



Phylodiversity to inform conservation policy: An Australian example



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HIGHLIGHTS

- We demonstrate tangible advantages of phylodiversity to conservation
- Study regions have a higher proportion of phylodiversity than species richness.
- Low regional phylogenetic endemism was found despite high numbers of endemics.
- High congruency found between PD and SR and between PE and WE within taxa
- Biotic responses to evolutionary processes are strongly influenced by life history

ARTICLE INFO

Article history:

Received 8 October 2014

Received in revised form 28 April 2015

Accepted 29 April 2015

Available online 12 May 2015

Keywords:

Phylogeny

Species

Conservation planning

Policy

Diversity

Phylogenetic diversity

Phylogenetic endemism

ABSTRACT

Phylodiversity measures summarise the phylogenetic diversity patterns of groups of organisms. By using branches of the tree of life, rather than its tips (e.g., species), phylodiversity measures provide important additional information about biodiversity that can improve conservation policy and outcomes. As a biodiverse nation with a strong legislative and policy framework, Australia provides an opportunity to use phylogenetic information to inform conservation decision-making.

We explored the application of phylodiversity measures across Australia with a focus on two highly biodiverse regions, the south west of Western Australia (SWWA) and the South East Queensland bioregion (SEQ). We analysed seven diverse groups of organisms spanning five separate phyla on the evolutionary tree of life, the plant genera *Acacia* and *Daviesia*, mammals, hylid frogs, myobatrachid frogs, passerine birds, and camaenid land snails. We measured species richness, weighted species endemism (WE) and two phylodiversity measures, phylogenetic diversity (PD) and phylogenetic endemism (PE), as well as their respective complementarity scores (a measure of gains and losses) at 20 km resolution.

Higher PD was identified within SEQ for all fauna groups, whereas more PD was found in SWWA for both plant groups. PD and PD complementarity were strongly correlated with species richness and species complementarity for most groups but less so for plants. PD and PE were found to complement traditional species-based measures for all groups studied: PD and PE follow similar spatial patterns to richness and WE, but highlighted different areas that would not be identified by conventional species-based biodiversity analyses alone.

The application of phylodiversity measures, particularly the novel weighted complementary measures considered here, in conservation can enhance protection of the evolutionary history that contributes to present day biodiversity values of areas. Phylogenetic measures in conservation can include important elements of biodiversity in conservation planning, such as evolutionary potential and feature diversity that will improve decision-making and lead to better biodiversity conservation outcomes.

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1. Introduction

Australia is one of 17 countries identified as biologically ‘megadiverse’ (Mittermeier et al., 1997). This reflects not only its sheer number of species, but the high degree of endemism (uniqueness) of its biodiversity – approximately 92% of higher plant species, 87% of mammal species, 93% of reptiles, 94% of frogs and 45% of bird species are found nowhere else (Chapman, 2009). This extraordinary biodiversity has evolved over many millions of years partly as a consequence of Australia’s geographical isolation from other continents.

Biodiversity refers to the variety of life, spanning genetic, species and ecosystem levels (Convention on Biological Diversity, 2006). However, for conservation evaluation and prioritisation, biodiversity is typically described and quantified using species level measures such as species richness, which is the count of the number of different species in a given area or region. Implicit in the application of such measures is the assumption that the species category as a unit of measurement is an appropriate surrogate for other facets of biodiversity (Soutullo et al., 2005) such as those represented by genes, traits and ecosystems.

Measures based on evolutionary history capture aspects of biodiversity missed by species level measures. Evolutionary history is usually represented by a phylogenetic tree (see Fig. 1), which depicts not only ancestor–descendent relationships among lineages of organisms but also the amount of evolutionary difference among those lineages. Phylogenetic diversity (PD) is a measure of the representation of evolutionary history (Fig. 1), and extends to a family of “phylodiversity” measures based upon the PD framework.

Importantly, calculating species richness alone does not identify areas where few species represent a significant amount of evolutionary history or phylogenetic diversity (Faith, 1992; Mooers and Atkins, 2003; Soutullo et al., 2005; Yek et al., 2009). This is because different sets of species can

differ greatly in the amounts of evolutionary history they represent (Faith, 1992; Mace et al., 2003; Isaac et al., 2007; Faith, 2008) as can geographic areas (Sechrest et al., 2002; Rosauer et al., 2009; Mishler et al., 2014). For example, the extinction of a species that does not have any close living relatives, such as the Wollemi pine (*Wollemia nobilis*), which is the sole living descendent of a 150 million year old lineage, would result in a greater loss of phylogenetic diversity than the extinction of a young species with many close relatives (May, 1990; Mace et al., 2003; Faith, 2008). A further advantage of phylodiversity is that, by shifting the measure of diversity from species to features or characters (i.e., units of phylogenetic variation), assessments of biodiversity/conservation value become relatively robust to taxonomic uncertainty and changes (Mace et al., 2003).

Explicitly considering evolutionary processes to address adequacy of conservation actions is frequently suggested but rarely undertaken in conservation planning (Klein et al., 2009; Winter et al., 2012). The paucity of work in this area is probably due to the challenges associated with understanding evolutionary processes and identifying spatial data to represent them (Possingham et al., 2005). The necessary phylogenetic trees and data have, until recently, been available for too few taxa to enable effective conservation planning. These factors (particularly data adequacy and coverage) are magnified when considering a large jurisdiction such as Australia. However, over the past 20 years there has been an exponential growth in the availability of phylogenetic trees for major taxon groups (Lyubetsky et al., 2014), and therefore methods that use them are increasingly relevant for conservation planning. In addition, the availability of comprehensive species data has improved in recent times. In the context of the current global extinction crisis, it is critical that conservation planning maximizes the capacity of biota to respond adaptively to environmental change, and it has been argued [e.g., Faith (1992), Moritz (2002)] that conserving phylogenetic diversity is the best way to achieve this.

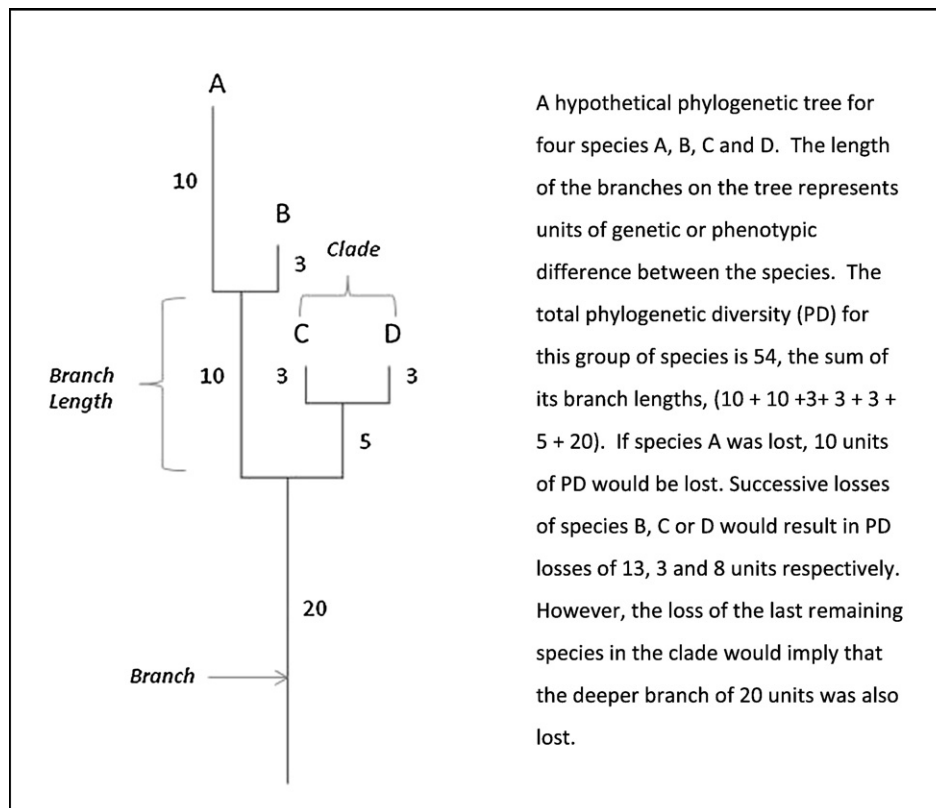


Fig. 1. A hypothetical example of phylogenetic diversity. Adapted from Faith and Richards, 2012.

Table 1

Conservation planning instruments and their recognition of phylogenetic or genetic diversity.

Instrument (policy, agreement, resolution, strategy)	Recognises phylogenetic diversity explicitly	Recognises phylogenetic diversity implicitly	Does not recognise phylogenetic diversity
International			
GEOBON	yes		
Convention on Biological Diversity (AICHI Target 11)		yes	
Global Biodiversity Strategy		yes	
World Heritage Convention		yes	
Millennium Ecosystem Assessment		yes	
Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES)	yes	yes	
IUCN Key Biodiversity Areas	yes		
Planetary Boundaries	Yes		
Edge of Existence (ZSL)	Yes		
National			
Australian Biodiversity Conservation Strategy 2010–2030		yes	
National Heritage List Guidelines	yes		
Climate Change Adaptation Framework and Research Plans		yes	
Australian National Strategy for the Reserve System			yes
National Framework for Management and Monitoring of Australia's Native Vegetation		yes	
Foundations for the Future; A long term plan for Australian ecosystem science	Yes		

Here we demonstrate the advantages of conservation measures that incorporate phylogenetic relationships. We investigate the family of phylodiversity measures based upon the PD framework (Faith, 1992; Faith et al., 2004), for a set of organismal groups representing flowering plants, vertebrates and invertebrates, for two regions of continental Australia. We show that analysing phylodiversity provides additional information to policy makers about the spatial distribution of biodiversity. This can enhance the assessment of conservation value, leading to a more complete and sophisticated understanding of the biodiversity of an area or region, how it evolved and why it is important to conserve.

1.1. Policy frameworks for conservation

Policy frameworks for biodiversity conservation exist as a hierarchy of international and national conventions and strategies, as well as their state or regional counterparts (Table 1). Prominent international agreements include the Convention on Biological Diversity, the World Heritage Convention and the Global Biodiversity Strategy (GBS). Many of these recognise three tiers of biological diversity – genetic, species and ecosystem – and aim to strengthen the capacity to conserve them. However, few of these agreements and strategies recognise phylogenetic diversity. The World Conservation Conference (WCC) in 2012 resolved to halt the loss of evolutionarily distinct lineages, and noted the related efforts of others, including IUCN's Save Our Species Fund, the Mohamed bin Zayed Species Conservation Fund, the Zoological Society of London's Evolutionary Distinct and Globally Endangered (EDGE) of Existence programme, the Amphibian Survival Alliance, the World Wide Fund for Nature (WWF) Global 200, US Fish and Wildlife Service's Endangered Species Grants.

With increased appreciation of phylogenetic diversity as an important aspect of biodiversity [e.g., Mace et al. (2003), Morlon et al. (2011)], there are increased efforts to better understand its links to important policy contexts. For example, the global biodiversity observation network, GEO BON (2011), has called for explicit consideration of phylogenetic diversity in the Convention on Biological Diversity's 2020 biodiversity targets, and the IUCN (2012) has suggested criteria for these targets based on phylogenetic diversity.

Due to strong legislative and policy frameworks, and also a rich information base, Australia provides an opportunity to highlight the potential for phylogenetic information to inform conservation decision-making. Broad areas of conservation policy in Australia relate to (i) protected area planning, (ii) threatened species management, (iii) mitigation of resource extraction (e.g., timber and mineral harvesting)

and (iv) amelioration of impacts of rapid climate change. For Australia, the key biodiversity conservation legislation is the *Environment Protection and Biodiversity Conservation Act 1995* (EPBC Act) and related inter-governmental strategies. One method the Australian Government uses to determine the conservation significance of a place is the natural heritage assessment requirements for listing areas as National Heritage Places under the EPBC Act. As part of these assessments, the most relevant criterion states that “the place has outstanding heritage value to the nation because of the place's importance in the course, or pattern, of Australia's natural or cultural history” (<http://www.environment.gov.au/topics/heritage/about-australias-heritage/national-heritage/national-heritage-list-criteria>). The Australian Heritage Council's assessment guidelines (AHC, 2009) suggest that the grounds on which a place might satisfy this criterion include evolutionary processes and centres of richness and diversity. The guidelines state that these include not only species richness and endemism (taxa with geographically restricted distributions, or ranges) but a variety of other measures, including phylogenetically distinct species, and that these places will demonstrate either the “richest concentration of species reflecting a particular evolutionary process in Australia, or the species present demonstrate an outstanding or unique aspect of evolutionary process”.

Within Australia, a range of current national strategies recognise the need to protect genetic (rather than phylo) diversity and to sustain evolutionary processes. They refer to these goals in the context of protecting climatic refugia and centres of endemism (areas with a concentration of endemic taxa), and in restoring habitat linkages to maintain natural evolutionary and ecological processes (Table 1). Some of the key international, national and state conservation planning instruments are listed in Table 1. For example the *Natural Resource Management Ministerial Council* (2010) recognised that biodiversity is not static but is increasing by evolutionary processes including genetic change. It describes three levels of biodiversity in terms of their attributes i.e., components, patterns and processes (including evolutionary processes).

In relation to protected area planning at the Australian national level, there are three main approaches driven by distinct legislation and policies. Both National and World Heritage sites are nominated by the public and, for sites of natural heritage significance, criteria refer to evolutionary processes and heritage. In contrast, the National Reserve System, primarily a government planning exercise, focuses more on encompassing the pattern of diversity (comprehensiveness and representativeness) and maximizing the resilience of protected areas (adequacy).

Areas of significant conservation value for the purpose of this study can be defined as areas containing globally, regionally or nationally

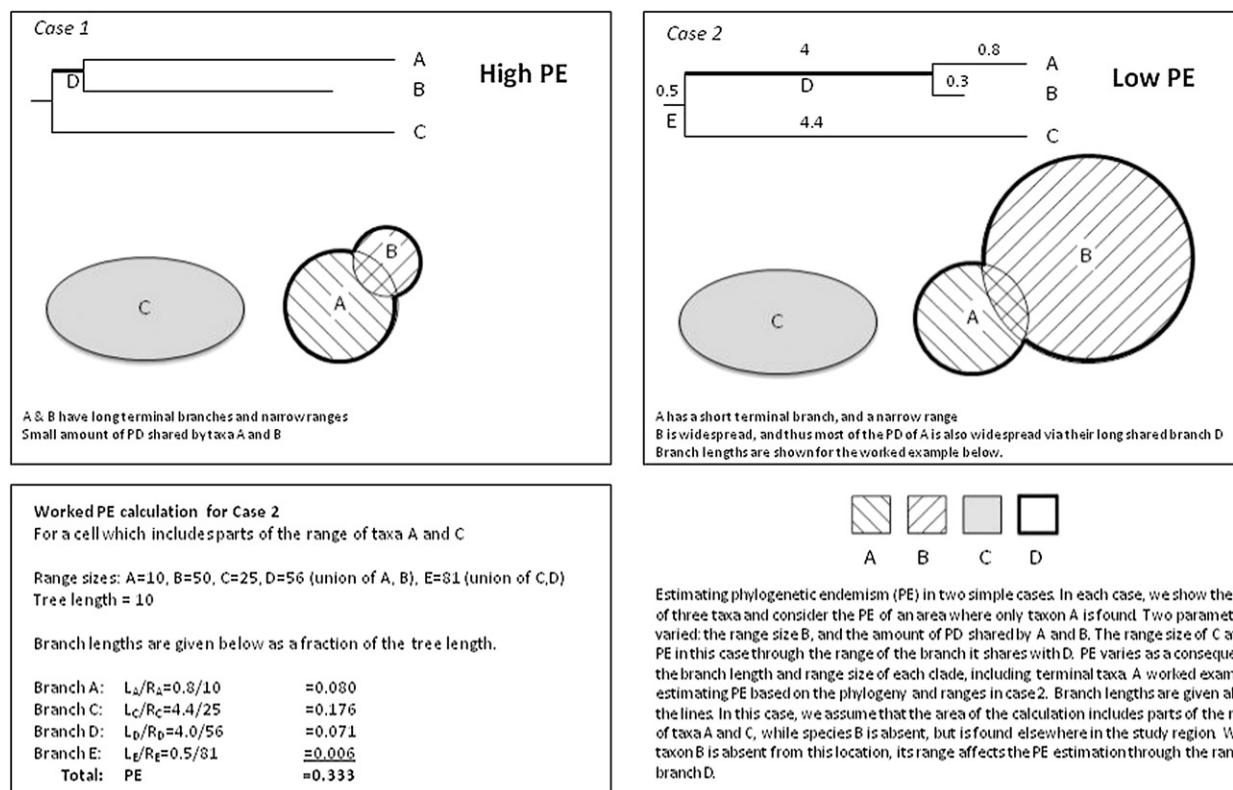


Fig. 2. Estimating weighted phylogenetic endemism.
Adapted from Rosauer et al., 2009.

significant concentrations of biodiversity values (e.g., high diversity, endemism, endangered species, and refugia). Therefore, we are identifying significant extant areas of biodiversity rather than setting priorities against some measure of threat.

1.2. Phylodiversity in conservation planning

The pioneering phylodiversity metric is phylogenetic diversity (PD; Faith, 1992). PD is regarded as the “phylodiversity metric of choice in conservation research” (Morlon et al., 2011). It is measured as the sum of the length of all branches on a phylogenetic tree for a species or set of species (an illustration of a hypothetical phylogenetic tree is given in Fig. 1 with formulae in Appendix 1). By summing the lengths of the branches linking a set of taxa to the root of the tree, PD accounts for shared evolutionary history to reflect the combined contribution of these taxa to the overall diversity of the set. PD is described as a measure of the degree of representation of evolutionary history (e.g., Faith and Williams, 2006; Faith, 2008). PD also can be described as a measure of feature diversity, where features can be genetic and morphometric (i.e., traits or forms that have evolved). PD provides a measure of the diversity of lineages that is not provided by species-based methods within a region. When used in conjunction, species and phylogenetic diversity can provide a more comprehensive picture of the conservation significance of an area (Faith, 1992; Moritz, 2002). PD is also applicable over a realistic range of information availability [i.e., varying types of tree from simple taxonomies to phylogenies with meaningful branch lengths (Faith, 1994)].

PD has several useful properties for conservation planning. In conservation assessment, giving priority to a species subset that maximizes represented feature diversity is justified as maximizing a form of ‘option value’ (Faith, 1994). Option value implies that feature variation is to be maintained as a way to ensure the possibility of future benefits from

unanticipated features. By using PD in conservation planning, the process may maximize represented feature diversity over those shared features of species that are explained by shared ancestry (Faith, 1992).

The richness and PD measures described above consider how much diversity is found in an area or region. However, one is often interested in the degree of endemism, or how restricted biodiversity is to a certain area. In the absolute case one would be interested in the number of species or the total length of unique branches of a phylogenetic tree, which are found only in a specific geographic area. For PD, this is the area's unique PD contribution or PD endemism (Faith et al., 2004). However, individual grid cells in a regional analysis are unlikely to have such strict endemism. Instead, we can score cells by giving partial credit for their representation of range-restricted elements (species or lineages). Weighted endemism (WE) (Crisp et al., 2001; Laffan and Crisp, 2003; Laffan et al., 2013) is a range weighted richness score, and is calculated as the sum of the proportions of each species' range found within the area considered (Appendix 1). Phylogenetic endemism (PE) (Rosauer et al., 2009) is range weighted PD and thus is equivalent to WE but takes into account the phylogeny. It is calculated as the sum of branch lengths weighted by the proportion of the range of each branch that is found in the area considered (an example is given in Fig. 2).

PE estimates the degree to which units of PD are restricted to particular areas (Fig. 2, Appendix 1). The PE measure for a region, unlike PD or WE, uses in its calculation the distribution of all species in the study system, not just those in the given region. A set of species may be restricted to a small area (high species endemism) but that does not necessarily mean that its PD is also highly restricted (i.e., it has a high PE) because closely related species may be more widespread, and thus their shared ancestral components (branches) will also be widespread. In such a case, only the short branches which differentiate an endemic species from its widespread close relative would be endemic (Rosauer et al., 2009).

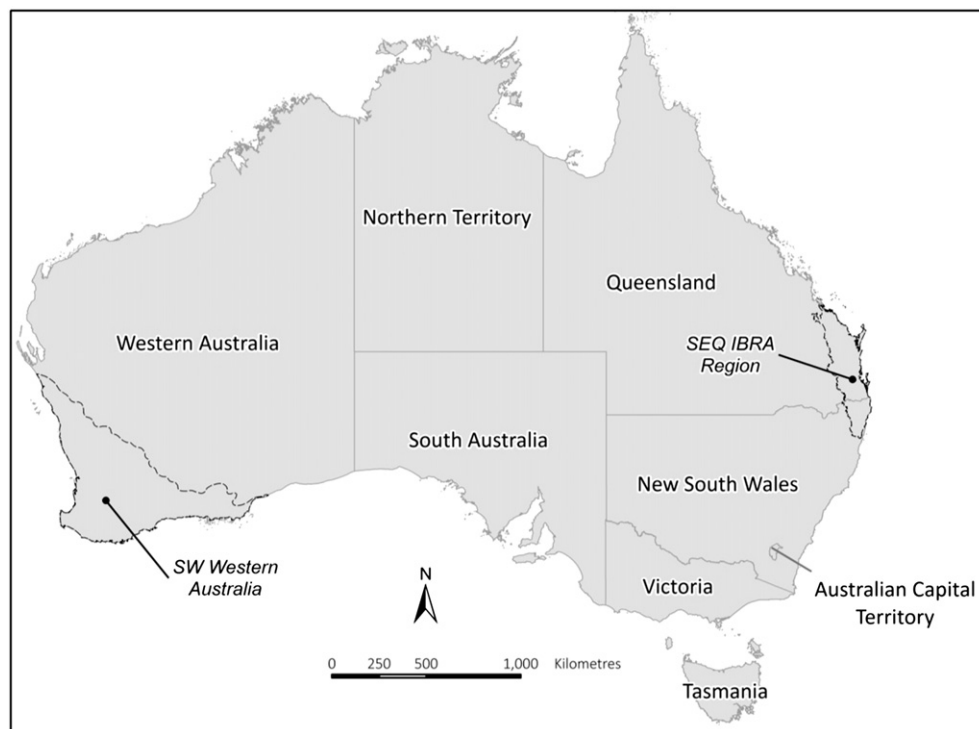


Fig. 3. Study regions in Australia. The South-east Queensland (SEQ) region is part of an eco-geographical transitional zone between sub-tropical and temperate environments representing a mix of diversity. South-west Western Australia (SWWA) represents a geographically isolated corner of the continent which has unique diversity features. They represent a Mediterranean woodland and scrub ecoregion (SWWA) that is an internationally recognised biodiversity hotspot (Myers et al., 2000) and a temperate broadleaf and mixed forest environment (SEQ).

Conservation planning for an area cannot be based solely on its total biodiversity scores for measures such as species richness, PD, WE or PE. The complementarity (Vane-Wright et al., 1991) score for an area indicates the additional biodiversity an area provides relative to some given existing set of areas. For example, a species-based complementarity analysis may be used to identify areas within a region that have a particular suite of species that do not occur anywhere else in the region. PD complementarity (Faith, 1992; Faith et al., 2004) is the sum of the additional branch length gained if an area is added to a set of areas. PE complementarity indicates how much the PE of a set or region increases if we add a given cell or area. In conservation planning, these weighted complementarity measures could identify areas not only having branches (or other elements) not found in the existing reserve system, but also having few substitute areas providing these un-represented elements. Thus, these measures greatly boost the applicability of PD and PE to conservation policy and planning.

2. Material and methods

2.1. Study regions and biological data

Two regions, South-west Western Australia (SWWA) and South East Queensland (SEQ) (Fig. 3), were chosen as focal areas for this study based on their importance in current conservation priority setting activities and their unique biodiversity.

SWWA is a recognised global biodiversity hotspot and contains five of the fifteen recognised national level biodiversity hotspots. It is a Mediterranean woodland and scrub ecoregion which covers approximately 300,000 km² that represents a geographically isolated corner of the continent with a unique diversity of taxa. Approximately 63–65% of the native vegetation in SWWA has been cleared since European settlement (Department of Environment, 2014; Lindenmayer and CSIRO, 2007). Over 5700 vascular plant, 700 vertebrate and 1800 invertebrate species

have been recorded in the region. Of these, approximately 4800 are endemic and 317 are listed as threatened under the EPBC Act (ANHAT data 2014).

The SEQ region covers approximately 78,000 km², is a temperate broadleaf and mixed forest environment and is part of an eco-geographical transitional zone between sub-tropical and temperate environments representing a mix of diversity. It is a region of the Interim Biogeographic Region of Australia classification (IBRA) (Department of Environment, 2015a) and is also a national level biodiversity hotspot. Approximately 45–55% of the native vegetation in SEQ has been cleared since European settlement (Department of Environment, 2014; Accad et al., 2013). Over 3000 vascular plant, 1000 vertebrate and 2000 invertebrate species have been recorded in the region. Of these approximately 790 are endemic and 201 are listed as threatened under the EPBC Act (ANHAT data 2014).

Both regions are considered distinctive phytogeographical regions for Australian plants (González-Orozco et al., 2014). Major threats to biodiversity in these regions (and indeed large areas of the continent) include land clearing for agriculture and urban development, habitat fragmentation, increased fire frequency, overgrazing, introduced plants and animals, salinisation, root rot fungus (*Phytophthora cinnamomi*) and change in ground water levels due to extraction and decreased rainfall (Department of Environment, 2015a,b).

We selected seven biotic groups on the basis of their broad representativeness of biological diversity and the availability of well-resolved phylogenetic trees. These were the mammals, hylid frogs, myobatrachid frogs, passerine birds, camaenid land snails, and the plant genera *Acacia* and *Daviesia*. Sources for each of these datasets and the phylogenetic trees used in these analyses are given in Table 2. We restricted the set of taxa considered in each group to be the intersection of the species in each region and the species found on the respective tree.

All species occurrence data used in this study were derived from the Australian Natural Heritage Assessment Tool (ANHAT) database.

Table 2
Datasets used in analyses.

Dataset	Data sources	Phylogenetic tree used	Records in ANHAT
Plants			
<i>Acacia</i>	Australian Herbaria State Conservation Agencies Western Australian Museum OBIS	Mishler et al. (2014)	524,701
<i>Daviesia</i>	Australian Herbaria State Conservation Agencies West Australian Museum	Rosauer et al. (2009)	45,760
Invertebrates			
Camaenid land snails	Australian Museums State Conservation Agencies CSIRO OBIS	(Hugall and Stanisc, 2011) Camaenid Land Snails of eastern Australia (not applicable to the South West Western Australia region)	27,764
Vertebrates			
Myobatrachid frogs	Australian Museums State Conservation Agencies Harry Hines CSIRO	Keogh et al., pers. comm.	141,483
Hylid frogs	Australian Museums State Conservation Agencies Harry Hines CSIRO	Rosauer et al. (2009)	112,267
Mammals	Australian Museums State and Commonwealth Agencies CSIRO OBIS AIMS	Bininda-Emonds et al. (2007)	689,653
Passerine birds	Australian Museums State Conservation Agencies Birdlife Australia CSIRO	Vane-Wright et al. (1991) and Hugall and Stuart-Fox (2012)	8,156,424

ANHAT is a map-supported database developed by the Commonwealth Environment Department (DOE). Data used in ANHAT have been collated from Australian Museums and Herbaria, CSIRO, Birdlife Australia, State and Territory Government Agencies and private collections.

ANHAT is used to help identify and prioritise areas of Australia for “outstanding national significance” – principally biodiversity – based on rigorous comparisons of specific natural values at a national scale. Determining national significance requires comparative information for the whole continent. As one of the sources of information used for natural heritage assessment, ANHAT enables quick analysis and comparison of recorded biodiversity values across Australia and provides scientifically robust and repeatable results. ANHAT is able to undertake marine and terrestrial analyses of all Australian vertebrate species (approximately 6700 species), the majority of Australian vascular plant species (>18,000 species) and a wide range of Australian invertebrate species (>26,000 species). In total there are close to 70 million records of Australian species that are available in ANHAT and it is used both internally within DOE and to satisfy external analysis requests from researchers and conservation bodies. As a database tool it has many applications and can be used for a variety of conservation assessment and planning analyses and tasks.

2.2. Biodiversity measurements

We used the Biodiverse software, version 0.19 (Laffan et al., 2010) for all spatial analyses. We aggregated observation data for the whole continent to 20 km × 20 km grid cells prior to analysis. We chose this resolution to reduce the effect of survey gaps while retaining sufficient level of detail for both national and regional extent analyses. We conducted analyses at the regional level, using assemblages of species across collections of cells, and then on a per-cell basis, using the assemblage of species in each cell individually.

We used the regional level analyses to obtain estimates of the total diversity represented by each region when considered as a whole. We calculated species richness (SR), phylogenetic diversity (PD), weighted endemism (WE), phylogenetic endemism (PE), absolute species endemism and PD-endemism for the sets of taxa across the cells comprising each of the SWWA and SEQ regions (see Appendix 1 for all formulae). We used the number of cells in which a species occurred as the distribution of the species for the endemism analyses. The SR, PD, WE and PE measures allowed an assessment of the overall diversity found in each region, while the absolute species endemism and PD-Endemism measures allowed an assessment of the amount of diversity that was uniquely found in each region.

Regional scale, aggregate measures of diversity are very useful for synoptic level analyses, but do not indicate where in each region the diversity is concentrated and thus how much each cell could contribute to opportunities for conservation unique to that region. To assess the spatial patterns of diversity across the continent we calculated SR, PD, WE and PE for the sets of taxa in each grid cell separately (referred to hereafter as per-cell analyses). We then calculated the complementarity of each cell in the study regions as the SR, PD, WE and PE in that cell not found outside the respective region (i.e., in the rest of Australia). This process allows an understanding of which cells are contributing most to the aggregate measures for each region. We identified cells which had >20% of their area within the reserve system (Department of the Environment, 2010) to identify areas currently conserved.

Species richness and PD are known to be correlated (Barker, 2002; Tucker and Cadotte, 2013), and there is evidence for a power curve relationship (Morlon et al., 2011). Given this, WE and PE are also expected to be correlated given their formulation as range weighted fractions of SR and PD. To assess this degree of congruence we fitted linear regression models (first and second order polynomial) on the per-cell surfaces of the SR versus PD, and WE versus PE indices. We also calibrated linear regression models for each region between all taxon groups for PD, and

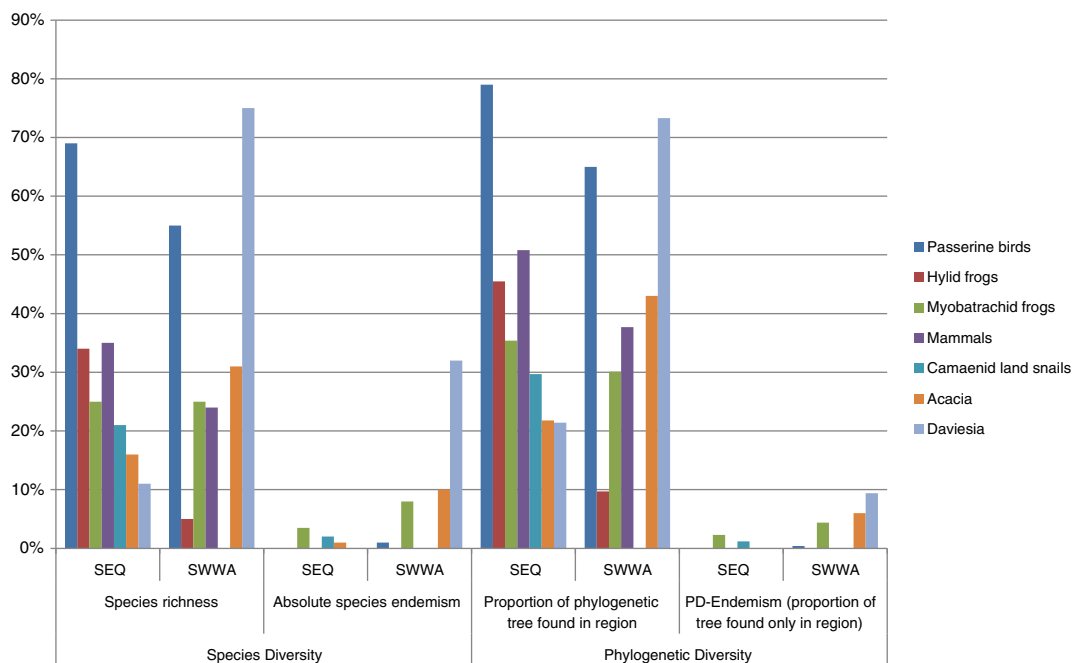


Fig. 4. Species and phylogenetic biodiversity metrics for the SEQ and SWWA regions as percentages of the total possible diversity for each group (all species or the sum of all branch lengths in the relevant phylogeny across Australia). Values in brackets are absolute species richness scores. The camaenid tree did not include species from SWWA.

PE and their complementarity surfaces to determine if there were any correlations in PD or PE across the biotic groups assessed.

An estimate of sampling redundancy was derived using a sample redundancy index (Garcillán et al., 2003) (Eq. (5), Appendix 1) to determine whether sampling bias was likely to affect the results. In this index, a value of zero means each species in a cell is sampled only once, with values increasing towards one as the ratio of samples to species increases.

3. Results

3.1. Regional level diversity metrics

Larger proportions of the species analysed within passerine birds, hylid frogs and mammals occurred within the SEQ region compared to SWWA. Conversely, larger proportions of the two floral groups analysed occurred in the SWWA region compared to SEQ (Fig. 4 and Table 1 in the Supplementary material).

Despite the relatively large percentages of faunal species that occur within the regions, very few were endemic to either region. In contrast, the number of endemics in SWWA for the plant groups analysed was very high (Fig. 4 and Table 1 in the Supplementary material).

Although taxonomic diversity is represented by absolute values, which means it is not standardised across all groups, we saw clear differences between regions in the maximum number of taxa and degree of endemism (left panel of Fig. 4). For example, species richness and endemism of animals were higher in SEQ than in SWWA but reversed for plants. The amount of proportional PD which represents the regional pool and is standardised against the rest of the continent, was greater in SEQ than SWWA for animals but not for plants (right panel of Fig. 4). Overall, the amount of PE unique to a region was greater in SWWA than SEQ.

Larger amounts of PD were found within the SEQ region for all faunal groups, whereas larger proportions of the PD for both plant groups were found in SWWA. Despite high proportions of passerine bird PD found in both SEQ and SWWA, very little (<1%) was endemic to SEQ or SWWA. In contrast, there were substantial proportions of PD in plant species

within SWWA (43% for *Acacia* and 73% for *Daviesia*) with 6% of *Acacia* PD and 9% of *Daviesia* PD being endemic to the region (Fig. 4).

3.2. Spatial patterns of diversity

Our results showed differences in the distribution patterns of species richness and PD across each region relative to the rest of Australia. For example, in the SWWA region the richness complementarity scores indicated that within any one cell there was a maximum of nine species of *Acacia* that only occurred in SWWA (see Map 6 in the Supplementary material). This cell, and other similar cells nearby, contributed to the high PD scores for cells in the mid-west of SWWA. Similarly for WE, the endemism complementarity analyses showed that there was at least one species that had its entire range restricted to one cell, thereby contributing to the high PE scores in the mid-west of the region (see Map 6 in the Supplementary material).

The per-cell WE results were not indicators of how many species are endemic to the region, rather they indicated how many species were endemic to one cell within the region. Similarly, the per-cell PD results were not an indicator of the total PD of the region for each taxon group; rather they showed areas of concentrated PD within the region. In this respect these measures can be used to assist in the identification of areas of conservation significance both within the region and compared to the rest of Australia.

In SWWA the richness complementarity scores showed that within any one cell there was a maximum of seven species of *Daviesia* that only occurred in the region and these contributed to the PD across the centre of the region (see Map 4 in the Supplementary material). Similarly for WE the complementarity scores for the region showed at least one species that had its entire range restricted to one cell in the region thus contributing to PE in the north-west of the region (see Map 4 in the Supplementary material). In SEQ there were only minor differences between WE and PE within the region. PD showed some significant differences, however, with more high diversity areas occurring in the south, west and north of the region in comparison with species richness (see Map 11 in the Supplementary material).

Although there was a large diversity of passerine birds in both regions, they were mainly restricted to the mid-west of SWWA and central east coast of SEQ (see Maps 5 and 12 in the Supplementary material). The PD for passerine birds was more widespread and more evenly distributed across both regions with the main concentration across the centre of the regions from south-east to north-west in SWWA and east to west in SEQ. Passerine birds tended to be more widespread and not endemic to the study regions. None of the species that occurred in SEQ and only one in SWWA was restricted to the region. PE for passerine birds in SWWA showed markedly different results compared to WE. In SEQ however, PE showed only slightly different results compared to WE.

The highest species richness for hylid frogs in any cell in the SEQ region was 16, and no species were endemic to the region. WE and PE of hylid frogs in this region followed similar patterns in their distribution with only minor differences (see Map 9 in the Supplementary material). However, species richness and PD varied slightly and there was higher PE than WE in the southern and northern parts of the region. This was similar for the myobatrachid frogs in SEQ with higher PD in the southern part of the region compared to species richness. The distribution of myobatrachid Frog PE and WE was similar within SEQ with only minor differences in the south east and north-west of the region. Species richness of this group followed a very similar pattern to PD in the region (see Map 7 in the Supplementary material).

Mammal species showed only slight variations in patterns of PE and WE and richness and PD within both regions (see Maps 1 and 8 in the Supplementary material). A maximum of 54 and 25 mammals occurred in any one cell in the SEQ and SWWA regions respectively. Camaenid land snails in the SEQ region also showed only slight variations in the pattern of PE and WE and richness and PD. There was a maximum of 15 species in any one cell and the complementarity scores showed only 1 species in any cell that did not occur outside the region (see Map 10 in the Supplementary material).

3.3. Congruence between and within biotic groups

There was no strong congruence (linear regression – see the Supplementary material for all regression results) between groups for either PD or PE in either of the two study regions. The strongest congruence for SEQ was for hylid frog vs myobatrachid frog PD (R^2 value of 0.66), with passerine bird vs mammal PD, mammal vs myobatrachid frog PD and hylid frog vs mammal PD having moderate congruence (R^2 values of 0.52, 0.53 and 0.52 respectively). The strongest congruence for SWWA was for mammal vs myobatrachid frog PD (R^2 value of 0.21). No significant congruence was found when comparing PE among taxa for either region.

There was, however, strong congruency (polynomial 2nd order) within groups when comparing PD with richness, and PE with WE, for both regions. Strong correlations were found for passerine birds, hylid frogs and myobatrachid frogs when comparing PD and species richness (R^2 values of >0.9 for both regions). Mammal PD and species richness were strongly correlated in SEQ (R^2 value of >0.9) and in SWWA (R^2 value of 0.87). The plant groups were also strongly correlated, with R^2 values of between 0.7 and 0.9 for SWWA and zero for SEQ.

Strong correlations (polynomial 2nd order) between PE and WE were found for passerine birds and mammals for both regions and hylid frogs for SWWA (R^2 values of >0.9). The plant groups were less strongly correlated with R^2 values of ≤0.8 for both regions.

Strong correlations (1st order) were found between PD-complementarity and SR complementarity for *Acacia*, *Daviesia* and myobatrachid frogs within SWWA. However, more than 20% of the species richness for plants and 10% of that for the myobatrachid frogs could not be explained by PD alone. Similarly in SEQ, 20% of the species richness for myobatrachid frogs could not be explained by PD (however, the SR complementarity is 2). The camaenid land

snails in SEQ were quite different in that 39% of their SR could not be explained by PD (only 1 species unique per cell).

SEQ had a higher congruence between PE complementarity and WE complementarity than SWWA, however the two plant groups had approximately 25% of their species richness not explained by PD in SEQ. All groups in SWWA had more than 10% of their PE complementarity unexplained by WE. Three of these groups (i.e., the plant groups and hylid frogs) had close to one quarter of their PE complementarity not explained by WE.

With the exception of mammals in SWWA, there was a good degree of sampling redundancy across both regions and for all taxa we analysed (i.e., redundancy scores of >0.3. See Maps 14 and 15 in the Supplementary material). Sample bias did not appear to affect the results for most taxa.

4. Discussion

We demonstrated consistent results from seven taxonomic groups spanning five separate taxonomic groups on the evolutionary tree of life at continental and regional scales. Although there was a demonstrated strong correlation between species based indices and phylogeny measures, in both our study regions and within all five Phyla, there were specific localities and taxa that had either marked or minor differences in the “hotspots” (areas highlighted as having high scores for species and phylogeny). Previous studies have illustrated that strong historical trends with important conservation implications can be identified from these small discrepancies between PD values, particularly when investigating areas with higher or lower PD than expected based on species richness (Forest et al., 2007; Costion et al., 2015). Our results were also consistent with previous studies that have shown that complementarity of phylogenetic diversity and species diversity is decoupled (Forest et al., 2007). Therefore conservation decisions based on species-only data may not capture feature diversity that can provide resilience to biodiversity loss (Faith, 1992) and areas (sometimes quite small) of important phylogeny will remain undiscovered and potentially unprotected. This was true particularly for passerine birds in both of the study regions and the two plant genera analysed for SWWA.

At the regional level, both SEQ and SWWA regions had a higher proportion of the phylogenetic tree represented per-cell than the proportion of species represented there (i.e., species richness). This suggests that the branches of the phylogenetic tree that connect these species are longer than expected and therefore potentially have more feature diversity. PE was low for both regions when compared to the rest of Australia, although a greater proportion of the species were endemic to each region, particularly for plants in SWWA.

The higher proportional PD, species richness and endemism of fauna in SEQ may be explained by the selection pressures that have been operating in this region over millions of years, together with the overlapping of species ranges from the north and south east of the continent (McFarland and Queensland CRA/RFA Steering Committee, 1998). This has led to well documented high richness in vertebrate groups in this area, including frogs (Roberts, 1993), birds and marsupials (Pianka and Schall, 1981) and small ground dwelling mammals (Catling and Burt, 1997).

SWWA's high species richness and even higher phylogenetic diversity for plants compared to the rest of Australia is well recognised (Hopper and Gioia, 2004), for example in species richness and endemism of *Acacia* (González-Orozco et al., 2011), and is one basis for its recognition as a biodiversity hotspot (Myers et al., 2000; Mittermeier et al., 2005). The high PD for plants may be due to an old and subdued landscape with high edaphic complexity and low nutrient soils which has provided an environment for both speciation and persistence of evolutionary lineages, with isolation since the mid Miocene and lack of extinction driving species and phylogenetic diversity in comparison to eastern Australia (Crisp and Cook, 2007; Byrne et al., 2011; Sniderman et al., 2013; Bui et al., 2014a,b; Byrne et al., 2014). While its faunal biota has not been considered as diverse as the flora, recent

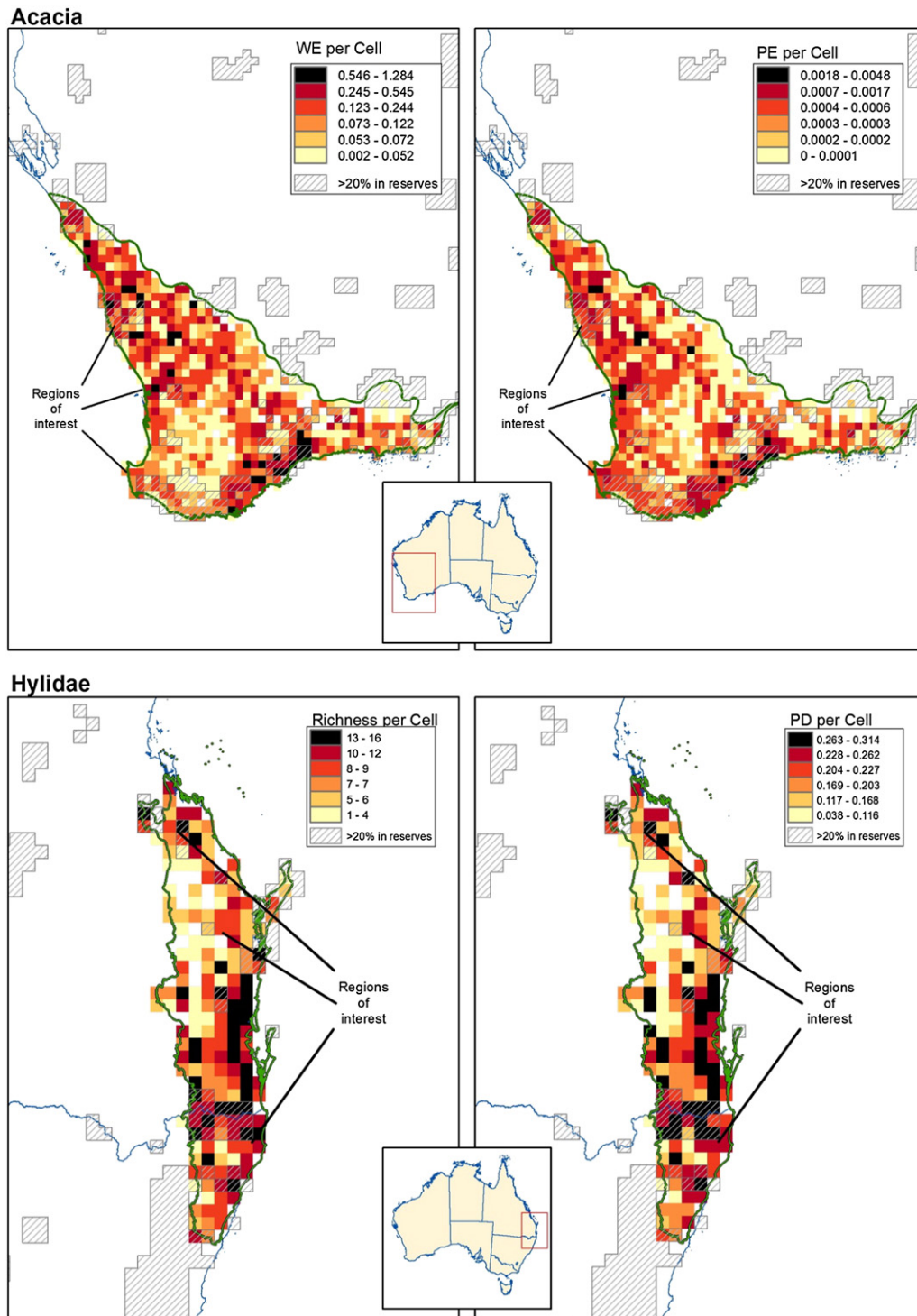


Fig. 5. Weighted endemism and phylogenetic endemism of *Acacia* in South West WA and Species Richness and Phylogenetic Diversity of hylid Frogs in South East Queensland (with areas of difference (interest) highlighted for each region).

analysis has identified high diversity, particularly in invertebrate and herpetofauna groups (Rix et al., 2014).

4.1. Diversity metrics per region

There was high congruence between PD and species richness and between PE and WE for many of the groups (particularly the faunal groups) but not when comparing PD between groups (e.g., passerine

bird versus mammal PD). Cases of high congruence between phylogenetic and species-based measures are well known in the literature (Barker, 2002; Tucker and Cadotte, 2013). Such congruence is expected within groups with (1) relatively 'balanced' phylogenies (i.e., groups in which evolutionary diversification – speciation and extinction – has been relatively constant throughout their history and among their component sub-lineages); (2) phylogenies which do not strongly reflect geography; (3) a tendency for old species to have smaller ranges;

and/or (4) a tendency for old species to occur in species-poor areas (Rodrigues et al., 2005).

Further, Barker (2002) found that, depending on the placement of species on the phylogenetic tree, PD can vary greatly between areas that have the same level of richness. Our results are consistent with this: all the comparisons between PD and richness for each group follow a polynomial 2nd order regression with the PD tapering off as richness reached a certain level because more of the phylogenetic tree was being included. Faith and Williams (2006) proposed that this relationship is not linear but follows a power curve, and the findings of Morlon et al. (2011) and the present study provides supporting evidence for that relationship.

However, of particular interest to conservation management are the areas where there is incongruence between phylogenetic diversity and species-based measures. Although there were quite similar patterns in the distribution of PD and species richness across both regions for all groups, there were many cases of clear discrepancies between the two, specifically areas which for certain groups exhibit high PD and low richness, high richness and low PD, high PE and low WE, and high WE and low PE (see Fig. 5).

Incongruence due to lower or higher than expected PD also has evolutionary and ecological explanations that have implications for conservation management. Lower than expected PD may be due to a high proportion of the species having originated recently or phylogenetic 'filtering' of lineages (in favour of related ones) during community assembly as a consequence of ecological and biogeographical constraints (Webb et al., 2002; Mishler et al., 2014). Conversely, Costion et al. (2015) found that areas with lower PD than expected in northeast Queensland were reliable indicators of ancient rain forest refugia whereas areas with higher PD than expected were correlated with extant rain forest that was both rich in immigrant lineages and unstable during glacial periods. Such complexities of a bioregion's natural history are masked by traditional species richness approaches as two areas may be equally diverse in both species and PD but could have evolved due to completely different historical processes as in the case of northeast Queensland (Costion et al., 2015).

For *Acacia* in SWWA areas of high PD occurred in areas of low species richness on the south west coast of the region. Calculating PD for *Acacia* in SWWA will add to the assessment of conservation value as the *Acacia* phylogenetic tree is unbalanced and the preservation of the areas of high PD and low species richness will ensure preservation of a larger suite of traits and therefore evolutionary history for this group (Rodrigues and Gaston, 2002; Pollock et al., 2015). Similarly, Mishler et al. (2014) found overlap in areas of high PE and endemism for *Acacia* but also identified additional areas with high PE and low WE. This led them to conclude that using phylogenetic diversity measures helps to identify areas of refugia and evolutionary history that would not necessarily be found using species-based measures alone. In a recent assessment of eucalypts, Pollock et al. (2015) found that a large proportion of *Eucalyptus* PD was not captured in existing reserves in Victoria, and that small changes in reserve design scenarios would improve protection of both *Eucalyptus* PD and species richness.

4.2. Implications for policy and conservation assessments

This analysis illustrates that the use of phylogenetic diversity provides valuable information for conservation planning, including strategies for adaptation to environmental change. Areas in which rapid evolutionary radiations have taken place may contain lineages that would be better able to adapt to a changing environment as they potentially contain species with a greater genetic variation. These species may be able to cope better with environmental changes as they have the potential to inhabit a wide range of environments and have relatively broad geographic ranges (Laverne et al., 2013). While this does not guarantee that this biodiversity will best adapt to changing conditions it does give conservation planners a quantitative assessment based on

the historical record of a given area. Pennington et al. (2004) state that understanding the history of an area can help to predict the response to future environmental changes and thus inform climate adaptation strategies. In addition, protecting maximum phylogenetic diversity provides both species and communities with the most resilience (options) to respond to changing environments (Collen et al., 2011).

In the context of Australian National Heritage Assessments, inclusion of phylogenetic diversity measures will enable the discovery of areas of significance with respect to evolutionary history and allow for their capture in the conservation estate. Phylogenetic diversity measures are being incorporated into ANHAT, which is used to assess the evolutionary heritage value of areas, particularly in natural resource management. Our analysis shows that inclusion of PD and PE in conservation assessment and planning tools such as ANHAT highlights areas that make a higher evolutionary contribution than species richness alone. While conservation actions themselves remain similar, assessment and prioritisation based on inclusion of phylogenetic diversity means this valuable component of diversity is captured.

In choosing phylogenetic diversity measures for application in conservation planning activities one needs to consider what is to be protected and the measures used to identify the most important places to protect it. For example, losing a widespread lineage will diminish the tree of life (PD) by exactly the same amount as losing an endemic lineage of the same total branch length. However, narrowly distributed lineages are, in general, more likely to be threatened and the choices of where to ensure their in-situ persistence are far more limited. Thus PE is a good indicator of places of importance for conserving PD.

The incongruence in patterns among groups suggests that different biotic lineages within an area may respond differently to the evolutionary and biogeographic processes operating on them in common. This result implies that a one-size-fits-all conservation and management strategy may lead to sub-optimal outcomes for at least some of the lineages.

4.3. Opportunities for further work

This study sets up the machinery and protocol not only for the calculation of current phylogenetic diversity and endemism patterns, but also for ongoing re-assessments. New patterns may be a consequence of range change, or may reflect scenarios of conservation planning. Ongoing assessments regionally and globally can take advantage of the increasing numbers of tools for calculating phylogenetic diversity measures. As one example, the Atlas of Living Australia (ALA – <http://www.ala.org.au/>) is a publicly available source of species information data for Australia and is developing PD analyses within their spatial toolset. Once available, these tools will be a useful resource for conservation assessment officers and planners within Australia.

Effective tools for policy and monitoring must face practical challenges. Analysis of phylogenetic diversity provides a good general indicator of feature diversity, but other complementary approaches are needed to fully capture functional trait diversity. Shared functional traits are often best explained by shared habitat/environment rather than shared ancestry. Functional trait diversity can be estimated by methods related to phylogenetic diversity measures, for example the functional environmental diversity (EDF) method outlined in Faith (2015a).

Phylogenetic uncertainty calculations can be used to determine confidence limits on phylogenetic analyses. Rosauer (2010) recommended that phylogenetic uncertainty assessments be included in conservation assessments using measures of PD and PE as they can potentially affect the results for conservation planning. This is a further avenue for improving use of phylogenetic diversity measures but was beyond the scope of this paper.

Null models also may be useful to investigate areas of phylogenetic overdispersion and underdispersion and would be a beneficial approach when using phylogenetic diversity measures in conservation assessment and planning. This approach would provide a means of quantitatively

identifying areas of congruence. One useful null model holds species occurrences (and thus species richness and WE constant) while randomising species position on the tree, to capture the component of PE due solely to phylogenetic relationships (Laffan and Crisp, 2003; Mishler et al., 2014; Rosauer and Jetz, 2015).

Determining the timelines of the past diversification events that gave rise to the extant biodiversity will, when aligned against timelines of past geological and environmental changes, help illuminate how biota may respond to change in the future. This requires dated phylogenetic trees for all groups, where branches are scaled to time by calibrating molecular evolutionary rates against an external reference such as fossils. The availability of such trees is rapidly increasing, with five of the seven trees used here being dated. Once such sufficient trees are available conservation planners will have the evidence base to design strategies to maintain phylodiversity (and the evolutionary processes that underlie it) into the future. We advocate a synthetic research agenda that seeks to understand biodiversity across time, space and phylogeny.

Recently, interest in Planetary Boundaries has pointed to the emerging strong link between phylogenetic diversity and conservation and global change policy. A Planetary Boundary (see Steffen et al., 2015) designates a point of change after which the planet is no longer in a “safe operating zone”. Beyond this point, further change can lead to tipping points where severe irreversible consequences emerge for human well-being. Planetary boundaries cover multiple aspects of the earth system, from climate change to biodiversity. The biodiversity boundary has been much debated. Following the proposal by Faith et al. (2010), Mace et al. (2014) recommended phylogenetic diversity (along with functional trait diversity) as an appropriate framework for monitoring and planning related to a biodiversity boundary (see also Steffen et al., 2015). Importantly, this framework presents a challenge for monitoring and planning that extends from a regional to a global scale. The analyses presented in this paper illustrate the foundations for the dynamic maps that will be needed.

One strategy for developing useful dynamic maps will be to take advantage of, and add value to, the well-developed observation systems at the species level that track change in range extent for species. Range change or loss is one of the key manifestations of climate change impacts on species, particularly in areas where warming is predicted or imminent (Araujo et al., 2013), but we do not know how this determines loss of phylogenetic diversity. PE scores for areas will change as the range extent for species and branches changes. PE scores can be recalculated as documented range changes for species are identified (for example, through ongoing monitoring of range extents in the Map of Life project (<http://www.mol.org>)). Such dynamic maps, for multiple taxonomic groups, may provide early warnings for a planetary boundary based on phylogenetic diversity – increased PE in many areas, for example, could indicate dramatic range losses. Further, groups such as GEO BON (the global biodiversity observation network; <https://www.earthobservations.org/geobon.shtml>) will also benefit from such dynamic maps, as a basis for monitoring of phylodiversity for many taxonomic groups.

Warnings of potential loss of global PD may be provided also by a related analysis of threatened phylogenetic endemism (TPE; Faith, 2015b). This measure calculates PE only for the threatened branches (i.e., only those branches with threatened descendants as indicated by IUCN red list or similar information). If an area shows an increase in the number of threatened species (and therefore in threatened branches) the TPE for the area will increase. Monitoring these values over time therefore provides an ongoing report on which areas contain many range-restricted threatened branches. This may provide another useful monitoring index in the context of Planetary Boundaries and GEO BON (see Table 1).

We note that biodiversity is just one of nine planetary boundaries and that it is only one of nine “society benefit areas” within GEOSS, the

umbrella organisation of GEO BON (atmosphere and geology are other areas). Our study therefore helps develop the framework enabling evolutionary history to be integrated into this broader multi-disciplinary framework of global observation systems for monitoring global change.

In summary, the use of phylodiversity measures in conservation assessments enhances evaluation of biodiversity by including an important dimension of biodiversity – evolutionary history – and will improve decision making for better conservation outcomes. The policy challenge is to identify local benefits and global issues regarding option values, planetary boundaries, tipping points and risk.

Acknowledgements

This work was initiated at a workshop (Integrating Measures of Phylogenetic and Taxonomic Diversity and Endemism into National Conservation Assessment) supported by the Australian Centre for Ecological Analysis and Synthesis (ACEAS). ACEAS is a facility of the Terrestrial Ecosystem Research Network (TERN) funded by the Australian Government National Collaborative Research Infrastructure Strategy (NCRIS). Further support was provided by John Stanistic, Andrew Hugall, Simon Ferrier, Jane Ambrose, Jonathan Face, Brian Prince, and the Australian Government Department of Environment.

We would also like to thank the two anonymous reviewers and Tom Bregman for providing constructive feedback and valuable comments on the manuscript.

This manuscript includes work done by Joe Miller while serving at the National Science Foundation. The views expressed in this paper do not necessarily reflect those of the National Science Foundation or the United States Government.

Appendix 1

Formula for the biodiversity measures used in the analyses. All analyses were done using the Biodiverse software [(Laffan et al., 2010); <http://purl.org/biodiverse>].

Species richness (ENDW_RICHNESS index in Biodiverse)

Count the number of species (taxa) in the set of taxa T. All species have equal weight.

$$Richness = \sum_{t \in T} 1$$

Weighted endemism (ENDW_WE index in Biodiverse)

Weighted endemism (WE) (Crisp et al., 2001; Laffan and Crisp, 2003) is a range weighted richness score, such that the contribution of each taxon t is weighted to be proportional to the fraction of its range that occurs across the area considered.

$$WE = \sum_{t \in T} \frac{r_t}{R_t} \quad (2)$$

where R_t is the full geographic range of taxon t , and r_t is the local range of taxon t (that part of its range found across the area considered). In this work the local and global ranges of a taxon are counted in units of number of square cells in which it is found.

Phylogenetic diversity (PD index in Biodiverse) is the sum of the branch lengths found in an area, where the branches are those along the minimum spanning path connecting the tips of the tree to the root node. The tips of the tree are the taxa found in that area, and each branch is counted only once.

$$PD = \sum_{\lambda \in \Lambda} L_{\lambda} \quad (3)$$

where L_{λ} is the length of branch λ in the set of branches Λ found across the area of interest.

Phylogenetic endemism (PE_WE index in Biodiverse) combines WE and PD to give an estimate of the degree to which branches that are found in an area are restricted to that area.

$$PE = \sum_{\lambda \in A} L_{\lambda} \frac{r_{\lambda}}{R_{\lambda}} \quad (4)$$

where R_{λ} is the full geographic range of branch λ in the set of branches Λ occurring across the area of interest, and r_{λ} is the local range of branch λ (that part of its range that occurs within the area). Note that the range of a branch is calculated as the union of the geographic range of the tips of the tree it subtends, so that a location containing more than one tip subtending an internal (ancestral) branch still counts only once for that branch. This ensures there is no double counting of locations when clade ranges are determined.

Absolute species endemism (END_ABS_ALL index in Biodiverse) is the sum of species found in an area and nowhere else. Its calculation is the same as for species richness except it only considers species unique to that area.

PD-endemism (PD_ENDEMISM in Biodiverse) is the sum of branch lengths found in a defined region and nowhere else. Its calculation is the same as for PD except it only considers branches unique to that area.

Sample Redundancy (Garcillán et al., 2003) is the ratio of labels to samples. Values close to 1 are well sampled while zero means there is no redundancy in the sampling

$$= 1 - \frac{\text{richness}}{\text{sum of the sample counts}} \quad (5)$$

Appendix 2. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.scitotenv.2015.04.113>.

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