Importance of cryptic species for identifying ‘representative’ units of biodiversity for freshwater conservation

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ABSTRACT

Nested systems of biodiversity classification are commonly used for designating protected area networks in terrestrial and marine realms. Whilst terrestrial-style protected areas are largely inappropriate for freshwater systems, the concepts of ‘representative’ biodiversity and ‘complementarity’ can be borrowed for freshwater conservation. Cryptic species are commonly found in freshwater macroinvertebrates and fish, and most have restricted distributions relative to the described conglomerate ‘species’. This indicates that ‘representative’ and therefore ‘complementary’ units of freshwater biodiversity may be smaller than previously appreciated. Using recently detected cryptic species in atyid shrimps from eastern Australia (Atyidae: Paratya australiensis, Caridina mccullochi and C. indistinca), we tested predictions about regional patterns of cryptic assemblage structure, endemism and Phylogenetic Diversity (PD) at the river scale, and discussed their implications for freshwater conservation. Patterns of distribution in these cryptic shrimp species largely corresponded with published distributional patterns of cryptic species in several freshwater fish in eastern Australia, and indicated the presence of four putative ecoregions within a previously recognised freshwater fish province (Eastern Province). However, some rivers had pronounced cryptic endemism, suggesting that rivers may not be ‘representative’ of one another’s biodiversity even within ecoregions. PD and endemism were largely correlated with one another, as endemics typically co-occurred with widespread species at the river scale. This study indicates that cryptic species can contribute to defining patterns of biodiversity at nested spatial scales that may be important for freshwater conservation.

1. Introduction

Spatially classifying biodiversity is fundamental for conservation (Margules and Pressy, 2000). Nested systems of classification (e.g. realms > provinces > ecoregions, Spalding et al., 2007) that reflect hierarchical levels of biotic distinctiveness are commonly used in terrestrial and marine bioregionalisation programs (Olson et al., 2001; Spalding et al., 2007). Typically, biotic distinctiveness is measured using presence and/or abundance data, critical species counts or phylogenetic distance among taxa (Vane-Wright et al., 1991; Faith, 1992; Clarke and Warwick, 1998; Whiting et al., 2000). The concepts of ‘representativeness’ and ‘complementarity’ underpin various approaches used to establish protected area networks, whereby multiple reserves that are representative of distinctive and therefore complementary units of biodiversity (e.g. ecoregions) are gazetted. For example, the National Strategy for the Conservation of Australia’s Biological Diversity (1996) requires governments to establish comprehensive, adequate and representative networks of terrestrial and marine protected areas (e.g. the Australian National Representative System of Marine Protected Areas). Whilst there are similar frameworks...
for establishing terrestrial and marine protected areas around the world [e.g., Canada’s Federal Marine Protected Areas Strategy (2005), IUCN’s World Commission on Protected Areas Strategic Plan (2005–2012)], there remains a global deficiency of frameworks and strategies for establishing freshwater protected areas (Saunders et al., 2002; Kingsford and Nevill, 2005; Dudgeon et al., 2006; Abell et al., 2007). While terrestrial approaches to establishing freshwater protected areas are likely to be inadequate for freshwater conservation (Saunders et al., 2002; Dunn et al., 2003; Dudgeon et al., 2006), the principles of representation and complementarity, as determined using regional systems of biodiversity classification, may be borrowed from the terrestrial and marine realms and applied to much needed freshwater conservation programs (Kingsford et al., 2005).

The importance of taxonomic resolution of benthic macroinvertebrates is contentious in freshwater ecosystem health bioassessment programs (Waite et al., 2004; Metzeling et al., 2006; Chessman et al., 2007; Heino and Soininen, 2007). However, species-level taxonomic resolution is of fundamental importance for defining representative units of biodiversity, as freshwater reserve systems aim to protect the full variety of species (Linke et al., 2007). Morphologically cryptic species are often detected in freshwater macroinvertebrates (Liu et al., 2003; Baker et al., 2004; Wellborn and Cothran, 2007; Hughes et al., 2008) and fishes (Waters and Wallis, 2000; Martin and Bermingham, 2000), many of which have small distributional ranges relative to the ‘ubiquitous’ morphospecies (e.g. Baker et al., 2003; Wellborn and Cothran, 2007). This suggests that ‘representative’ units of freshwater species diversity may be smaller than previously appreciated. Cryptic species are likely to represent units of evolution that are important for conservation, rather than conglomerations of morphologically similar species, which may not even be closely related (Crandall et al., 2000; Bickford et al., 2006; Page et al., 2007). Despite the common detection of cryptic freshwater species, biogeographical patterns (upon which measures of representativeness and complementarity are based) have rarely been compared between formally described species and their cryptic composites.

In eastern and southern Australia, three genera of freshwater atyid shrimp (Decapoda: Atyidae: Paratya, Caridina and Australatya) are common in lotic systems and used in conservation planning and bioassessment programs (e.g. Metzeling et al., 2006; Linke et al., 2007). The genera Paratya and Australatya are each represented by a single described species (Paratya australiensis Kemp, 1917; Australatya striolata McCulloch and McNeil, 1923), whereas Caridina is represented by two described species in these regions [Caridina mccullochi J. Roux, 1926 (New South Wales, the Australian Capital Territory, Victoria and South Australia) and Caridina indistincta Calman, 1926 (South East Queensland)]. However, recent phylogenetic studies have shown that Paratya is a complex of at least nine cryptic species in south eastern Australia (Cook et al., 2006), several of which occur sympatrically and are reproductively isolated, indicating they are biological species (Hughes et al., 2003; Cook et al., 2007). Similarly, molecular phylogenetic data invalidates C. mccullochi and C. indistincta as monophyletic species, and suggests that the C. mccullochi-indistincta complex may also contain about nine cryptic species (Page et al., 2005a; Page and Hughes, 2007a,b; Page et al., 2007), several of which are also known to be reproductively isolated (Chenoweth and Hughes, 2003) and consistently different in morphology (Page et al., 2005a). The contrasting levels of diversity between described and cryptic species in these genera make them interesting systems with which to explore bioregional patterns that may be relevant for conservation.

The purpose of this study was to present a case study of ‘representative’ units of biodiversity using biogeographic patterns in cryptic species in the genera Paratya and Caridina at the river scale in eastern Australia. Whereas the described taxa would suggest no biogeographical pattern (e.g. Paratya) or a split at the Queensland/New South Wales border (C. indistincta, C. mccullochi), recorded presence/absence of cryptic species in these genera (Cook et al., 2006; Page and Hughes, 2007b) may elucidate more complex and evolutionarily valid patterns of freshwater bioregionalisation. We used measures of assemblage similarity, endemism and Phylogenetic Diversity (PD, Faith, 1992) to test predictions about bioregional patterns of cryptic species diversity in these shrimp. The PD of an area is an index of the phylogenetic branch length spanned by lineages in that area in relation to the overall phylogenetic length spanned by lineages in all areas, and thus contributes information for conservation assessment about the evolutionary history of an area (Faith et al., 2004). Specifically, we predicted that assemblage similarity would reflect recognised east Australian hydrographic regions (i.e. Central Queensland, South East Queensland, North Coast New South Wales, South Coast New South Wales, Australian Water Resources Council, 1976; Fig. 1), and be correlated with geographical distance among rivers, as distance is a factor that may influence spatial patterns of biodiversity (MacArthur and Wilson, 1967). Furthermore, as β-diversity (i.e. species diversity among rivers within regions) is high for various taxonomically unambiguous freshwater groups (Revenga et al., 2005; Dudgeon et al., 2006), we expected to detect pronounced endemism in some rivers or groups of nearby rivers. Finally, we predicted that patterns of PD would be correlated with endemism, as endemic species are theoretically geographically restricted relics and are thus likely to have longer phylogenetic branch lengths than more widespread taxa (Erwin, 1991). We compared cryptic bioregional patterns in these shrimp with other cryptic freshwater taxa in eastern Australia, and discussed global implications of cryptic freshwater species for conservation programs.

2. Materials and methods

Thirty-two coastal rivers across four regional areas in eastern Australia between Rockhampton in the north (23°22′23″S) and Sydney in the south (33°51′57″S) were selected for this case study as they represent the major area of distributional overlap between the genera Paratya and Caridina (Table 1; Fig. 1). Seven COI mitochondrial DNA P. australiensis lineages occur in these rivers (Cook et al., 2006), as do seven COI lineages in the C. mccullochi-indistincta complex (Page et al., 2005a). Presence/absence of these 14 taxa at the river scale, as reported in the aforementioned published studies, were used to calculate assemblage similarity, endemism and phyloge-
nentic diversity at the river scale. All calculations were made for each genus separately and when both genera were included in analyses, where possible.

The performance of community similarity indices is dependent on sample size and species diversity, and the choice of index is further governed by the available data (i.e. whether abundance or presence-absence data is available) and if a missing species is known to be a real absence (Wolda, 1981; Janson and Vegelius, 1981; Faith et al., 1987). Whilst cryptic species diversity in the genera Paratya and Caridina is high relative to the described taxa, it is low in the context of analysis of community similarity. Furthermore, in some cases it is unknown whether missing species are really absent from a river in which it was not found in the earlier studies. We therefore selected Jaccard's community similarity coefficient (Jaccard, 1912) to examine assemblage similarity in cryptic species of shrimp among rivers, as it does not take into account shared absences and is suitable for presence-absence data (Vargas et al., 1998). Pairwise calculations were made using the formula: \( J = j/(a + b - j) \), where \( j \) is the number of species in both rivers, \( a \) is the number of species in the first river, and \( b \) is the number of species in the second river. Values for \( J \) range from zero, where the assemblages in each river have no species in common, through to one, where the assemblages have identical species composition. Pairwise matrices of \( J \) among rivers were analysed using multi-dimensional scaling (MDS) in PRIMER version 5.2.8 (Clarke and Gorley, 2001) using 5000 permutations. As \( J \) is sensitive to sample size, and low numbers of taxa (as in the case of cryptic species of Paratya and Caridina) may inflate values for \( J \) (Vargas et al., 1998), we examined the relationship between \( J \) and number of taxa using Pearson's correlation coefficient in PRIMER using 5000 iterations. The relationship between assemblage similarity and geographic distance (i.e. shortest coastline distance among river mouths) was analysed using a Mantel test (Man tel, 1967) in PRIMER using 5000 iterations.

Endemism is a measure of range-size rarity and we used the Site Endemism Index (SEI, Rebelo and Siegfried, 1992) to compute endemism for each river using the formula: \( \text{SEI} = \sum \frac{k}{ai} \), where \( k \) is the total number of sites (i.e. rivers) and \( ai \) is the number of sites at which species \( i \) occurs. This index ranges from one, where all species at a site have broad geographical ranges, through to infinity, with large values indicating the presence of species with range-size rarity (i.e. rivers with high endemism). We determined the relationship between SEI and sampling effort (i.e. number of sampled sites and number of genotyped individuals), and the relationship between SEI and latitude, using Pearson's correlation coefficient in SPSS.

PD is a measure that integrates phylogeny, complementarity and endemism (Faith, 1992) and ranges from zero, where an area (i.e. river) has low endemism and complementarity with respect to the total phylogeny of the taxa, through to infinity, with large values indicating that a given area has high endemism and complementarity. In order to calculate PD for each river, we firstly determined branch lengths among the taxa with respect to appropriate outgroups: Paratya, outgroup = P. howensis, Lord Howe Island (GenBank accession number = AY622605, Page et al., 2005b); C. mccullochi-indistincta complex, outgroup = C. typus (GenBank accession number = DQ478478, Page et al., 2007). Where possible, two haplotypes from each lineage that were reported from coastal rivers in eastern Australia were selected as ingroup taxa for each genus, giving a total of 62 haplotypes for Paratya and 74 haplotypes for Caridina (see supplementary material for GenBank Accession numbers). It was not possible to calculate PD for rivers using the Paratya and C. mccullochi-indistincta complexes combined as the respective original studies used non-homologous fragments of the COI mtDNA gene. However, we added values of PD from their respective separate analyses to give some indication of their combined patterns of PD. Maximum likelihood (ML) analysis as implemented in PHYML (Guindon and Gascuel, 2003), using 1000 bootstrap replications, was used to create a tree file that included branch lengths for each genus using input parameters as determined in MODELTEST (Posada and Crandall, 1998). Tree files from PHYML were then used to estimate PD for each river for each genus in CONSERVE IV (Agapow and Crosier, in preparation, see also Crosier et al., 1999). To remove the branch length of the outgroup for values of PD for each river, whilst maintaining their relative branch length distances from the outgroup, we subtracted the smallest value for PD for each river, whilst determining the relationship between PD and
sampling effort (i.e. number of sampled sites per river and number of genotyped individuals), and the relationships of PD and latitude, were analysed using Pearson’s correlation coefficient in SPSS. Finally, the relationship between PD and endemism, and the relationship between the branch length of each cryptic taxon and the number of rivers the taxon was found, were tested using Pearson’s correlation coefficient.

3. Results

3.1. Patterns in lineages of Paratya

Analysis of assemblage similarity within the genus Paratya gave \( J \) values ranging from zero to one. The Kolan, Burnett, Mary, Maroochy, Richmond, Hunter and Hawkesbury Rivers had identical species composition \( (J = 1) \). \( P. australiensis \) lineage 4 was the only taxon reported in these rivers, as did the Gold Coast, Logan, Bellinger and Manning Rivers \( (P. australiensis \) lineage 6 was the only taxon reported in these rivers; Fig. 2a). \( J \) was not correlated with number of taxa used in each pairwise comparison \( (\rho = -0.318, P = 0.999) \), but was related to geographic distance among rivers \( (\rho = 0.133, P = 0.048) \). Rivers from each region overlapped to some extent, although rivers from the Sydney region were more distinct than the other regions (Fig. 2a). Endemism in lineages of Paratya varied markedly among rivers, with the Tweed, Clarence and Shoalhaven Rivers having very high values (Fig. 3). There were no significant relationships between endemism and number of sites sampled in each river or number of individuals genotyped (Table 2). Endemism was not correlated with latitude (Pearson’s coefficient = 0.276, \( P = 0.214 \)).

MODELTEST selected the General Time Reversible model with a significant amount of invariable sites and gamma distributed rate heterogeneity (GTR + I + G) as the Akaike’s Information Criterion (AIC) best-fit model of nucleotide substitution for the data and other parameters as follows: alpha (i.e. gamma shape parameter) = 1.3138, pinvar (i.e. proportion of invariable sites) = 0.5992, number of rates = 4, base composition – \( A = 0.258, C = 0.206, G = 0.197, T = 0.344 \).
Analysis of assemblage similarity among rivers within the C. mcullochi-indistincta complex gave J values ranging from zero to one, and showed that rivers in South East Queensland were distinct from rivers in Central Queensland and northern NSW, and that Central Queensland and northern NSW were only partly overlapping (Fig. 2b). J was not correlated with number of taxa (\( r = -0.239, P = 0.998 \)) but was related to geographic distance among rivers (\( r = 0.383, P = 0.001 \)). Endemism in lineages of the C. mcullochi-indistincta complex was moderately variable among rivers, although no river had exceptionally large values relative to other rivers (Fig. 3). Endemism was significantly correlated with sampling effort (Table 2), and was not correlated with latitude (Pearson's coefficient = 0.210, \( P = 0.294 \)).

MODELTEST selected TrN + I + G as the AIC best-fit model of nucleotide substitution and the other parameters as follows: alpha = 1.239, Pinvar = 0.579, number of rates = 4, base composition – A = 0.280, C = 0.251, G = 0.144, T = 0.325. Bootstrap support for each lineage was high (Fig. 4b). The Fitzroy, Calliope, Boyne and Kolan Rivers all had relatively low levels of PD, whereas all other rivers had relatively high PD (Fig. 5). PD was not correlated with latitude (Pearson's coefficient = 0.272, \( P = 0.179 \)). Branch length of the lineages was not correlated with the number of rivers where the lineages were found (Pearson's correlation = 0.486, \( P = 0.329 \)).

### 3.3. Patterns in lineages of Paratya and Caridina combined

Analysis of assemblage similarity within Paratya and the C. mcullochi-indistincta complex among rivers showed that South East Queensland, northern NSW and Central Queensland were not overlapping (Fig. 2c), although the spread of rivers within each region was large. J was not correlated with number of taxa (\( r = -0.382, P = 1.000 \)) but was correlated with geographic distance among rivers (\( r = 0.321, P = 0.003 \)). Endemism was highest for the Tweed and Clarence Rivers, although the Mary, Brisbane and Hastings Rivers also had high values (Fig. 3). Combined endemism was not correlated with latitude (Pearson's coefficient = 0.055, \( P = 0.840 \)) or sampling effort (Table 2), and endemism was not correlated between the genera Paratya and Caridina (Pearson's coefficient = –0.055, \( P = 0.846 \)). When values of PD for the two genera were added, results show variable patterns of PD, with the Kolan and Brisbane Rivers having the lowest and highest values for PD, respectively (Fig. 5). PD in genera Paratya and Caridina were not correlated (Pearson's coefficient = 0.220, \( P = 0.430 \)), and PD was not correlated with endemism (Pearson’s correlation coefficient = 0.494, \( P = 0.052 \)) or sampling effort (Table 2).
Fig. 3 – Site endemism index (SEI) for each river as determined using cryptic species in *Paratya* (black bars), *Caridina* (white bars) and *Paratya* and *Caridina* combined (gray bars). The rivers are arranged north–south down the y axis.

Table 2 – Pearson’s correlation coefficients for tests of Site Endemism Index (SEI) and Phylogenetic Diversity (PD) and sampling effort (i.e. number of sites per river and number of individuals per river)

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Site endemism index</th>
<th>Phylogenetic diversity</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sites per river</td>
<td>Individuals per river</td>
</tr>
<tr>
<td><em>Paratya</em></td>
<td>0.298 (0.202)</td>
<td>0.158 (0.506)</td>
</tr>
<tr>
<td><em>Caridina</em></td>
<td>0.604 (0.001)</td>
<td>0.455 (&lt;0.001)</td>
</tr>
<tr>
<td><em>Paratya</em> and <em>Caridina</em></td>
<td>0.228 (0.414)</td>
<td>0.222 (0.427)</td>
</tr>
</tbody>
</table>

*P* values are given in parenthesis and significant results are indicated in bold.
4. Discussion

Our analysis of assemblage similarity, endemism and phylo-
genetic diversity in cryptic species of freshwater shrimp in
eastern Australia indicated units of biodiversity that contrast
markedly with those indicated using their conglomerate de-
scribed ‘species’. However, it should be noted that our analy-
sis represents a demonstration of the potential for cryptic
species in identifying ‘representative’ units of biodiversity.
More comprehensive sampling would be needed to determine
the true distribution of the lineages within and among rivers,
as measures of shrimp cryptic species diversity at the river
scale tended to be positively correlated with sampling effort.
Our analysis of assemblage similarity, in which we predicted
rivers within known hydrographic regions (i.e. Central
Queensland, South East Queensland, northern New South
Wales, and Sydney, Fig. 1) to be more similar with each other
than with rivers from other regions, gave contrasting results
between the genera *Paratya* and *Caridina*. For genus *Caridina
the prediction was largely supported, although rivers in
which only *Caridina* lineage B was found caused some degree
of overlap between the Central Queensland and northern New
South Wales regions. Better sampling would likely reveal
the presence of lineage D in these rivers from Central Queens-
land and lineages C4 and E in rivers of northern New South
Wales, thereby indicating greater biotic distinction between
these regions. For genus *Paratya* the expectation for regional
groupings of rivers was only partly apparent for the Sydney
region and there were no distinctions between Central
Queensland, South East Queensland and northern New South
Wales. However, it is likely that the true distribution of the
three widespread lineages (i.e. *Paratya* lineages 4, 6 and 8) is
more continuous within regions than their apparent disjunct
distributions that have been reported to date. For example,
*Paratya* lineages 4 and 6 have recently been found to co-occur
at the river scale throughout South East Queensland, includ-
ing the Logan and Gold Coast rivers, although lineage 8 has
not been found (T. Rodriguez, unpublished data). Presuming
that the distribution of lineage 8 is more continuous among
rivers throughout northern New South Wales than is cur-
rently reported, each region is very likely to have unique com-
binations of cryptic species of *Paratya* (excluding species
demic to a single river) [i.e. Central Queensland – lineage
4, South East Queensland – lineages 4 and 6, northern New
South Wales – lineage 4, 6 and 8, and Sydney – lineages 1, 4
(whitch is rare in this region), 6 and 8]. Whilst values of Jac-
cards community similarity coefficient (J) can be inflated by
analyses using only a small number of taxa (Vargas et al.,
1998), J was not correlated with the number of taxa used in
pairwise analyses for *Paratya*, *Caridina* or when the genera
were combined. In this study, incomplete sampling and
uncertainty about ‘missing’ species were more important fac-
tors that have likely influenced analyses of assemblage
similarity.

Whilst analyses of assemblage similarity in genera *Paratya
and Caridina* in eastern Australia did not always give strong
indications for regional groupings, the reported distributions
of cryptic species in other freshwater taxa indicate biotic dis-
inctiveness among the four regions. For example, three allo-
patric and very divergent clades were detected in the ornate
rainbowfish, *Rhadinocentrus ornatus* – Central Queensland,
South East Queensland, northern New South Wales (Page
et al., 2004). Similarly, the genus *Hypseleotris* (Teleostei: Eleo-
tridae) is a complex of five closely related species in central

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Fig. 4 – Maximum likelihood (ML) trees used to calculate phylogenetic diversity (PD) for (a) *Paratya* and (b) *Caridina*. Numbers at
nodes are bootstrap values and clade labels represent the lineage name as given in Table 1. Central Queensland – open
diamonds, South East Queensland – grey diamonds, northern New South Wales – black triangles, Sydney region – open
triangles.
and eastern Australia, three of which occur in coastal drainages (Thacker et al., 2007). Of these three, one is distributed from Central Queensland to northern New South Wales (H. klunzingeri), one is distributed from South East Queensland to Sydney (H. galii), and the third is found in Central and South East Queensland (Hypseleotris sp. 5 Midgley's) (Thacker et al., 2007). Finally, distinct genetic (allozyme) groups, which likely correspond to cryptic species, have been revealed with-

![Phylogenetic Diversity](image)

Fig. 5 – Phylogenetic diversity (PD) in each river for Paratya (black bars), Caridina (white bars) and Paratya and Caridina combined (gray bars). The rivers are arranged north–south down the y axis.
in Australian smelt (Retropinna semoni) – Central Queensland, South East Queensland, South East Coast (includes northern NSW and Sydney regions), and two additional groups from inland and southern Australia, respectively (Hammer et al., 2007). Thus, there is striking concordance in cryptic bioregional patterns in various freshwater taxa in eastern Australia, which align closely with biotic patterns of species richness in described species of freshwater crayfish (genus Cherax, Whiting et al., 2000). These ‘ecoregions’ lie within a recognised freshwater fish ‘province’ (Eastern Province, Unmack, 2001), demonstrating the importance of cryptic species for identifying nested systems of biodiversity. Whilst our case study is an Australian example, the detection of cryptic species in freshwater taxa has shown strong biogeographic regionalisation elsewhere. For example, the distribution of cryptic species within the freshwater isopod genus Mesaphiesopus was distinct between Cape Peninsula and the Hotentots Holland Mountains regions of South Africa (Gouws et al., 2004), distinct regional distributions of cryptic species of crayfish genus Paranephrops were found in New Zealand (Apte et al., 2007), and cryptic species in the rosyface shiner complex, genus Notropis, showed striking bioregional patterns in the eastern United States (Berendzen et al., 2008). Distinct cryptic species diversity among regions is thus of fundamental importance for defining spatial units of biodiversity important for conservation (i.e. ecoregions).

In addition to among region biodiversity, diversity among rivers within regions (i.e. β-diversity) is reported for other freshwater faunas and is important for conservation (Reagven et al., 2005; Dudgeon et al., 2006). We predicted variable levels of cryptic species endemicity among rivers or groups of nearby rivers. This prediction was supported for Paratya (e.g. Tweed, Clarence and Shoalhaven Rivers), although more endemic lineages could be revealed by better sampling. For example, P. australiensis lineage 7 was found in only a single upland tributary of the Goulburn River (King Parrot Creek, Victoria), despite good sampling in that system (15 sites, 141 individuals; Cook et al., 2006), suggesting that multiple tributaries and elevations need to be sampled within each river to detect the presence of all cryptic taxa. For Caridina, however, cryptic β-diversity was relatively low for all rivers, perhaps as a consequence of the much earlier colonisation of Australia by Caridina than Paratya and subsequent longer evolutionary time for dispersal (Page et al., 2007). Note however that cryptic species within Caridina are endemic to particular sand islands off the east Australian coast (Page and Hughes, 2007a). Interestingly, the east Australian continental shelf becomes wider with decreasing latitude, suggesting that there should be lower endemicity to the north on account of increased opportunities for among river dispersal during periods of lowered sea-levels (Unmack, 2001; Thacker et al., 2007). Whilst the most northerly rivers sampled for each genus had low endemicity (Fig. 3), particularly for Caridina, endemicism was not significantly correlated with latitude in either genus, indicating that latitude is not a predictor of ‘hotspots’ of diversity.

Striking cryptic endemicism in eastern Australia was reported in ornate rainbow fish (Rhadinocentrus ornatus) for Searys Creek (South East Queensland, Page et al., 2004), spiny crayfish (genus Euastacus) for the Shoalhaven River (Sydney region, Baker et al., 2004), and eel-tailed catfish, genus Tandanus, for northern New South Wales (Jerry, 2008). Similar patterns of cryptic endemicism and strong β-diversity among geographically proximate rivers have been also reported elsewhere for macroinvertebrates (e.g. freshwater crabs in South Africa, Daniels et al., 2003; springsnails in south-western USA, genus Pyrgulopsis, Liu et al., 2003; caddisflies in south-western USA, genus Gymnagia, Jackson and Resth, 1998) and freshwater fish (e.g. central American catfish, genus Pimelodella, Martin and Bermingham, 2000; rosyface shiners, genus Notropis, in the Eastern Highlands of the eastern United States, Berendzen et al., 2008). Thus, even within ‘ecoregions’, cryptic species endemicism in some rivers indicates that these rivers are neither ‘substitutable’ nor ‘replaceable’ conservation units (Dudgeon et al., 2006; Linke et al., 2007). Rivers within the same ecoregion, therefore, may not be ‘representative’ of one another’s biodiversity.

Phylogenetic diversity (PD) is a measure that integrates phylogeny and endemicism (Faith, 1992), and our analyses showed that PD was correlated with our measure of endemicism (SEI). A possible explanation for this is the premise that endemic species are geographically restricted relics (Erwin, 1991), implying that endemic species have long branch lengths. However, there were no correlations between the branch length of a given cryptic species and the number of rivers in which it was found. The correlation between PD and endemicism, therefore, is due to the fact that endemics were typically found in rivers where widespread species were also found. However, several rivers with low endemicism for Paratya had high PD, as multiple widespread species incorporated a larger proportion of the phylogenetic tree of the genus. However, if our presumption that the widespread lineages have more continuous distributions within regions is true, then rivers which also harbour endemic species will have higher PD than rivers without endemics. As PD and endemicism (i.e. SEI) in Paratya and Caridina was not correlated, these shrimp cannot be used as surrogates for one another when spatially classifying biodiversity, which is a result shown for other freshwater biota (Hess et al., 2006).

PD can be used to prioritise taxa or areas for conservation (Faith, 1992). For example, analysis of PD in spiny crayfish (genus Euastacus) from the Sydney Water Supply Catchment identified one species (Lineage B, sensu Baker et al., 2004) as a priority, as its sister species (Lineage A) is thought to have recently gone extinct (Faith and Baker, 2006). Similarly, South American freshwater crabs in the genus Aegla contain cryptic species that are endemic to particular hydrographic regions (Pérez-Losada et al., 2002). One region (i.e. Tucapel, Imperial and Tolteúén Rivers) was ranked with the highest conservation priority because it had the highest PD (Pérez-Losada et al., 2002). Rather than using PD to rank the conservation value of particular cryptic taxa in Paratya or Caridina, PD may be more useful for identifying particular rivers which could be considered to have conservation priority (Faith, 1992; Pérez-Losada et al., 2002).

Whilst our analysis considered cryptic species-level diversity at the river scale, cryptic diversity at other geographic or systematic scales also has importance for conservation programs. For example, cryptic species may be endemic to a specific part of a river (e.g. Paratya lineage 7 is restricted to a single tributary of the Goulburn River, Cook et al., 2006; crypt-
tific species of rosyface shiners, genus Notropis, are endemic to particular tributaries of the Mississippi River, USA Berendzen et al., 2008), or sub-specific phylogeographic breaks (i.e. evolutionarily significant units, ESUs) may occur within or among rivers or regions (Avise, 1992; Crandall et al., 2000; Moritz, 2002). For example, Caridina lineage B contains ESUs that correspond to Central Queensland, South East Queensland and northern New South Wales, respectively (Page and Hughes, 2007b). Whilst species-level taxonomy (and sub-specific taxonomy) represents part of the biodiversity information challenge (Faith and Baker, 2006) the resolution of cryptic species is fundamental for the effective protection of evolutionary valid taxa in freshwater conservation planning programs.

REFERENCES


