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TITLE: Environmental, spatial and phylogenetic determinants of fish life-history traits and functional composition of Australian rivers.

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ABBREVIATED TITLE: Determinants of fish life-history traits and functional composition of Australian rivers.

KEY WORDS: Trait-environment, variance partitioning, spatial autocorrelation, community assembly, fish biogeography.

## Summary

1. The biogeography freshwater fish is determined in part by large scale filters such as phylogenetic history, the spatial arrangement of catchments and environmental variability. Species are filtered from the regional pool if they possess a combination of functional traits enabling them to persist in the local environment. This paper aims to quantify the relative importance of these large scale filters in determining spatial variation in freshwater fish life history traits and functional trait composition of Australian river basins.

2. We developed a database of 10 life history traits for 141 native freshwater fish species and compiled species distribution data for 123 river basins across the Australian continent. In order to partition the variation in life-history trait distribution into unique and overlapping components, we also quantified the degree of phylogenetic relatedness among species, the geographic arrangement of river basins throughout the landscape and 12 broad-scale environmental factors. We then related life-history trait composition to gradients of environmental variation by constrained multivariate ordination and simple linear regression.

3. Our explanatory matrices accounted for 86.8% of the total variation in life-history trait composition at the river basin scale, of which, 59.4% could be attributed to phylogeny and spatially structured environmental variation. This component represents the overlap among the broad-scale filtering processes of phylogenetic history, spatial autocorrelation and environmental variability in accounting for the distribution of life-history traits across Australian river basins.

4. Our analysis showed strong associations between suites of life-history traits that define generation time and reproductive output and a strong climate-hydrological gradient across the landscape. We also showed significant correlations between specific environmental variables and a

number of key life history traits that highlight the importance of trait-mediated environmental filters at broad spatial scales.

5. This study advances our conceptual understanding of broad-scale community assembly theory and has revealed trait-environment relationships at scales relevant to restoration and conservation of aquatic biodiversity. Our study provides greater insight into the determinants of spatial variation in fish species distributions and potentially addresses key scientific challenges, such as understanding how fish communities are assembled, and identifies the potential threats and responses of these communities to environmental change.

## INTRODUCTION

Predicting community responses to spatial and temporal gradients of environmental variation is a key challenge for contemporary ecologists, given the perceived extent of current and potential environmental change (Dudgeon et al., 2006). Central to this investigation is the link between species and their environment mediated by trait-habitat interactions at several scales (Frimpong & Angermeier 2010; Olden et al., 2010). The current view is that regional species pools are regulated by landscape-scale connectivity, dispersal limitation and phylogenetic history, from which hierarchically structured spatial and temporal environmental variability (sensu 'the habitat template'; Townsend & Hildrew, 1994) filter those species least suited to a specified set of environmental conditions via their traits (i.e. characteristics of an organism that are linked with fitness and performance) (Emerson & Gillespie 2008; Peres-Neto, Leibold & Dray 2012). Examples relating variation in species traits to local and regional environmental gradients are numerous for plants (e.g. Ackerly & Cornwell, 2007; Campetella et al., 2011), invertebrates (e.g. Stutzner, Dolédec & Hugueny, 2004; Poff et al., 2006) and fish (e.g. Blanck, Tedesco & Lamouroux, 2007; Eros, Heino & Rask, 2009; Pease et al., 2012). For freshwater fish, much of this research has focussed on associations between reach scale trait composition and environmental factors at several spatial scales. For example, Pool et al. (2010) showed how a number of human related environmental drivers, such as hydrological alteration and catchment land use, partly explained fish trait functional diversity in the lower Colorado River Basin. Further, Pease et al. (2012) found relationships between morphological and ecological traits and both local and landscape-scale environmental variables along a fluvial gradient in tropical Mesoamerica. While these studies (and others) have led to a general understanding of trait-environment relationships at a fine spatial grain, there are relatively few studies focussing on the relationships between broad-scale trait composition and environmental gradients characterised at the river basin scale.

The river basin is an ideal grain size with which to address these issues, as it corresponds more closely to the broad-scale filtering concepts central to community assembly theory and has the

potential to elucidate patterns not previously described with finer spatial resolution (Angermeier & Winston, 1998; Unmack 2001; Stewart-Koster et al., 2007; Hermoso & Kennard, 2012). In order to explain spatial patterns in basin-scale trait composition it is important to consider the role of broader biogeographic patterns, phylogenetic history and the spatial arrangement of basins, as well as landscape-scale environmental conditions (Borcard & Legendre, 2002; Poff et al., 2006; Sternberg & Kennard, in press). For natural systems, phylogenetic history in-part determines the type and range of traits present in the regional species pool and is likely to be important in driving a number of key structuring processes, such as niche conservatism and phylogenetic dependence (Olden et al., 2010), while the spatial arrangement of river basins structures the distribution of species across the landscape such that that neighbouring basins are more similar in their species composition than distant basins (i.e. spatial autocorrelation) (Legendre, 1993; Poff et al., 2006). Moreover, the geographical distribution of river basins determines the broader environmental gradient that ultimately selects suites of species (and traits) from the regional pool (Peres-Neto et al., 2012). Identifying the important environmental and ecological factors underpinning species distributions and biodiversity patterns is essential for addressing key scientific challenges, such as understanding how fish communities are assembled, and identifying the potential threats and responses of these communities to environmental change (Jackson, Peres-Neto & Olden, 2001; Olden et al., 2010). Furthermore, the knowledge derived from such analyses conducted over large spatial extents and of a coarse grain (e.g. river basins) is appropriate for informing the local restoration and conservation of aquatic biota (Fausch et al., 2002).

Life-history traits are a major determinant of species fitness and may ultimately influence the distribution and abundance of fish across gradients of hydrological and environmental variation (e.g. Winemiller & Rose, 1992; Blanck et al., 2007; Tedesco et al., 2008; Olden & Kennard 2010). Winemiller & Rose (1992) suggested that the distribution of species could be predicted across a range of habitat types based on the relationships between some key life-history traits and hydrological and environmental variation. Small bodied species with short generation times, early

maturation and low juvenile survival should be characteristic of hydrologically unstable environments dominated by frequent disturbance events (Winemiller & Rose, 1992). Large bodied, highly fecund species with late maturation and low parental care are expected in environments dominated by periodic/seasonal flow regimes, while species of intermediate body size, low fecundity, large egg size and high parental care should dominate in resource limited environments with stable flows and low spatial and temporal heterogeneity (Winemiller & Rose, 1992). These life-history strategies represent 'opportunistic', 'periodic' and 'equilibrium' strategies respectively, and represent trade-offs between generation time, fecundity and juvenile survival (Winemiller & Rose, 1992). Subsequent research has resulted in mixed support for these associations (reviewed in Frimpong & Angermeier, 2010), although such predictions allow us to test our conceptual understanding of life-history theory and trait-environment relationships. Testing trait-environment associations in this manner helps to reduce some of the complexity of natural systems derived from multiple direct and indirect interactions among species, traits and the environment, while providing support for future conservation efforts and advancing predictive models (Welcomme, Winemiller & Cowx, 2006; Mims et al., 2010).

The present study aimed to identify broad-scale trait-environment relationships and quantify the relative importance of phylogenetic, spatial and environmental predictors for explaining the composition in terms of life-history traits of freshwater fish assemblages across river basins in continental Australia. Given Australia's long isolation and high proportion of endemic fish, it represents an ideal setting in which to investigate how phylogenetic history and environmental variation has shaped the distribution of the extant fish fauna and understand the role of life-history traits in this filtering process. We tested the predictions of Winemiller & Rose (1992) that hydrologic and climatic variation will explain differences in the distribution of life history strategies across our study region. We also quantified the relative importance of phylogenetic, spatial and environmental predictors to fish trait distribution by partitioning the variation among these components. We

discuss our results in the context of life history theory, and how they contribute insight into patterns and processes of biogeographical variation in fish species distributions.

## METHODS

### Study Area, Fish Distribution and Trait Information

We assembled functional trait information for freshwater fish occurring in 123 river basins within six primary Australian drainage divisions: North-East Coast, South-East Coast, Murray-Darling Basin, Lake Eyre Basin, Timor Sea and Gulf of Carpentaria (Fig. 1). The region covers more than 4,300,000 km<sup>2</sup> of the Australian continent and is characterised by a diversity of landforms, climate, flow regimes, and aquatic habitat types. This covers approximately 55% of the Australian continent and contains over 90% of the freshwater fish species occurring in Australia (Allen, Midgley & Allen, 2003), hence encompassing the range of life-history strategies and evolutionary pathways of the Australian fauna. Thus these data are ideal for identifying potential broad-scale determinants of variation in life history trait composition at a resolution appropriate for testing our hypotheses.

We considered only fish species in our study region that complete their entire life cycle in freshwater. This maximises our ability to detect trait-environment relationships based on factors structuring fish trait composition that are largely freshwater in nature, whereas the distribution of marine or estuarine vagrants and diadromous species may more closely reflect oceanic processes, such as marine currents and pelagic productivity (Unmack, 2001). Furthermore, preliminary analysis that included diadromous species (194 species in total) explained a lower proportion of trait composition at the river basin scale (data not shown). In total, 141 native freshwater (i.e. excluding translocated and alien species) fish species from 22 families were investigated. Present day species distribution data were assembled using information from published sources (Allen et al., 2003; Pusey, Kennard & Arthington, 2004; Lintermans, 2007; Unmack, 2013) and our own unpublished surveys.

We quantified 10 life-history traits based on our current knowledge and the information available for the majority of focal species (Table 1). These traits describe longevity, age at maturation (female), length at maturation (female), spawning substratum, spawning frequency, reproductive guild (following Balon, 1975), total fecundity, egg size, degree of parental care (PC)

(following Winemiller, 1989) and maximum length. Trait assignments were based on a number of sources of information, including species accounts in comprehensive texts (i.e. McDowall, 1996; Allen et al., 2003; Pusey et al., 2004; Lintermans, 2007), species descriptions from the primary literature, state agency reports, university reports and graduate theses, and electronic databases available on the World Wide Web (e.g. FishBase). All trait information was assigned based on a majority of evidence rule with preference given to adult female measurements where possible (see Olden & Kennard, 2010 for more details on trait assignments). Ordinal data were assigned a single trait state and median values were recorded when ranges were presented for continuous data. Functional traits with no information were inferred from closely related species (Olden, Poff & Bestgen, 2006; Tedesco & Hugueny, 2006; Olden & Kennard, 2010).

To analyse variation in the distribution of functional traits throughout our study area we developed a matrix of trait frequencies in each river basin. To accomplish this we were first required to categorise continuous traits into discrete states based on quartiles, which were shown to be an appropriate delineation via frequency histograms. Categorical traits were retained unchanged. Trait frequencies were then calculated by multiplying the species-trait matrix and the species-distribution matrix and dividing by basin richness to give the proportion of species present in each river basin possessing each trait (response data).

## Environmental, spatial and phylogenetic data

### Environmental data

We quantified 27 catchment terrain, river network, climatic, productivity and hydrological variables derived from the National Catchment and Stream Environment Database at the 1:250,000 scale (Stein et al., 2010). From these we chose a final set of 12 variables after testing for redundancy and co-linearity using a combination of Principal Components Analysis (PCA) and Spearman-Rank correlations (Table 2). All variables in the final analysis had a variance inflation factor less than 10 (Quinn & Koeugh, 2002).

Environmental variables were chosen best to represent the extent of variation in environmental conditions present in our study area and to encapsulate a range of ecologically important environmental determinants reported in the primary literature. Catchment terrain variables (catchment area, relief ratio, % lowland, % upland, catchment storage, stream density) describe the habitat size, connectivity and aquatic habitat availability. Climate and productivity variables (temperature, temperature range, net primary production) describe the amount and range of physical energy available to the system. Hydrologic variables (runoff, coefficient of variation, perenniality) describe the magnitude, frequency, timing and duration of flow in the system. The final set of 12 environmental explanatory variables was then normalised (mean of 0, unit variance).

#### Spatial data

To investigate the influence of spatial arrangement of river basins on patterns in the trait distribution data we recorded the latitude and longitude of each river basin outlet and centred these variables on their mean to reduce co-linearity (Anderson & Gribble, 1998). As stream capture is considered to be a relatively rare event and not a major determinant of extant freshwater fish distributions in Australia (Unmack 2001), we considered it more appropriate to use basin outlet as our measure of the spatial proximity of river basins to one other. We then employed multivariate trend-surface analysis by calculating all the terms of a cubic trend surface regression to give the following nine spatial variables:  $x$ ,  $y$ ,  $x^2$ ,  $xy$ ,  $y^2$ ,  $x^3$ ,  $x^2y$ ,  $xy^2$ ,  $y^3$ , where  $x$ =latitude and  $y$ =longitude (Borcard & Legendre, 2002). These terms were then used to model broad-scale spatial structures in later analysis and identify the degree of spatial autocorrelation in the response data.

#### Phylogenetic relationships

To quantify the variation in functional traits that can be attributed to phylogenetic dependence we first developed a matrix containing the species richness of each river basin at the family level. We chose this departure from traditional comparative approaches (Webb et al., 2002)

because we wished to quantify the explanatory power of phylogeny in our analysis instead of accounting for phylogenetic signal. Due to the large number of explanatory variables (22 families) we chose to reduce this dimensionality using Principal Co-ordinates Analysis (PCoA) based on a Bray-Curtis dissimilarity matrix. The first five principal components (which explained 97% of total variation) were retained as explanatory phylogenetic variables for later analysis.

### Statistical Analysis

Before analysis, we conducted Detrended Correspondence Analysis (DCA) to measure the degree of species turnover along our distribution gradient based on the length of the ordination axis (ter Braak, 1986). This analysis revealed that a linear response model was an appropriate assumption for future analysis, i.e. trait frequency was assumed to vary linearly along our measured environmental gradient (Gauch, 1982).

We quantified the degree of variation in trait frequency distribution that could be attributed to environmental, phylogenetic and spatial variables and the variation shared by these components using Partial Redundancy Analysis (pRDA) (Borcard, Legendre & Drapeau, 1992; Anderson & Gribble, 1998). This (pRDA) is a variance partitioning method that identifies relationships between one set of response variables and set of predictor variables after partialling out the effects of a third matrix of co-variables. This procedure partitioned the total variation in trait frequency distribution into eight unique components: 1) pure environmental (E); 2) pure phylogenetic (P); 3) pure spatial (S); 4) phylogenetically structured environmental (PE); 5) spatially structured environmental (SE); 6) spatially structured phylogenetic (SP); 7) spatially and phylogenetically structured environmental (SPE); 8) unknown component (U) (Table 2). See Anderson & Gribble (1998) for further explanation of these components and the steps required for their calculation.

The relationship between trait frequency distribution and environmental characteristics at the river basin scale was assessed using Redundancy Analysis (RDA). RDA is a constrained scaling procedure that seeks to explain a linear combination of response variables (trait frequencies) from a

linear combination of predictor variables (environmental factors) while preserving the Euclidean distance between the objects (Quinn & Keough, 2002). It produces constrained eigenvectors that are useful for exploring the relationships between environmental variables and species data simultaneously via scaling/ordination.

We examined the relationship between basin-scale frequencies of key life history traits describing maximum length, maturation size, total fecundity and egg size (e.g. Winemiller & Rose, 1992) and a subset of important environmental variables identified in the RDA analysis using simple linear regression. These regression plots allowed us better to understand the nature of key trait-environment relationships and further test our research hypothesis.

All data analyses were performed in R (v2.14.2; The R Foundation for Statistical Computing, 2011).

## RESULTS

### Variance Partitioning

Partitioning the variation in trait frequency distribution into environmental, phylogenetic and spatial components showed that between 70.9% and 75.5% of the variation in life history composition of river basins could be explained by each set of explanatory variables (Table 3). The amount of overlap in this variation explained is shown in the subsequent steps. The total amount of the variation in trait frequency distribution explained by each of the components of variation (E, P, S, SE, PE, SP, SPE) was 86.8%; with 13.2% of the variation in trait frequency distribution left unexplained (U) (Table 4). The component that accounted for the most variation in fish trait frequency distribution was the spatially and phylogenetically structured environmental variation (SPE) (59.4%). This component represents the amount of variation that can be explained by the unique overlap between landscape-scale environmental conditions, the spatial arrangement of catchments and the effects of phylogenetic dependence, and was notably larger than the next most important component of variation (Table 4). The unique explanatory power of the environmental, spatial and phylogenetic variables (after accounting for the overlap among these components) was low, explaining only 3.1%, 4.3% and 5.9% of the broad-scale variation in freshwater fish functional trait frequency distribution respectively (Table 4).

### Trait-Environment Relationships

Redundancy analysis revealed a number of relationships between trait frequency distribution and environmental features at the catchment scale. An examination of the resulting biplot showed a clear temperature-perenniality gradient associated with the first RDA axis, which accounted for 58.1% of the total variation in trait-frequency distribution (Fig. 2). Small bodied, egg guarding fish that reach maturity at small size and spawn on various gravel and organic substrata were more frequent in environments with perennial flow and low mean annual temperature, as can be shown from the correlation among these components in negative ordination space on the first

RDA axis (Fig. 2). This ordination space was dominated by river basins from the South East Coast drainage division. Conversely, larger bodied, non-egg guarding, highly fecund fish with small eggs and late maturity were more frequent in environments with high mean annual temperature and temporary flow, as can be seen in positive ordination space on the first RDA axis (Fig. 2). Positive ordination space on the first RDA axis was also dominated by river basins from the Timor Sea division, Gulf of Carpentaria division and to a lesser extent the North East Coast division (Fig. 2). The second RDA axis explained a much lower proportion of the total variation in trait frequency distribution (5.0%) as shown by the minor vertical separation of traits in ordination space (Fig. 2c). Fish characterised by larger eggs and intermediate age and length at maturity were more frequent in environments typified by a high gradient, high stream density, high net primary production and low variation in mean annual temperature (Fig. 2). These environmental features were important for separating river basins in the Timor Sea and Gulf of Carpentaria from North East Coast river basins in ordination space as shown on the vertical axis (Fig. 2a).

Regression slope plots identified a number of strong relationships between the frequency of species possessing key life history traits and environmental characteristics of river basins (Fig. 3). The proportion of larger bodied fish was strongly positively associated with catchments characterised by higher mean annual temperature (MaxL3  $r^2=0.83$ ;  $n=122$ ), while small bodied fish were negatively associated with this environmental gradient (MaxL1  $r^2=0.69$ , MaxL2  $r^2=0.50$ ;  $n=122$ ) (Fig. 3a). In catchments with perennial flow, fish tended to reach maturity earlier (LenMat1  $r^2=0.52$ ;  $n=122$ ), while the opposite was true for catchments with intermittent flow (LenMat3  $r^2=0.60$ ;  $n=122$ ) (Fig. 3b). Species that produce fewer eggs were more likely to be found in catchments with high NPP (TFec1  $r^2=0.38$ ;  $n=122$ ), while highly fecund fish showed a negative association with NPP (TFec4  $r^2=0.37$ ;  $n=122$ ) (Fig. 3c). Egg size showed no relationships with catchment storage (a surrogate for the amount of floodplain/wetland type habitats).

## DISCUSSION

There have been several successful attempts to relate fish functional trait composition to gradients of environmental variation (Eros et al., 2009; Pool et al., 2010; Pease et al., 2012). However, our study is one of the few to quantify the relative importance of phylogenetic, spatial, and landscape-scale environmental factors to explain the composition of life-history traits across many river basins. We showed that spatially and phylogenetically structured environmental variation could explain the majority of variation in trait distribution across the Australian continent. Our study also found strong associations between suits of traits that define 'periodic' and 'opportunistic' life-history strategies (sensu Winemiller & Rose, 1992) and a climate-hydrologic gradient. We also showed strong correlations between some important environmental variables and a number of key life history traits defining maximum body size, generation time and total fecundity.

Landscape-scale environmental conditions, the spatial arrangement of catchments and the effects of phylogenetic dependence all explained a high proportion of the variation in life-history trait distribution in this study (70.9%, 73.2% and 75.5% respectively). Large scale studies with many sampling locations are often better able to detect relationships between predictor and response variables, because they encompass the entire response gradient instead of narrow window of this gradient defined by the finer scale (Jackson et al., 2001). Our results highlight the potential importance of the broad-scale biogeographic processes responsible for shaping present day trait distributions. However, when we partitioned the variation in life-history traits into the environmental, spatial and phylogenetic components we found that the unique explanatory power of these variables independent of the other was relatively low (5.1%, 8.9% and 1.9%, respectively). This indicates that very little of the variation explained by the predictor variables was due to the unique effects of individual environmental, spatial or phylogenetic components and, in fact, much of the explanatory power of these predictor variables is derived from the overlap among them (SPE= 50.1%). This component represents the spatially and phylogenetically structured environmental variation related to the distribution of life-history traits throughout our study area. The results of our

variance partitioning procedure are consistent with community assembly theory (Emerson & Gillespie, 2008, Peres-Neto et al., 2012), whereby phylogenetic history and landscape connectivity define the range of traits present in a regional species pool, from which spatially structured environmental habitat filters traits that maximise a species fitness and reproductive success. The components of our variance partitioning procedure explained 86.8% of the total variation in life-history trait distribution, from which more than two thirds could be accounted for by this 'filtering' process. Quantifying the relative importance of these components of variation has provided strong support for our current conceptual understanding of the way in which the environment, space and phylogeny influence the observed distribution of traits throughout the landscape and highlights the importance of considering phylogenetic and spatial factors (and their interaction) when investigating the role of environmental variation for structuring variation in life-history composition.

We found strong associations between a number of key life-history traits and environmental variables measured at the catchment scale. Redundancy analysis revealed a strong association between large bodied, late maturing broadcast spawners that produce large numbers of small eggs, with river basins dominated by high mean annual temperature and low perenniality. This suite of traits is associated with the 'periodic' endpoint strategy of Winemiller & Rose (1992), who predicted a higher frequency of this life-history strategy in areas subjected to seasonal or periodic episodes of favourable conditions. In our analysis, traits associated with the 'periodic' strategy were more frequent in river basins from the Northeast Coast, Gulf of Carpentaria and Timor Sea drainage divisions, where seasonal and periodic patterns of wetting and drying are common. The majority of these river basins are located north of the Tropic of Capricorn and consequently show an association with high mean annual temperature. In our analysis, high mean annual temperature is most likely a surrogate for high seasonality where species are expected to maximise reproductive success by delaying maturity to a size sufficient for producing large clutches of eggs and for adult survival during suboptimal conditions (Winemiller & Rose, 1992). This size-seasonality association is strongly reflected in our linear regressions plots where the frequency of moderately large bodied fish was

very strongly associated with high temperature (seasonality), and the converse was true for smaller fish. Identifying these key trait-environment relationships across broad spatial scales and with species from disparate phylogenetic backgrounds offers important insight into the environmental and biogeographic determinants of functional trait composition (Olden & Kennard 2010)

We observed a strong association between small bodied, egg guarding substratum spawners with low fecundity and moderately small eggs, and river basins dominated by perennial streams and low mean annual temperature. This suite of traits is commonly associated with the 'opportunistic' strategy of Winemiller & Rose (1992) who predicted this life-history strategy in areas subjected to frequent, unpredictable disturbance. These strategies are also reportedly more common in North and South American fish from warmer climates (Winemiller & Rose, 1992; Mims et al., 2010). In contrast, our results for Australian fish indicate that life-history traits associated with the opportunistic strategy are more frequent in colder, more perennial river basins, such as those in the Southeast Coast drainage division. This is contrary to theoretical predictions and may be explained in a number of ways. Firstly, we may be unable to detect the small scale ecological responses to unpredictable disturbance important to short-lived opportunistic species. River basins in the Southeast Coast division have, on average, a higher percentage of land >250m in altitude and higher catchment slope, where such environments are conducive to 'flashy', disturbed river systems. Secondly, the contemporary distribution of species possessing opportunistic life-history traits, such as the Atheriniformes, may have been established as much as 20 million years BP (Crowley, 1990; Unmack, 2001), at a time when the Australian continent was further south and environmental conditions more favourable for opportunistic species. Filipe et al. (2009) reported that river basin boundaries were more important for segregating species composition than contemporary climate variables in the Iberian Peninsula, south-western Europe, and concluded that historical factors may exert greater constraints on native freshwater fish assemblages than present environmental conditions. Thus our inability to detect relationships between opportunistic strategists and unpredictable environments may be because we cannot capture spatial, phylogenetic and/or

environmental variation at an appropriate spatial and temporal scale (Fausch et al., 2002; Stewart-Koster et al., 2007).

The temperature-perenniality gradient accounted for much of the variation in trait frequency distribution; however, there was a weaker relationship between traits describing low fecundity and moderately larger egg size, and river basins with high NPP, more stream network per catchment area, and higher relief ratios. Linear regression plots also indicated a correlation between river basins with high NPP and species with low fecundity. These trait-environment associations are consistent with the 'equilibrium' life-history strategy of Winemiller & Rose (1992), where stable, highly productive environmental conditions allow species to invest in juvenile survival by producing fewer larger eggs.

The broad geographic scale of our study, coupled with the large grain size of our sampling units (i.e. the river basin scale), provided us with the opportunity to test the importance of large-scale and long-term factors, such as phylogenetic history and the spatial arrangement of river basins to community assembly and life-history trait composition. Our study provides environmental managers with key ecological information at a scale and grain size appropriate for landscape scale restoration efforts (Fausch et al., 2002), and the identification of large-scale protection areas (Abell et al., 2007). Such information is particularly relevant, given that freshwater systems are currently considered among the most endangered worldwide (Dudgeon et al., 2006).

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List of Tables:

Table 1. 10 Life-history traits quantified for 141 Australian native freshwater fish species.

Trait	Description	Abbreviation
Longevity*	Maximum potential life span (years)	Long
Age at maturation*	Mean age at maturation (years)	AgeMat
Length at maturation*	Mean total length at maturation (cm)	LenMat
Spawning substratum	Mineral (e.g. gravel, rocks)	SPSUB1
	Organic (e.g. plants, wood)	SPSUB2
	Various (mineral and organic)	SPSUB3
	Pelagic	SPSUB4
	Other (e.g. buccal)	SPSUB5
Spawning frequency	Single spawning per season	SPFRQ1
	Batch/repeat/protracted spawner per season	SPFRQ2
	Single spawner per lifetime	SPFR3
Reproductive guild	Nonguarders (open substratum spawners)	REPG1
	Nonguarders (brood hiders)	REPG2
	Guarders (substratum choosers)	REPG3
	Guarders (nest spawners)	REPG4
	Bearers (internal)	REPG5
	Bearers (external)	REPG6
Total Fecundity*	Total number of eggs or offspring per breeding season	TFec
Egg size*	Mean diameter of mature (fully yolked) ovarian oocytes (mm)	EggS
Parental care	Metric representing the total energetic contribution of parents to their offspring sensu Winemiller (1989)	PC
Maximum body length*	Maximum total body length (cm)	MaxL

\*Continuous trait characteristics that were discretised for functional community analysis included longevity (1: 0-3.0 years; 2: 3.1-4.0 years; 3: 4.1-6.0 years; 4: >6.0 years); age at maturity (1: 0-0.9 years; 2: 0.91-1.00 years; 3: 1.01-2.00 years; 4: >2.00 years); length at maturity (1: 0-3.3 cm; 2: 3.4-6.0 cm; 3: 6.1-20.0 cm; 4: >20.0 cm); total fecundity (1: 0-500; 2: 501-3000; 3: 3001-40000; 4: >40000); egg size (1: 0-5.200 mm; 2: 5.201-1.000 mm; 3: 1.001-1.300 mm; 4: >1.300 mm); and maximum body length (1: 0-8.0 cm; 2: 8.1-15.0 cm; 3: 15.1-40.0 cm; 4: >40.0 cm).

Table 2. Description and summary statistics (mean  $\pm$  SE, range) for the final set of 12 environmental variables that were characterised for 123 Australian river basins and used in the trait-environment analyses.

Basin Scale Variables	Abbreviation	Description	Mean $\pm$ SE	Range
<b>Terrain</b>				
Catchment Area	AREA	Catchment area upstream of river basin outlet (km <sup>2</sup> )	25501 $\pm$ 7868	443 - 836102
Relief ratio	REL_RATIO	(Maximum upstream elevation - river basin outlet elevation)/maximum flow path length)	0.0069 $\pm$ 0.0006	0.0005 - 0.0446
% Lowland	LOWLAND	% of catchment <10m (%)	12.4 $\pm$ 0.9	0.2 - 52.2
% Upland	UPLAND	% of catchment >250m (%)	20.1 $\pm$ 2	0.0 - 93.8
Catchment storage	STORAGE	% catchment defined as 'Valley Bottom' (%)	17.9 $\pm$ 1	0.1 - 48.2
<b>Network</b>				
Stream density	STREAM_DENS	Total length of the stream network / catchment area (km/km <sup>2</sup> )	0.74 $\pm$ 0.2	0.11 - 1.29
<b>Climate</b>				
Temperature	TEMP	Mean annual catchment temperature (°C)	21.6 $\pm$ 0.4	10.4 - 27.5
Temperature range	TEMP_RANGE	Mean annual catchment temperature range (°C)	10.4 $\pm$ 0.4	1.6 - 18.5
<b>Productivity</b>				
Net primary production	NPP	Mean catchment net primary production (pre-1788) (tC ha <sup>-1</sup> )	3.99 $\pm$ 0.23	0.24 + 9.76
<b>Hydrology</b>				
Runoff	RUNOFF	Discharge/catchment area (ML/km <sup>2</sup> )	1830894 $\pm$ 371177	191 - 31512887
Coefficient of variation	CV	Coefficient of variation of the discharge	1.00 $\pm$ 0.05	0.35 - 4.15
Perenniality	PEREN	% contribution to mean annual discharge by the six driest months of the year (%)	4.8 $\pm$ 0.6	0.0 - 22.9

Table 3. The percentage of variation in life-history trait data (T) explained by each of the 12 steps of analysis to partition the variation into its eight components, using the phylogenetic (P), spatial (S) and environmental (E) data matrices.

Step	Description	% Variation explained
1	RDA of T constrained by E	70.9
2	RDA of T constrained by S	73.2
3	RDA of T constrained by P	75.5
4	RDA of T constrained by E with S used as covariables	7.7
5	RDA of T constrained by E with P used as covariables	7.0
6	RDA of T constrained by E with S and P used as covariables	3.1
7	RDA of T constrained by S with E used as covariables	10.0
8	RDA of T constrained by S with P used as covariables	8.1
9	RDA of T constrained by S with E and P used as covariables	4.3
10	RDA of T constrained by P with E used as covariables	11.6
11	RDA of T constrained by P with S used as covariables	10.5
12	RDA of T constrained by P with E and S used as covariables	5.9

Table 4. Summary of calculations used to derive the percent of variation explained in life-history trait composition by each of the eight components of variation.

Component of Variation	Calculation for variation partitioning (numbers refer to steps in analysis; see Table 3)	Variation Explained (%)
Pure environmental (E)	6	3.1
Pure spatial (S)	9	4.3
Pure phylogenetic (P)	12	5.9
Spatially structured environmental (SE)	SEP-SPE = (1-4)-SPE	3.8
Phylogenetically structured environmental (PE)	PES-SPE = (1-5)-SPE	4.5
Spatially structured phylogeny (SP)	SPE-SPE = (2-8)-SPE	5.6
Spatially and phylogenetically structured environmental variation (SPE)	[9 + (2-7) + (2-8) -2], or [6 + (1-4) + (1-5) -1], or [12 + (3-10) + (3-11) -3]	59.4
Total Explained ( $\Omega$ )	(1 + 7 + 12), or (2 + 4 + 12), or (3 + 5 + 9), or E + S + P + SE + PE + SP + STE	86.8
Unexplained ( $\epsilon$ )	100% - $\Omega$	13.2

List of Figures:

Figure 1. Distribution of the 123 river basins and six drainage divisions (shaded area) included in the study area. Symbols are unique to each drainage division and are used in later figures.

Figure 2. Ordination bi-plot showing redundancy analysis (RDA) results for the life-history trait matrix constrained by environmental factors. The horizontal and vertical axes represent 58.1% and 5% of the total variation in life-history trait composition, respectively. a) The distribution of river basins grouped by drainage division (see Fig. 1 for symbol definition) in ordination space defined by life-history trait variation and the environmental gradients. b) Eigenvector plot of environmental characteristics associated with variation on the first two ordination axes (see Table 2 for abbreviations). c) The distribution of life-history traits on the first two ordination axes (see Table 1 for abbreviations).

Figure 3. Simple linear regression plots showing the regression slopes for relationship between key environmental variables (horizontal axis), and the relative frequency of key life-history traits (vertical axis). For clarity, individual data points (123 river basins per life-history trait category) are not shown.

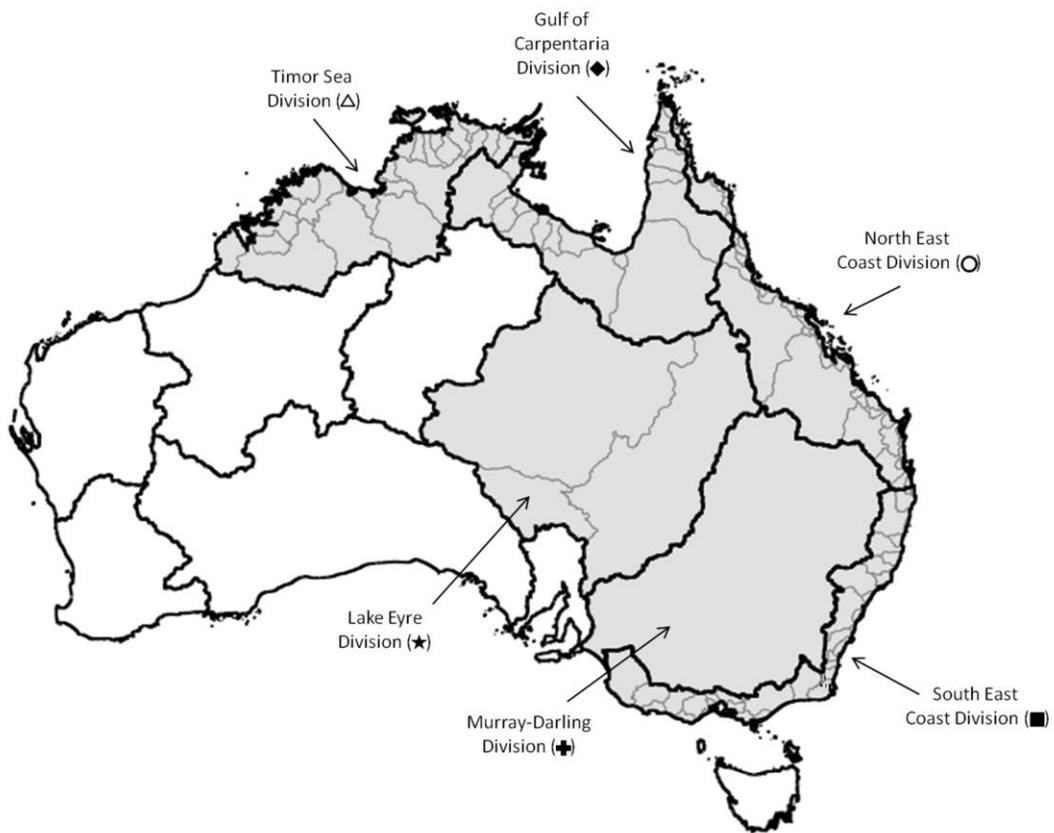


Figure 1.

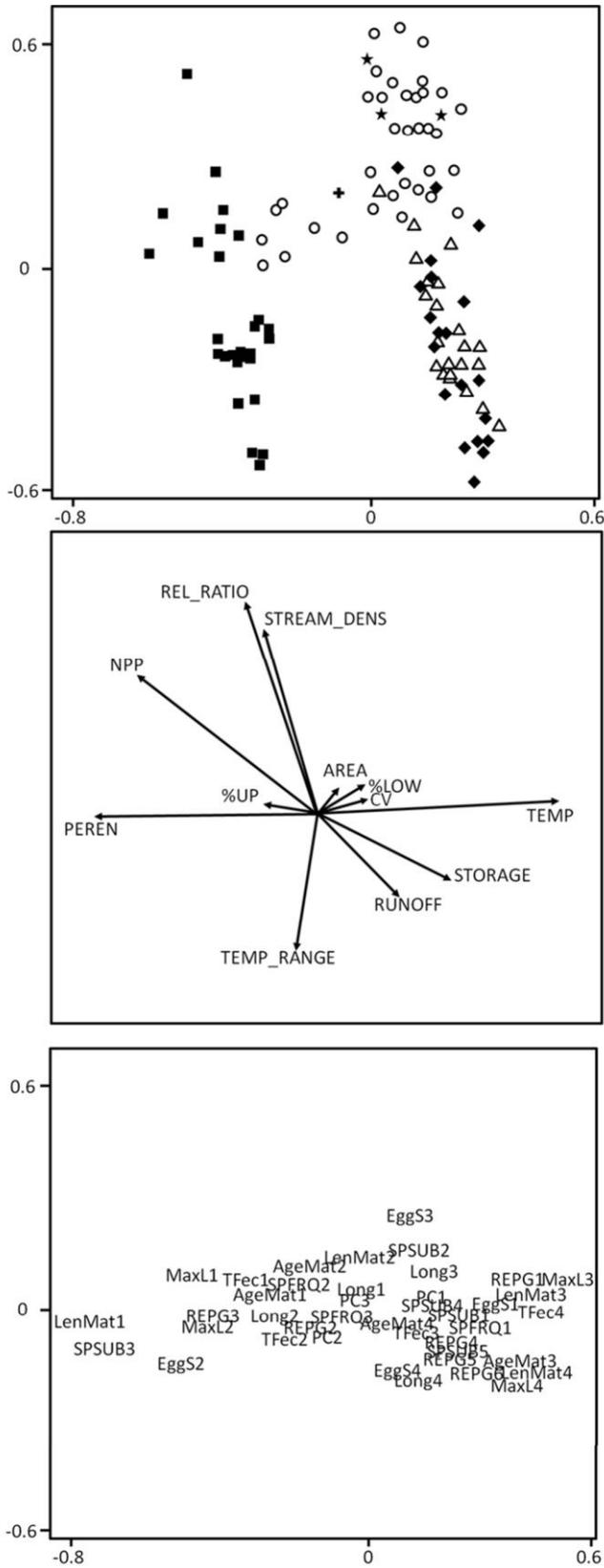


Figure 2

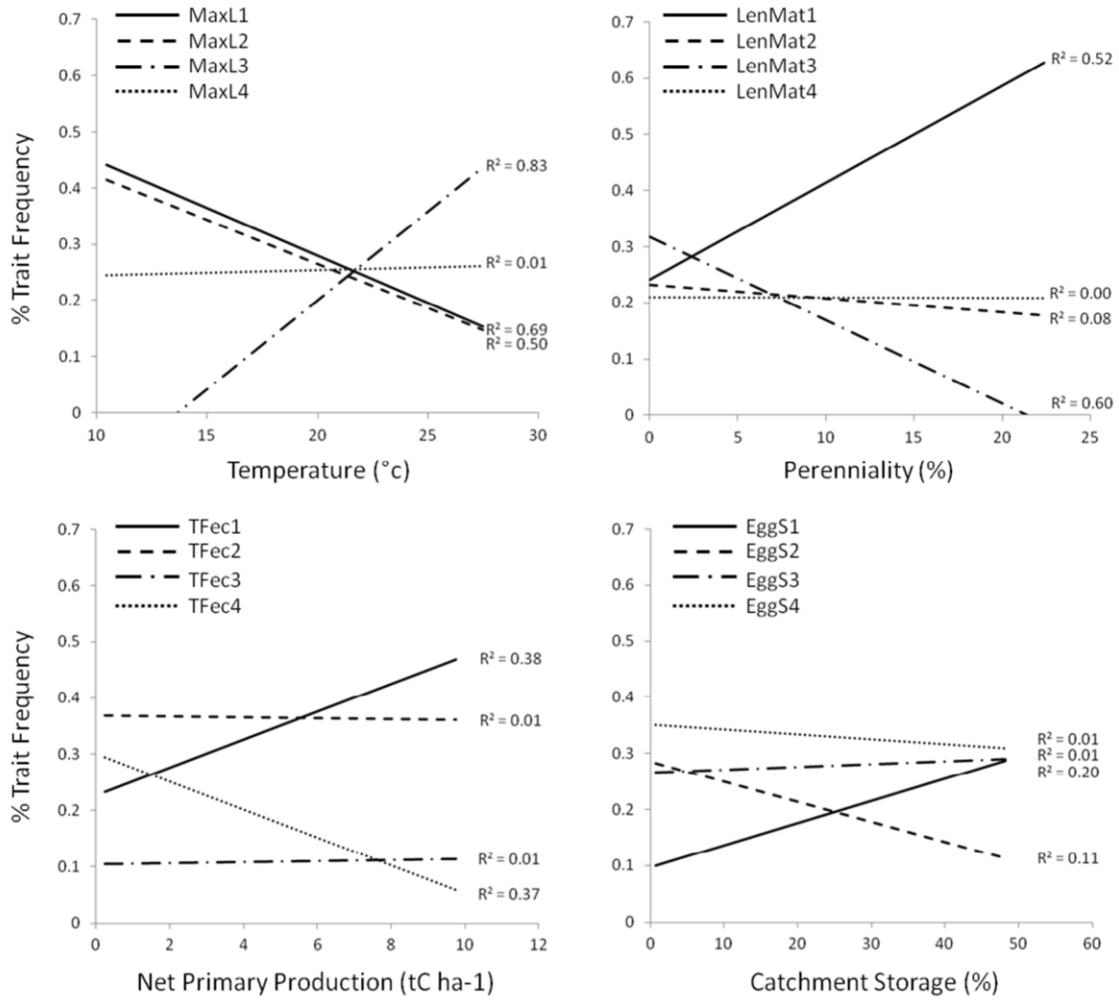


Figure 3.