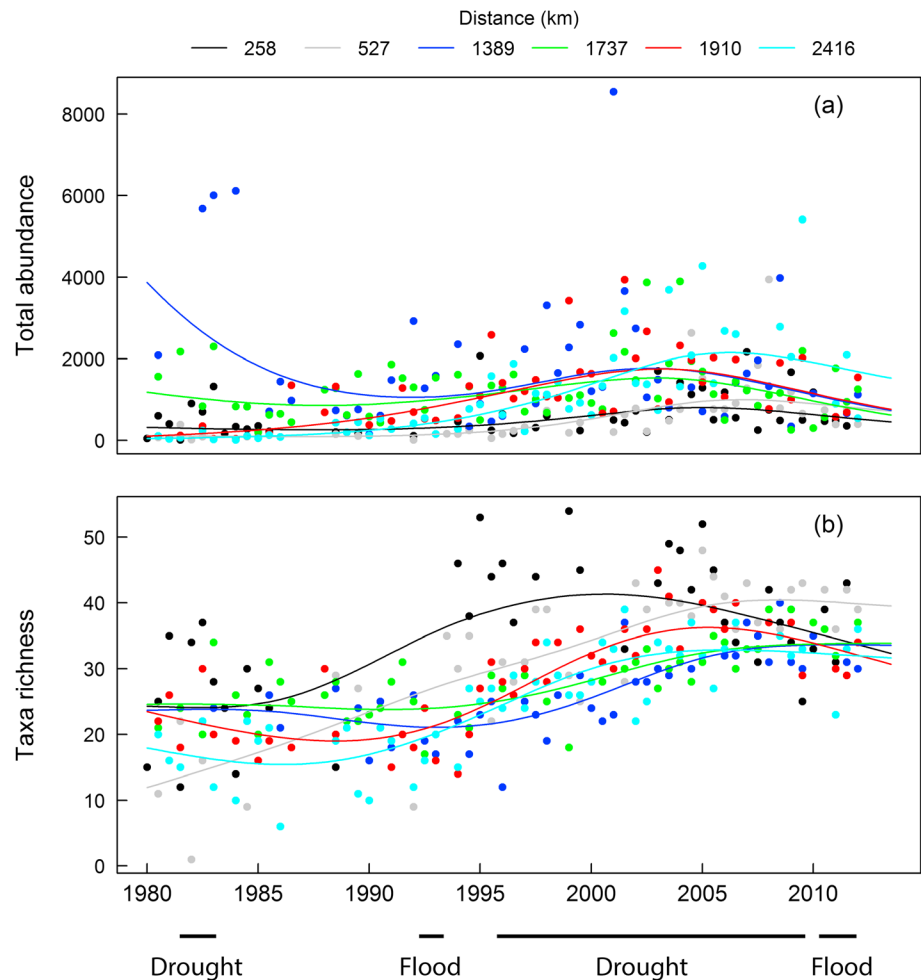


Figure 3. Space-time plots of (a) total abundance and (b) taxa richness. Lines fitted by generalized additive models. Color indicates site distance from source (km). Sites 808, 811, and 812 at distances 1389, 1737, and 1910 km are located within the semiarid region. Periods of drought and flood are indicated with horizontal lines beneath the time axis.

3.2. Abundance and Richness of the Macroinvertebrate Community

Taxa richness and total abundance of macroinvertebrates began to increase across all sites after the 1993 flood and declined after peaking during the Millennium drought (Figure 3). Abundance displayed a unimodal response to EC with a peak at about $300 \mu\text{S}/\text{cm}$, whereas it decreased with increasing turbidity, varied seasonally with temperature, and increased with time after the 1993 flood (Figures 4a–4d). Richness decreased with increasing EC and pH, whereas it varied seasonally with temperature, and it increased with time after the 1993 flood (Figures 4e–4h).

3.3. Macroinvertebrate Community Structure

Various diagnostic tools were used to determine the number of PCO axes that potentially contain interpretable structure. Scree plots showing the results obtained by each of these methods are given in Figure 5. The first three methods compare the observed distribution of eigenvalues to a distribution expected for unstructured multivariate data having the same number of dimensions, and the fourth uses bootstrapped confidence intervals of the eigenvalues. The broken-stick model (Figure 5a) and conditional random permutation method (Figure 5c) suggest that there were 11 or 12 nontrivial axes out of a total of 268. The holistic random permutation method (Figure 5b) suggests that there were five or six nontrivial axes, and the bootstrapped eigenvalues (Figure 5d) indicate that there were two nontrivial axes. Space-time plots of individual PCOs indicated there was spatial and temporal structure in the first four PCOs, including a

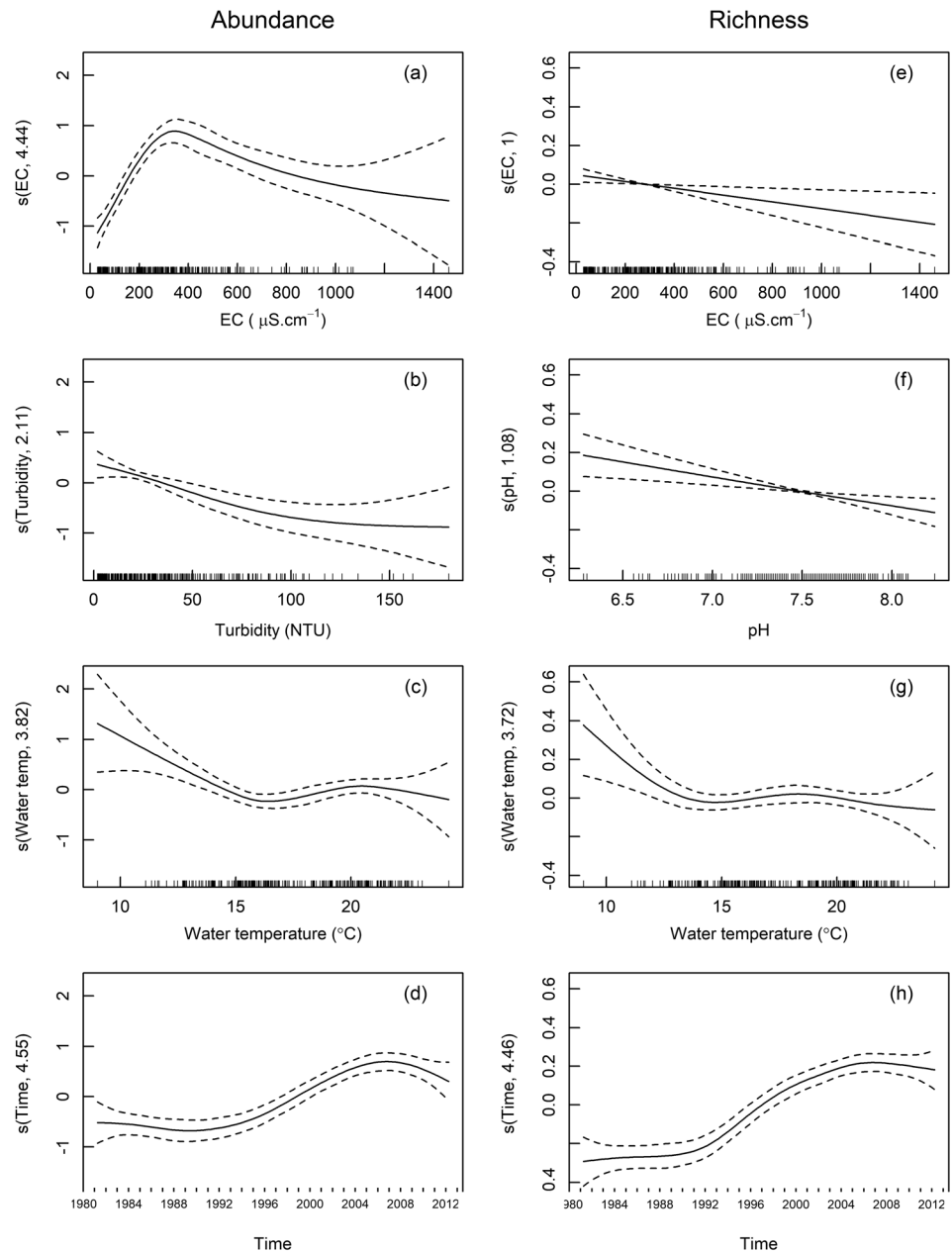


Figure 4. Plots of smooth components of GAMs for total abundance (a–d) and taxa richness (e–h) against the corresponding explanatory variable. The effective degrees of freedom for each smooth term is given in parentheses on the y axis (higher values indicating greater *wiggleness* of the smooth), and the rug plots (small tick marks above the x axes) indicate values of the explanatory variable. EC = electrical conductivity.

seasonal pattern in the third and fourth axes, but there was no clear spatial structure in subsequent axes, only a gradually decreasing seasonal pattern up to PCO12.

On the basis of patterns in the first four PCOs (Figure 6), a spatiotemporal dbRDA model was fitted to the data. Orthogonal polynomial terms in the model accounted for the quadratic relationship between community structure and distance from source (particularly apparent in PCO1; see Figure 6a), a cubic polynomial trend over time, and the interaction between the two. A cosine term was added to account for seasonality. All parameter estimates were statistically significant at the 0.05 level. However, there was some evidence from residual diagnostic plots that Site 804 did not entirely conform with the spatial component of the model, which we attribute to an effect of the Yarrawonga weir (4 km upstream) on the basis of an earlier study (Bennison

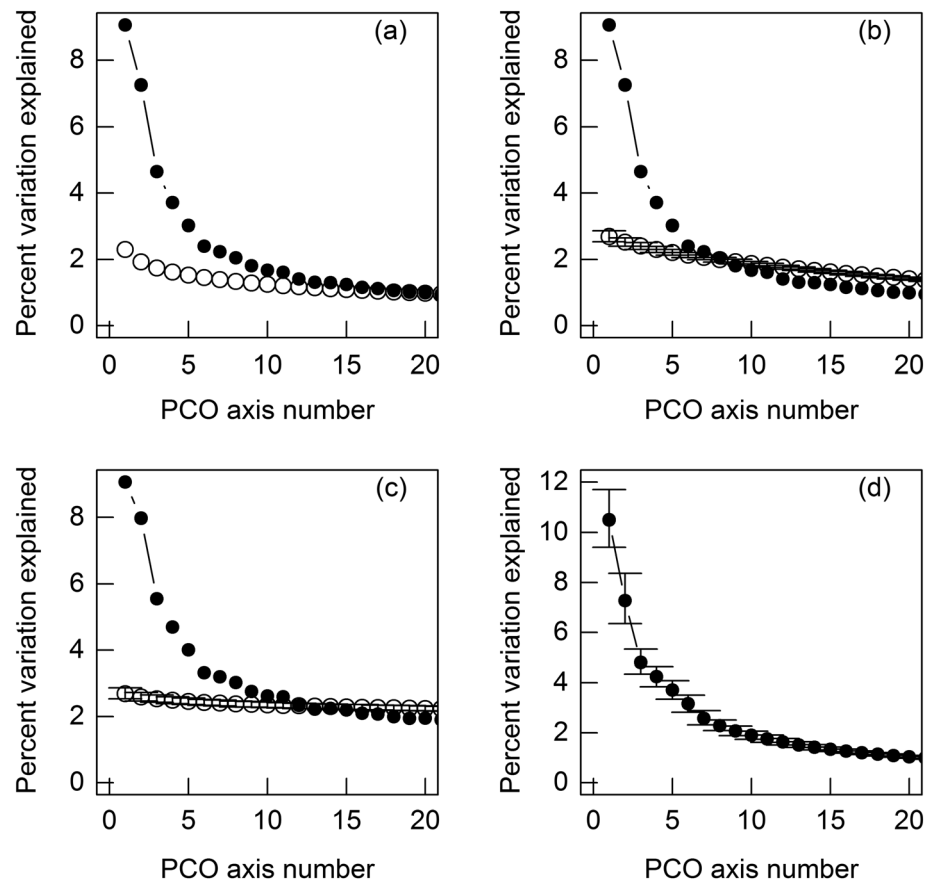


Figure 5. Scree plots for the principal coordinate (PCO) analysis with (a) the broken-stick model, (b) 95% permutation confidence intervals from a null model of no structure, where percentages represented by each axis are taken holistically as a fraction of the total variation; (c) as in (b), except percentages represented by each axis are taken conditionally as a fraction of the variation remaining after removing that which is explained by prior axes; and (d) 95% bootstrap confidence intervals for eigenvalues.

et al., 1989). The indicator variable [dist = 527] was therefore added to the model to account for the shift in community structure at this site. The analysis of variance table for the final model is given as Table 1. The dbRDA model explained 24% of the total variation. Fitted values from the model are overlaid on the space-time plots for the first four PCOs (Figures 6a–6d), with Spearman correlations between each PCO axis and the environmental variables provided above each plot.

PCO1 represented 9.1% of the total variation in the macroinvertebrate community. The primary pattern in PCO1 is a quadratic spatial trend along the Murray River, and a convergence of PCO sample scores toward those of the mid-Murray sites over time (Figure 6a). This pattern appears consistent with that of rainfall and water temperature, and PCO1 was positively correlated with temperature (weakly) and negatively with rainfall. PCO1 was also moderately positively correlated with pH, turbidity, and EC.

PCO2 represented 7.3% of the variation in the macroinvertebrate community and displayed a spatial trend along the river (Figure 6b). While Site 814 remained in the higher region of the PCO2 scores, there again was a pattern of increasing similarity of PCO2 scores among sites over time, indicating a loss of spatial variability of community structure throughout the river system. EC was most highly correlated with PCO₂, followed by turbidity and pH. This suggests that PCO2 reflects changes in community structure attributable to water quality.

PCO3 and PCO4 represented 4.6% and 3.7% of the variation, respectively (Figures 6c and 6d). Unlike later axes, these two axes still contain an appreciable spatial component. Spatially, PCO3 appears to reflect a difference between the lowermost site and all other sites, whereas PCO4 appears to distinguish the two

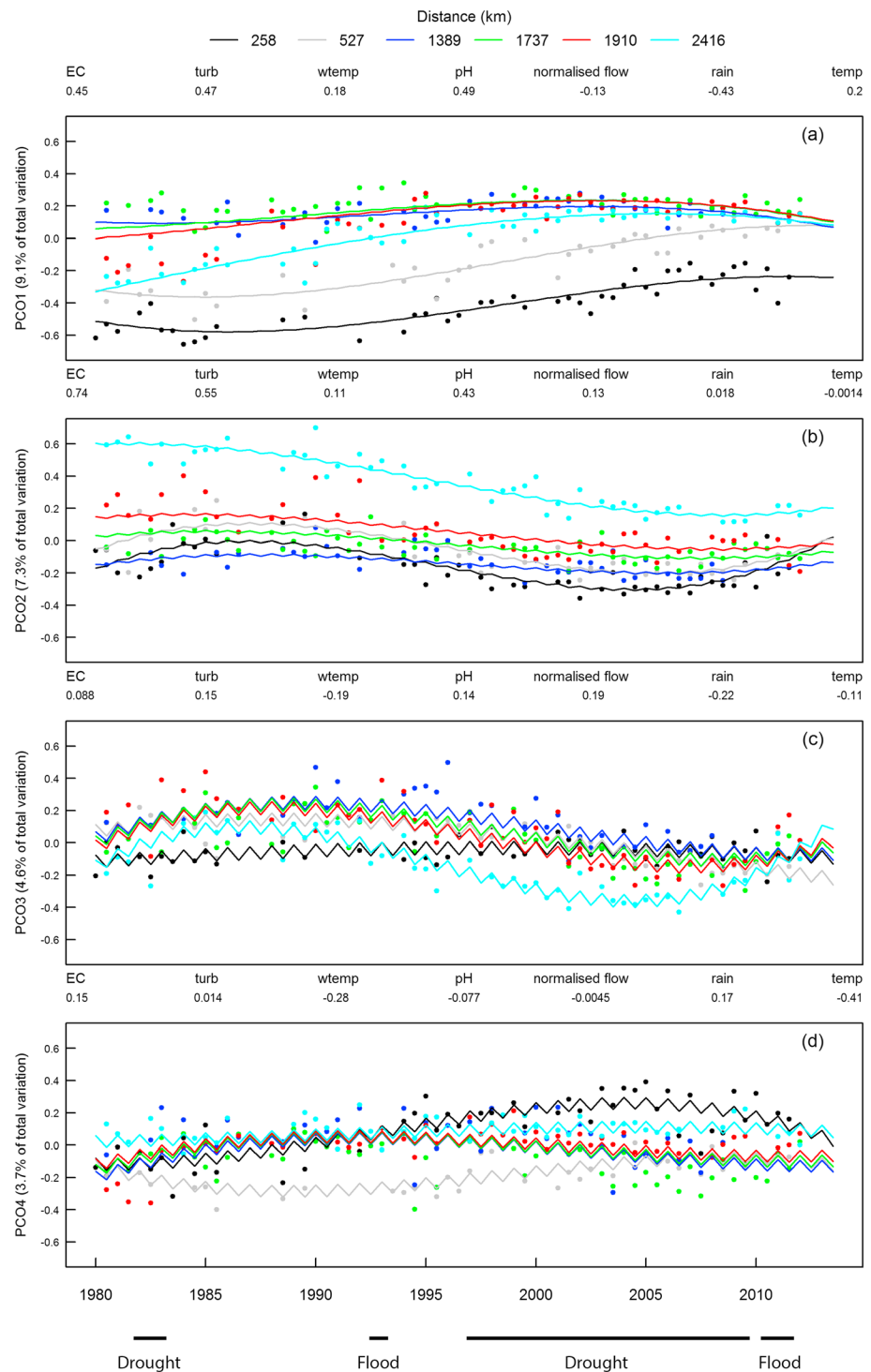


Figure 6. Space-time plots for principal coordinate (PCO) axes 1–4 (a–d, respectively) with fitted values (lines) from the distance-based redundancy analysis model with space and time as predictors. Spearman rank correlations between each PCO axis and the environmental variables are given above each graph. Color indicates site distance from source (km). Sites 808, 811, and 812 at distances 1,389, 1,737, and 1,910 km are located within the semiarid region. Periods of drought and flood are indicated with horizontal lines beneath the time axis. EC = electrical conductivity.

uppermost sites from lower sites. Both axes exhibit cubic polynomial trends in time, which were also evident in the first two axes and might be related in part to the 1993 flood, and a seasonal pattern that was not evident in the first two PCO axes.

Table 1
ANOVA Table for dbRDA Model With Space and Time as Predictors

Source	Df	SS	F	p
Poly (Dist, 2)	2	11.6	16.4	0.001
Cos ($\pi \times$ Time)	1	1.8	5.0	0.001
Poly (Time, 3)	3	5.5	5.2	0.001
[Dist = 527]	1	1.8	5.2	0.001
Poly (Dist, 2) \times Poly (Time, 3)	6	5.2	2.4	0.001
Poly (Time, 3) \times [Dist = 527]	3	1.9	1.8	0.001
Residual	252	88.9		

Note. ANOVA = analysis of variance.

The macroinvertebrate community composition was then modeled with dbRDA as a function of EC, turbidity, water temperature, pH, TKN, TP, normalized flow, rainfall, temperature, and both distance and time. Scatter plots of PCOs against environmental variables indicated the relationships were approximately linear, and distance and time were included in the dbRDA model in the same forms as in the previous spatiotemporal model. Some variables or terms were dropped from the model on the basis of significance tests, multicollinearity diagnostics, and the AIC/BIC (see Akaike and Bayesian Information Criteria for distance-based linear models in Anderson et al., 2008); the final model included EC, turbidity, water temperature, normalized flow, pH, rainfall, the indicator variable for Site 804, and a cubic term for time. The analysis of variance table for

the final model is given as Table 2. The model explained 16% of the total variation, with the main sources of variation being EC and the polynomial trend in time. A conditional dbRDA indicated that the environmental variables (not including the indicator variable or time) accounted for 10% of the variation in community structure, while the terms from the previous spatiotemporal model explained a further 16% of the variation. This indicates that the environmental variables, for which data were available, account for only 38% of the spatiotemporal variation and thus provide only a partial explanation of the observed spatiotemporal patterns.

3.4. Taxa Response Curves Along Ordination Axes

Shade plots displaying the response curves of individual taxa along the first four PCOs are given as Figure 7. The taxa are clustered in 30 coherent groups (A–AD), according to the similarity in their patterns of abundance through space and time. It is evident from Figure 7 that some taxa have a narrow coverage of the underlying environmental gradients whereas others span the full range of those gradients and that the shapes of the curves are generally either monotonic or unimodal. The ordering of the coherent groups accords principally with the first two PCOs, which represent variation in the macroinvertebrate assemblage that we attribute primarily to responses to climate (rainfall and temperature) and water quality (EC and turbidity). The explained deviances for individual smooth PCOs in the GAMs (Table 3) similarly indicate that coherent group abundances load mostly on the first two PCOs. Figure 7 also indicates there are ecological important patterns in PCO3 and PCO4, in groups L, K, B, P, O, and C, in particular. Group P, in fact, loads almost exclusively on PCO3, as shown in Table 3. Nine coherent groups that were most strongly associated with the patterns in the ordination axes (Table 3), and which span the ordering shown in Figure 7, were chosen for a more detailed examination.

From Figure 7, taxa from groups K and L are generally restricted to sites with higher rainfall, lower water temperature, and good water quality. These groups occurred mainly in the uppermost site. Groups K and L were composed of taxa that are generally associated with cool, well oxygenated, flowing water, and typically considered pollution sensitive, such as *Coloburiscoides* sp. and *Atalophlebia* spp. (mayflies), *Leptoperla* spp. (stoneflies), *Cheumatopsyche* spp. (net-spinning Caddisfly), *Austrosimulium* spp. (filter-feeding diptera), and *Simsonia* spp., *Notriolus* spp. and *Austrolimnius* spp. (riffle beetles). These two groups generally increased in abundance at Site 801 from the 1990s and appeared to decrease near the end of the study period (e.g., see Figure 8a).

Groups E, C, and P displayed a general increase in abundance, more so at one particular site (different for each group), from around 1990 onward. Taxa within group E cover a range of climates but generally occur where the water quality is better. This group was most abundant at Sites 801 and 804. Group E comprised three, highly mobile, predatory taxa, including one dragonfly species (*Apocordulia macrops*) that is considered pollution sensitive, with a SIGNAL2 score of 10 (SIGNAL2 scores ranging from 1 for pollution tolerant to 10 for pollution sensitive have been ascribed to most families of Australian macroinvertebrates; see Chessman, 2003), as well as a nonbiting midge (*Rheotanytarsus* spp.) that is considered

Table 2
ANOVA Table for dbRDA Model With Environmental Variables, and Space and Time as Predictors

Source	Df	SS	F	p
EC	1	5.1	13.4	0.001
Turbidity	1	1.2	3.3	0.001
Water temperature	1	1.9	5.0	0.001
Normalized flow	1	1.2	3.1	0.001
pH	1	1.8	4.7	0.001
Rainfall	1	0.9	2.5	0.001
[Dist = 527]	1	1.6	4.1	0.001
Poly (Time, 3)	3	5.2	4.6	0.001
Residual	258	97.8		

Note. ANOVA = analysis of variance; dbRDA = distance-based redundancy analysis.

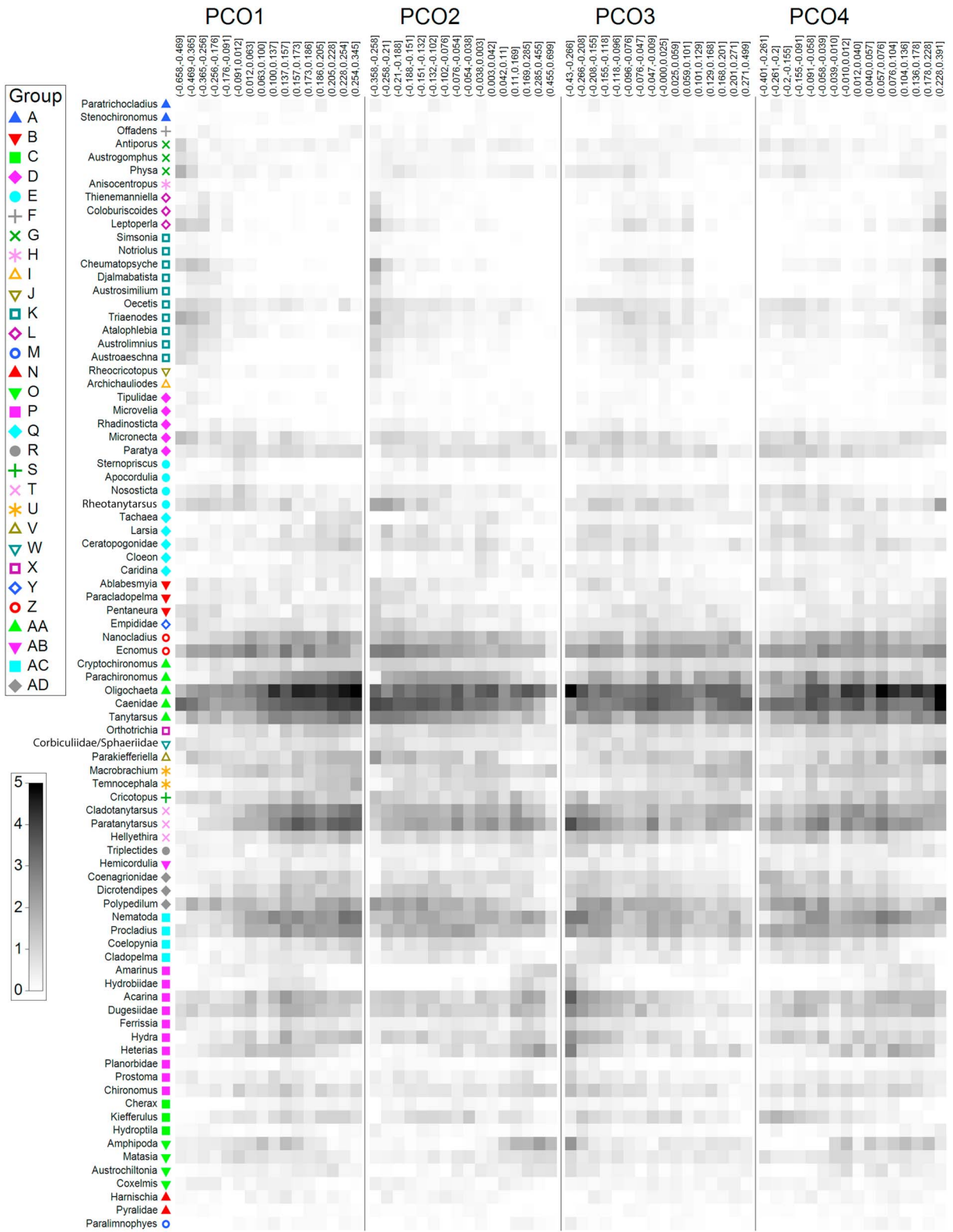


Figure 7. Shade plots of fourth-root abundances against principal coordinates (PCOs) 1–4. Coherent species groups can be identified from the colored symbols shown in the legend at top left. A common abundance scale, based on fourth-root abundances, was used for all plots.

Table 3
GAMs of Coherent Group Fourth-Root Average Abundances Against PCOs

Group	Explained deviance per smooth term				Explained deviance (%)	Null deviance
	s (PCO1)	s (PCO2)	s (PCO3)	s (PCO4)		
L	41.7	13	1.8	6	89.8	402.6
P	6.7	2	35.6	3.7	88.4	1146.8
K	23.4	10.5	1.2	3	87.1	333.8
AA	10.8	14.6	0.3	2.1	84.7	1720.8
AD	9	15	8.1	5.7	76.2	1016.4
T	20.4	1.4	1.5	1.6	76	1023.7
G	21.3	3	8.5	0.2	75.3	339.5
E	16	16	1.1	6.4	72.5	357.6
AC	11.3	7.1	6	3.6	66.5	720.5
C	10.6	7.1	7.8	6.8	65.7	314.4
O	1.9	10.9	2.5	9.3	64.7	355
U	9.1	0	10.3	−0.1	61.1	615.2
F	3.7	3.8	1.9	3.4	59.8	87.3
I	18.7	4.1	6.7	1.3	56.7	63.9
J	0.2	1.3	4.6	4.2	55.8	137.1
Q	9.5	0.3	3.5	0.5	55.7	272.4
A	1.2	3.5	8.1	3.4	53.4	73.2
M	4.4	1.1	0.9	3.6	53.2	96.2
V	2.6	4.5	4.2	1.2	53.1	507.8
D	10.9	0.6	11.4	10.3	52.9	198.3
H	1.1	7.4	10.7	2.9	47.3	96.6
B	3.7	12.4	0	4	47.1	310.8
Y	2.6	4	1.5	0.4	44.2	390
Z	4.5	3.2	0.9	0.9	43.2	546
R	1.4	2.2	2.4	2.7	42.8	332.1
N	2.8	12.5	0.6	10.5	39.2	100.3
S	1.2	2.6	1.4	1.3	32.7	391.5
X	3.7	0.6	0.9	0.2	26.7	340.6
W	1.2	0.1	0.6	0.3	21.3	299
AB	0.1	3.8	2.8	0.7	19.1	218.8

Note. GAM = generalized additive model; PCO = principal coordinate.

tolerant to pollution (SIGNAL2 score of 3). Group C occurred at warmer climates and all but the poorest of water quality. Group C, which included the freshwater yabby (*Cherax destructor*), a chironomid (*Kiefferulus* spp.), and a caddisfly (*Hydroptila* spp.), occurred mostly at the midreach site 811 (1,737 km) and gradually increased in abundance from 1990. Group P covered a range of climates and water quality, except for *Amarinus lacustris* and Hydrobiidae which were restricted to the higher salinities. Group P (Figure 8b) increased in abundance across all sites, with a rapid population increase in the early 1990s at Site 814, followed by a decrease again in the mid-2000s to become comparable in abundance to the other sites. This group consisted of highly tolerant, benthic taxa, including two snails, a flat worm, a proboscis worm, and a freshwater crab. The freshwater crab (*Amarinus lacustris*) occurred exclusively at Site 814, and the mud snail (Hydrobiidae) occurred almost exclusively at this site. These two taxa are known to inhabit brackish waters.

Groups AA, AC, and AD exhibited a wide coverage of climate and water quality, but with a slight bias toward warmer temperatures and a tendency to avoid the more saline and turbid waters. These groups exhibited an increase in abundance over time (Figure 8c), and all displayed the quadratic spatial pattern seen in PCO1, with higher abundances in the mid-Murray. However, the magnitude of this spatial pattern diminished over time for Group AA as abundances increased mainly at the upper and lower sites, resulting in a convergence with the mid-Murray sites. Groups AA, AC, and AD are composed of highly pollution-tolerant taxa with low SIGNAL2 scores (2–4). Chironomidae made up the majority of taxa, but these groups also contained Oligochaeta (worms), Nematoda (roundworms), and Caenidae (mayflies), which were the most numerous taxa collected overall.

Many of the taxa in these groups increased in their frequency of occurrence after the flood of 1993. These included taxa from Ephemeroptera (Caenidae), Plecoptera (Gripopterygidae), Trichoptera (Hydroptilidae), Odonata (Protoneuridae, Austrocorduliidae), Diptera (Chironimidae, including the subfamily Tanypodinae and tribes Chironomini and

Tanytarsini, Orthoclaadiinae, and Simuliidae), Nematoda, Crustacea (Parastacidae), Mollusca (Planorbidae, Hydrobiidae, and Ancyliidae), Acarina (Halacaridae), Hydrozoa (Hydridae), Coleoptera (Elmidae and Dytiscidae), and Tricladida (Dugesiidae). Apart from a few predatory species within Tanypodinae, Dytiscidae, Odonata, and Dugesiidae, most of which occurred within group E at Site 804, representatives from the other families were mostly shredders, collectors, and scrapers that feed on detritus and plants, and the majority have more than one generation per year (MDFRC, 2013; Schäfer et al., 2011).

3.5. Counterfactual Analysis to Elucidate how Environmental Changes Have Influenced Groups of Taxa

The predicted abundances of the 30 coherent groups of taxa under various scenarios are shown in Figure 9 for a selection of sites in winter 2011. The purpose of this analysis was to assist in understanding what the community structure might have been near the end of the study period if certain conditions were different, including EC. Winter 2011 was chosen for this analysis because it was the only sampling occasion near the end of the study period that had macroinvertebrate data for all six sites; though, it was repeated for summer 2010 with a subset of sites, and similar patterns were observed. In the following we focus mainly on the nine coherent groups described in the previous section.

The scenarios for Site 801 included predictions under actual conditions (i.e., the observed abundances), a pH that was 0.3 units higher, and a water temperature that was lower by 2.5 °C. The actual conditions in 2011 are given in Table 4. Results suggest that groups E, AC, and AD would have been in higher

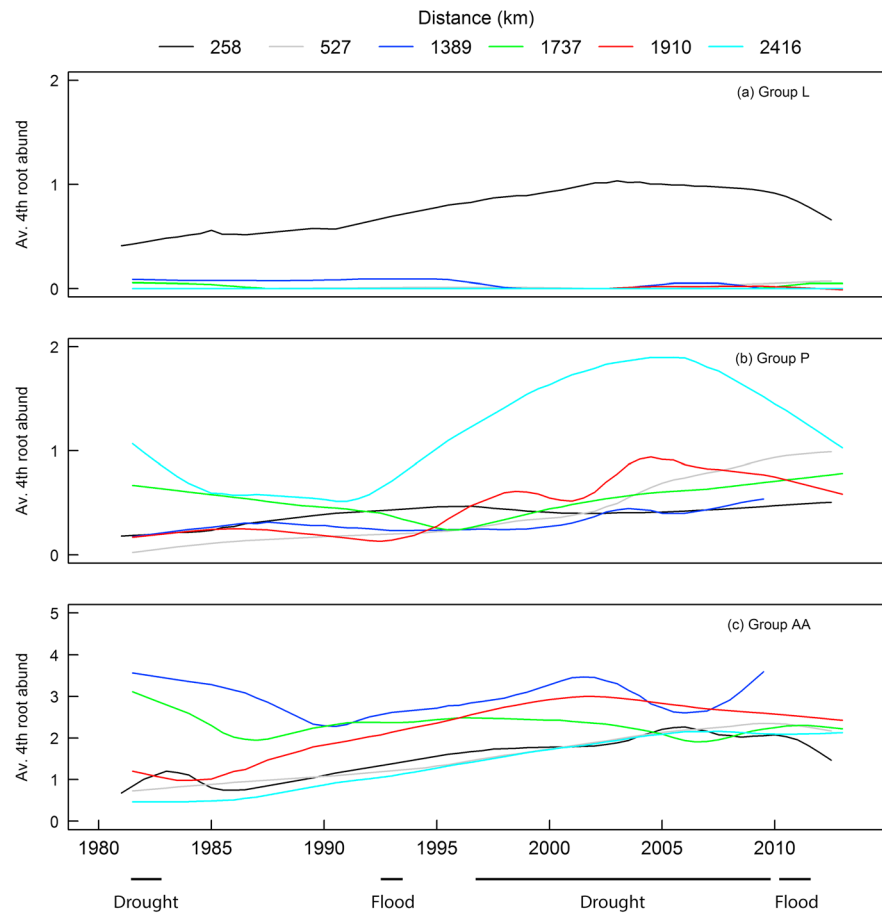


Figure 8. Space-time plots of averaged fourth-root abundances for selected coherent groups of taxa: (a) Group L, (b) Group P, and (c) Group AA. Color indicates site distance from source (km). Sites 808, 811, and 812 at distances 1,389, 1,737, and 1,910 km are located within the semiarid region. Periods of drought and flood are indicated with horizontal lines beneath the time axis.

abundance if the pH was 0.3 units higher, that is, if the pH had been about 7.3 as it was in 1980. Had the water temperature been 2.5 °C cooler in 2011 abundances would have been higher for groups K and L, and lower for groups E, AC, and AD.

The shift in community structure at site 804, which we attributed to the proximity of Yarrawonga weir 4 km upstream, appears to be due to a lower abundance of several groups of taxa, including groups AA and AC, whereas groups C and E were in higher abundance. This was inferred by setting the indicator variable [dist = 527] to zero in the dbRDA model then predicting abundances from the new PCO scores resulting from the change. For simplicity we refer to this intervention as *no weir* in Figure 9. Group E would have been more abundant if the water temperature had been 2.0 °C cooler, whereas Groups C, AC, and AD would have been less abundant.

The most notable scenario at Site 814 is that several groups of taxa would have been more or less abundant if the EC had have been higher by 150 $\mu\text{S}/\text{cm}$, as it was predicted to be at Morgan (between Sites 812 and 814) in the absence of salinity mitigation strategies, or 400 $\mu\text{S}/\text{cm}$ higher, as it was in 1980. Group P would have been more abundant, whereas groups E, AA, AC, and AD less abundant. Furthermore, the GAMs presented in Figures 4a and 4e suggest that total abundance and taxa richness would have been lower under these two scenarios of higher EC, although 95% confidence intervals for predictions suggest that the evidence is weak. Predictions with approximate 95% confidence intervals (in parentheses) under actual conditions, and EC higher by 150 and 400 $\mu\text{S}/\text{cm}$ are, for abundance, 1,366 (750, 1982) individuals, 999 (527, 1471) individuals, and 628 (284, 972) individuals, respectively; and for richness, 33 (30, 36) taxa, 32 (29, 35) taxa, and 31 (27, 34) taxa. Of these, the only difference in means that is statistically significant is between the mean

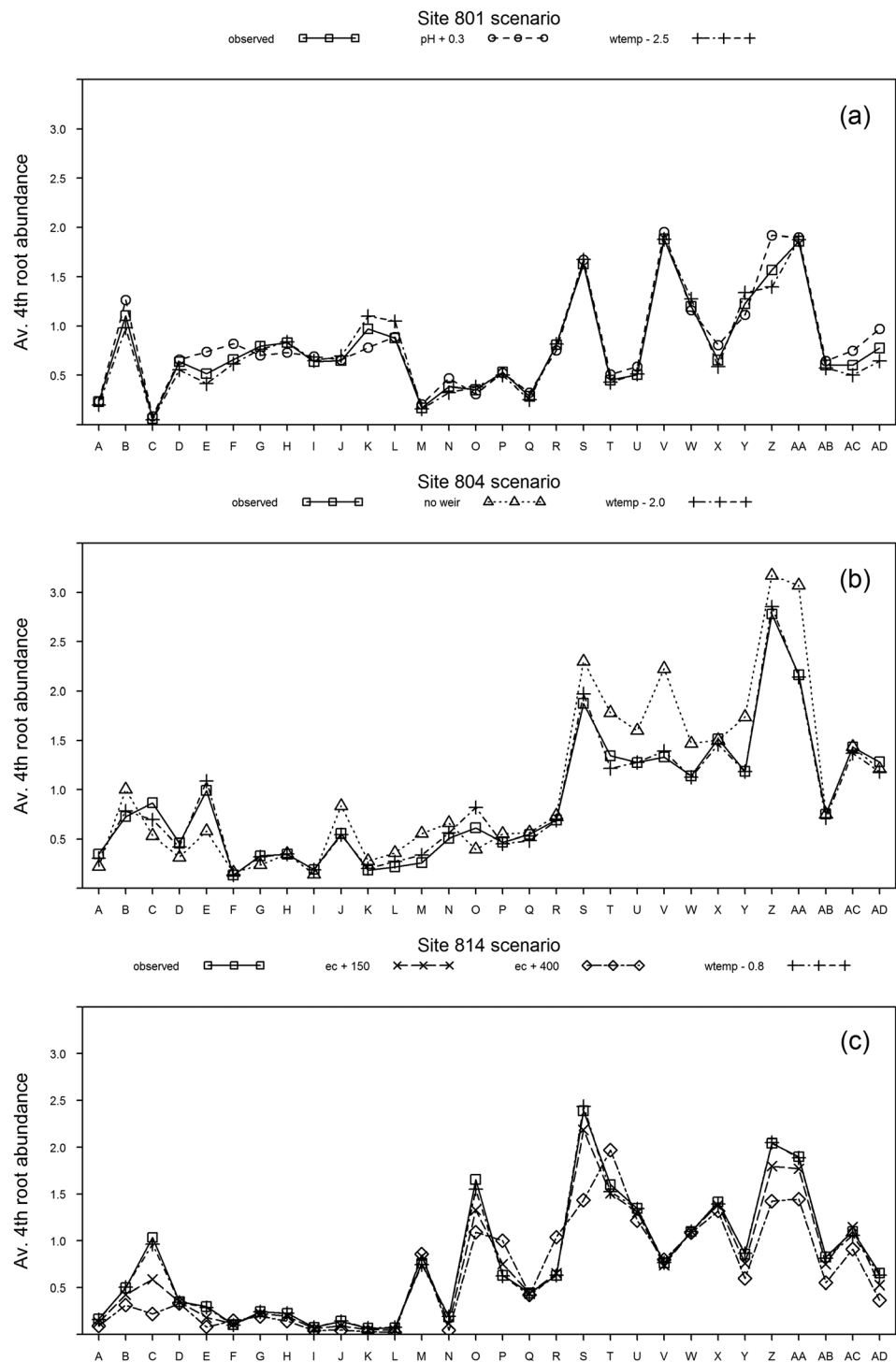


Figure 9. Plots of averaged fourth-root abundances for coherent groups of taxa, at selected sites –(a) Site 801, (b) Site 804, and (c) Site 814 –under various scenarios: (i) observed abundances under the actual conditions of the winter of 2011 (see Table 4); (ii) predicted abundances if the pH had been 0.3 units higher at Site 801; (iii) predicted abundances if the water temperature had been cooler by 2.5, 2.0, and 0.8 °C for Sites 801, 804, and 814, respectively; (iv) predicted abundances if the indicator variable for Site 804 was set to zero, which for simplicity we refer to here as no weir (at Yarrowonga); and (v) predicted abundances if the electrical conductivity had been higher by 150 and 400 $\mu\text{S}/\text{cm}$ at Site 814.

Table 4
Actual Conditions in Winter 2011

Variable	Site 801	Site 804	Site 814
EC ($\mu\text{S}/\text{cm}$)	44	71	373
Turbidity (NTU)	4	14	126
Water temperature ($^{\circ}\text{C}$)	11.7	15.5	15.1
Normalized flow	0.02	0.13	1.54
pH	7.0	7.9	7.5
Rainfall (mm/day)	1.4	0.7	1.5

Note. EC = electrical conductivity.

abundance under actual conditions and the mean abundance at 400 $\mu\text{S}/\text{cm}$ higher EC, with the approximate 95% confidence interval for the difference being (46, 1428) individuals.

4. Discussion

The WQMP began in 1980 with the purpose of evaluating measures to control salinity and nutrients and restore flows, as well as detecting other problems that might be affecting aquatic ecosystems of the Murray River. Since its inception there have been several major flooding events, with widespread flooding in 1993 and 2010–11, and droughts,

including the 1982–1983 drought and the Millennium drought from 1997 to 2009. Taxa richness and total abundance of macroinvertebrates increased across all sites after the 1993 flood then began to decline after peaking during the Millennium drought. Richness decreased with increasing EC and pH, whereas it varied seasonally with temperature, and it increased with time after the mid-1990s. Abundance displayed a unimodal response to EC with a peak at about 300 $\mu\text{S}/\text{cm}$, whereas it decreased with increasing turbidity, varied seasonally with temperature, and increased with time after the mid-1990s. The changes in community structure were similarly related to EC, pH, turbidity, and water temperature and also to normalized flow and rainfall. The temporal trends in the univariate and multivariate analyses indicate something other than the measured environmental variables was responsible for the persistent changes in richness, abundance, and community structure following the flood of 1993. Moreover, in the multivariate analysis, the environmental variables (EC, turbidity, water temperature, normalized flow, and rainfall) accounted for only 38% of the systematic variation through space and time. This suggests that flood was a major determinant of community structure, which accords with the stream literature (Death, 2008; Lake, 2000; Reice et al., 1990; Resh et al., 1988).

These observations are consistent with our first hypothesis: that the number of taxa would increase in response to floods, in agreement with the intermediate disturbance hypothesis. However, we also observed an increase in total abundance. It is well known that floods can have many indirect effects on the structure of macroinvertebrate communities and that these can manifest over a range of time scales. Numerous studies have reported that richness and density decrease in response to high flows—as individuals are washed out, crushed by moving substrate and debris, or take refuge—and that recovery generally happens within a few weeks (Brooks & Boulton, 1991; Death, 2008; Mannes et al., 2008; Robinson, 2012; Scrimgeour & Winterbourn, 1989). Floods can also have a major effect on habitat—including scouring and aggradation/degradation of streambeds, removal of plants, nutrient input, and deposition of detritus (Lake, 2000)—and these effects can last from years to decades (Lake, 2000; Madej & Ozaki, 1996). Natural floods in the Rhône River resulted in an increase in richness (Daufresne et al., 2007; Fruget et al., 2001) and abundance of some macroinvertebrate taxa (Daufresne et al., 2007), particularly the abundance of eurytolerant and invasive taxa, that persisted for more than a decade without any apparent sign of recovery. We found that the immediate effect of high flows was negligible, which might be a result of the long deployment periods for artificial substrates, but that the 1993 flood appeared to have a sizeable longer-term impact. Daufresne et al. (2007) hypothesized a switch to an alternative stable state (Scheffer et al., 2001) as an explanation for the persistent increase in richness observed in their study, but in our study there were signs of recovery after about a decade, and we suspect the explanation lies in the indirect effects of floods on habitat (e.g., see Townsend & Scarsbrook, 1997).

Apart from a few predators, all of the taxa that became more prevalent after the 1993 flood were shredders, collectors, and scrapers that feed on detritus and plants, and the majority have more than one generation per year (MDFRC, 2013; Schäfer et al., 2011). This could indicate that the flood had a long-lasting effect on community structure through the promotion of taxa capable of exploiting inputs of detritus and debris from the floodplain (Death, 2008; Junk et al., 1989), and possibly the periphytic algal biomass that might have increased in response to nutrient inputs (Baldwin & Mitchell, 2000; Cummins & Klug, 1979; Rier & Stevenson, 2006). In the longer term, future monitoring could include variables thought to mediate the effects of floods on community structure—such as substrate composition, periphytic algal biomass, and

both fine and coarse particulate organic matter—but, in the short term, the models presented here could be further developed to include lagged flows that might account for the delayed effects of floods.

In addition to the effects of floods, we hypothesized that warming would alter the geographical ranges of some species and shift the community toward eurytolerant taxa. Water temperature increased by about 2.5 °C over the 33-year period at Site 801, while at Site 804 it increased by 2.0 °C, and at all other sites it increased by an average of 0.8 °C. There was evidence that the increase in water temperature of 2.5 °C at Site 801 reduced the abundance of Groups K and L, including taxa such as *Coloburiscoides* sp. and *Atalophlebia* spp. (Ephemeroptera), *Leotoperla* spp. (Plectoptera), and *Cheumatopsyche* spp. (Trichoptera), all of which are generally associated with cool water and occur in relatively high numbers at Site 801 in winter. Conversely, Groups AC and AD—which include tolerant taxa from Chironomidae, Oligochaeta, Nematoda, and Caenidae that are generally found across a range of sites—were in higher abundances. For example, Nematoda and *Cladopelma curtivalva* (Chironomidae) were rarely detected at the upper sites until the onset of the Millennium drought in the summer of 1996 and are now present in quite high numbers. Similarly, *Polypedilum* spp. (Chironomidae) were in very low numbers until the onset of the drought. Prior to the drought, these taxa were mostly abundant in the warmer midreaches of the river. This would suggest a shift in the geographic range of these taxa, although abundances generally decreased again when the drought ended. These findings are in agreement with the majority of long-term studies of macroinvertebrates (Chessman, 2009; Daufresne et al., 2007; Durance & Ormerod, 2007; Flourey et al., 2013; Fruget et al., 2001, 2015).

The increase in water temperature in the Murray River appears to have occurred during the drought of 1997–2009, after which it began to fall again. There was no clear directional trend in the air temperature data through time, only an apparent long-term cycle with a trough occurring in the early 1990s, and this pattern was consistent across all sites. Further, the observed increases in water temperature are consistent with those reported by others during times of drought (see Mosley, 2015), which have ranged from 1.3 to 7 °C. Accordingly, we believe that the variation along the river in water temperature increases is largely due to local factors such as lower water levels and reduced groundwater inputs.

Our third hypothesis concerned the response of the macroinvertebrate community to decreasing salinity levels. EC decreased in the Lower Murray over the 33-year period—at Site 814 it decreased from an average of 800 to about 400 $\mu\text{S}/\text{cm}$ —and this can, in part, be attributed to salinity mitigation strategies. Species richness is believed to peak at an EC of between 300 and 490 $\mu\text{S}/\text{cm}$, with a statistically significant decline at <99 and $>1,500$ $\mu\text{S}/\text{cm}$ (Kefford et al., 2011). Kefford et al. (2011) found that family richness similarly appears to peak at 300–490 $\mu\text{S}/\text{cm}$, but with a statistically significant decline detected only at $>4,000$ $\mu\text{S}/\text{cm}$. Our results indicate that richness (mostly at the level of genus and family) decreases with increasing EC, but abundance displayed a unimodal response with a peak at about 300 $\mu\text{S}/\text{cm}$. Moreover, counterfactual predictions indicate that many taxa had increased in abundance as a result of reduced salinities, while some decreased. For example, *Cherax destructor* (Crustacea) and *Hydroptila* spp. (Trichoptera) began to appear with increasing abundance in the Lower Murray from the early 1990s. *Hydroptila* spp. are known to have a relatively low tolerance to salinity (Horrigan et al., 2005; Rutherford & Kefford, 2005), whereas *Cherax destructor* survives experimentally in salinities up to 25 g/L (Mills & Geddes, 1980) and has an estimated maximum field salinity tolerance of 16.1 g/L (Rutherford & Kefford, 2005), though anecdotal evidence suggests it tends to favor salinities between 100 and 1,580 mg/L (approx. 780–2,500 $\mu\text{S}/\text{cm}$) in the field (Hart et al., 1991). Conversely, the freshwater crab *Amarinus lacustris*, which is known to inhabit freshwaters with higher salinities and only occurred at Site 814, appears to have decreased in abundance with the lower salinity. This suggests that the geographic ranges of some taxa may be shifting in response to changing salinity in the Lower Murray, due to either a direct sublethal effect or an indirect effect mediated by biotic interaction.

Unexpectedly, we also observed an appreciable decrease in pH at the uppermost site (Site 801). The pH at this site ranged between 6.3 and 7.8, with the mean varying from about 7.3 in the 1980s to 6.6 in 2005, and increasing again to 7.0 in the 2010s. The pH levels below 5.0 and above 9.0 are known to be toxic to most macroinvertebrates (Hussain & Pandit, 2012), but within this range Graca et al. (2004) found that richness decreases with increasing pH. We similarly observed a decrease in richness with increasing pH. We also found that some taxa at Site 801 were in lower abundance at the lower pH levels, including from

the Chironomidae tribes Tanytarsini and Chironomini, and subfamilies Orthoclaadiinae and Tanytopodinae, and also Coenagrionidae (Odonata), and Hydroptilidae and Economidae (Trichoptera). It may be that these taxa have pH optima above 7 (Tripole et al., 2008). Site 801 lies within a subcatchment known to suffer from soil acidification (Chapman et al., 2007), and the lower pH in the Murray River might be the result of acid runoff during periods of high rainfall (Billett & Cresser, 1992; Krug & Frink, 1983). The use of lime to counter soil acidification has increased exponentially in this region since the early 1990s (Scott et al., 2007), and this, together with lower runoff during the Millennium drought, might explain the increasing pH at Site 801 from the mid-2000s.

Floods, droughts, climate, land use, weirs, and water quality, therefore, appear to have contributed to the spatial and temporal changes in macroinvertebrate communities. The taxonomic data presented here indicate two dominant spatial patterns: one being a quadratic trend that is, at least partly, related to climate (rainfall and temperature); and the other a monotonic trend related to water quality (particularly EC). There was also a noticeable decrease below the Yarrawonga weir in the abundance of gathering collectors (Cummins & Klug, 1979), which feed on detritus in sediments, and this accords with the serial discontinuity concept (Ward & Stanford, 1983). Over time, the spatial trends diminished, as taxa from the mid-Murray expanded their range and communities converged due to increases in temperature at the uppermost sites and decreases in salinity at the lower sites. It is possible that the 1993 flood also contributed to the convergence of communities over time, especially taxa within group AA such as dipterans, mayflies, and perhaps nematodes. Importantly, against this backdrop of climate and water quality variability, we believe we have been able to distinguish a continuum of change in community structure along a salinity gradient, and that salinity mitigation has contributed to the changes that have occurred over the 33-year period of this study.

Of the management interventions that have been implemented since the 1980s—salinity mitigation, reducing nutrient pollution, capping water diversions and allocating water for environmental flows (see section 1)—we can be more certain about the impact of salinity mitigation principally because an estimate of the reduction in salinity that resulted was available from a previous study. Our results suggest that rising salinity had impacted macroinvertebrate communities in the past and that mitigation strategies may be effective in reversing that impact. We acknowledge there is some uncertainty in the modeled improvement in EC attributed to salinity strategies (MDBMC, 2015), but the reported contribution of 150 $\mu\text{S}/\text{cm}$ is an appreciable proportion of the average reduction of 400 $\mu\text{S}/\text{cm}$ in the Lower Murray over the study period. We also acknowledge that there were spatial and temporal patterns in the communities that we were not able to explain with the available data, and that confounding bias might therefore be an issue. Further research is needed to identify the processes underlying these patterns if we are to reduce uncertainty in the estimated effects of salinity and mitigation strategies, as well as detect other anthropogenic impacts. This is an important next step because salt loads are projected to increase in the MDB (MDBMC, 2015), and elsewhere around the world (Cañedo-Argüelles et al., 2013), and a better understanding of the ecological risks is needed to guide future policy and programs. It is less clear from our results whether pollution abatement and environmental watering strategies have had an impact on macroinvertebrate communities. While there appeared to be a gradual reduction in TKN and TP over the 33 years, it is not possible to attribute this to the algal (and nutrient) management strategy owing to the difficulty in quantifying the effect of this intervention (MDBMC, 1994). Further, both TKN and TP were highly correlated with turbidity, making it difficult to separate their effects on macroinvertebrates in the modeling that was done, and unfortunately, measurements of soluble nutrient concentrations (nitrate, nitrite, and filterable reactive phosphorus) were infrequent in the data set that was available. With regard to environmental flows, we know that regulation of the Murray River has reduced the magnitude of average annual floods (annual exceedance probability 50%) by more than 50%, but big floods (average recurrence interval of 20 years or more) have been little affected (Maheshwari et al., 1995). Given the apparent importance of large floods on macroinvertebrate communities, evident from our analysis, it is unclear whether environmental flows have had or could have an appreciable effect on in-channel macroinvertebrate communities, especially with the constraints placed on such flows to avoid inundation of private property and infrastructure (MDBA, 2014). Further research is required on the (delayed) effects of floods of various magnitudes to better understand the impact of floods and environmental flows on the aquatic macroinvertebrates of the Murray River.

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