











Real-world conservation planning for evolutionary diversity in the Kimberley, Australia, sidesteps uncertain taxonomy

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Abstract

Targeting phylogenetic diversity (PD) in systematic conservation planning is an efficient way to minimize losses across the Tree of Life. Considering representation of genetic diversity below and above species level, also allows robust analyses within systems where taxonomy is in flux. We use dense sampling of phylogeographic diversity for 11 lizard genera, to demonstrate how PD can be applied to a policy-ready conservation planning problem. Our analysis bypasses named taxa, using genetic data directly to inform conservation decisions. We highlight areas that should be prioritized for ecological management, and also areas that would provide the greatest benefit if added to the multisector conservation estate. We provide a rigorous and effective approach to represent the spectrum of genetic and species diversity in conservation planning.

KEYWORDS

conservation planning, evolutionary diversity, gekkonidae, lizard conservation, Marxan, phylogenetic diversity, Scincidae, the Kimberley

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1 | INTRODUCTION

In the face of rapid biodiversity loss, the use of phylogenetic diversity (PD; Faith, 1992) in conservation assessments holds the promise of better prioritizing investment for biodiversity conservation (Carvalho, Velo-Antón, & Tarroso, 2017; Forest, Grenyer, & Rouget, 2007; Pollock, Rosauer, & Thornhill, 2015; Rosauer, Pollock, Linke, & Jetz, 2017) including genetic and species diversity. Conserving evolutionary diversity contributes to ecosystem stability (Cadotte, Dinnage, & Tilman, 2012) and the adaptability of species (Sgrò, Lowe, & Hoffmann, 2011), however, effectively representing species and genetic diversity in a single, fully integrated planning process has not previously been possible. In spatial planning exercises, where nature conservation is assessed alongside competing resource uses, considering evolutionary relationships, rather than counting species as independent units of diversity, should help target sets of areas that best capture regional evolutionary diversity.

An advantage of PD-based conservation assessment that has received limited attention (Asmyhr, Linke, Hose, & Nipperess, 2014; Rosauer, Blom, & Bourke, 2016; Thomassen, Fuller, & Buermann, 2011), is that it does not depend on using named taxa. This is potentially important for at least three reasons. First, it is clear from dated phylogenetic analyses that species are not equivalent in representing evolutionary diversity—the quantum of diversity represented by a species (or any other taxonomic level) varies widely (Isaac, Turvey, Collen, Waterman, & Baillie, 2007). Second, divergent evolutionary lineages, sometimes referred to as evolutionarily significant units (Moritz, 1994), are often nested within species. Third, in many taxa, even among well-known vertebrates, taxonomy is in flux or does not adequately represent the PD. Conservation assessment based on phylogenetic lineages has the potential to address these issues by representing spatial patterns of diversity independent of taxon names, if we can define evolutionary units and describe each unit in terms two questions: “*where does it occur?*” and “*how is it related to other units on the phylogeny?*” This does not imply that species do not matter for ecology, but rather reflects the reality that biological diversity is a continuum, from local variants to species, genera, and beyond.

Phylogenetic conservation strategies offer great potential for improved outcomes from limited resources, but to achieve actual benefits, conservation assessment must connect to existing policy and management priorities (Laity, Laffan, & González-Orozco, 2015). We demonstrate this here through a collaborative study in a biodiverse region (Kimberley, northwest Australia) involving biodiversity researchers and key landholders including the state government, conservation organizations, Indigenous communities, and some private leaseholders, who have common interests

in managing their country to sustain natural ecosystems and evolutionary diversity. The then state government committed, in its Kimberley Science and Conservation Strategy (Government of Western Australia, 2011), to building and managing a multisector conservation estate.

The Kimberley region comprises the western portion of Australia's monsoonal tropics (AMT; Figure 1) covering 421,000 km². It is a major centre of species diversity and endemism (Bowman, Brown, & Braby, 2010), with a rapid rate of recent species discovery (Pepper & Keogh, 2014). Ongoing phylogeographic and phylogenetic analyses of low dispersal species are revealing high levels of taxonomically unrecognized lineage diversity (Afonso Silva et al., 2017; Laver, Doughty, & Oliver, 2017; Moritz, Fujita, & Rosauer, 2016; Oliver et al., 2017; Potter, Bragg, Peter, Bi, & Moritz, 2016; Potter, Eldridge, Taggart, & Cooper, 2012) and sometimes misconstrued species boundaries (Catullo, Lanfear, Doughty, & Keogh, 2014; Rabosky, Hutchinson, Donnellan, Talaba, & Lovette, 2014). Thus, current taxonomy for these groups does not adequately represent the evolutionary diversity of the system. We focus here on lizards, because they are climatically sensitive, have low rates of dispersal, strong spatial structure, and are thus likely to assist in identifying evolutionary refugia and areas of importance for conservation.

The Kimberley is similar in area to California, yet sparsely populated, with less than 40,000 residents (Kimberley Development Commission, 2011). Almost half the region's residents are Indigenous, which is reflected in land ownership and management under a variety of tenures, including Indigenous Protected Areas (IPAs) in which Aboriginal traditional owners undertake to sustain biological and cultural values as part of Australia's National Reserve System. In 2016, 25% of the Kimberley was already in conservation reserves (IUCN categories 1–6), including 7% in government conservation areas, 14% in Indigenous conservation arrangements including IPAs, and 2.1% managed by the Australian Wildlife Conservancy. Another 1% is designated for new reserves. Some private grazing properties (1.4% of the region) are also managed principally for conservation, but for the purposes of this analysis were not included as reserves.

Despite substantial ecological effects of fire and grazing regimes, the limited impact of intensive land uses such as cultivation, mining, and urbanization across the Kimberley provides flexibility for effective conservation planning to proceed before, rather than after, intensive development. Existing public conservation areas, while having substantial biodiversity value, were not allocated under a systematic conservation planning approach (Margules & Pressey, 2000). In the context of the government conservation priorities, we combine new evidence on phylogeographic diversity with systematic planning tools to identify areas that: (1) have highest priority for ecological management, irrespective of tenure, and (2) given a 5% expansion target, make the greatest additional contribution

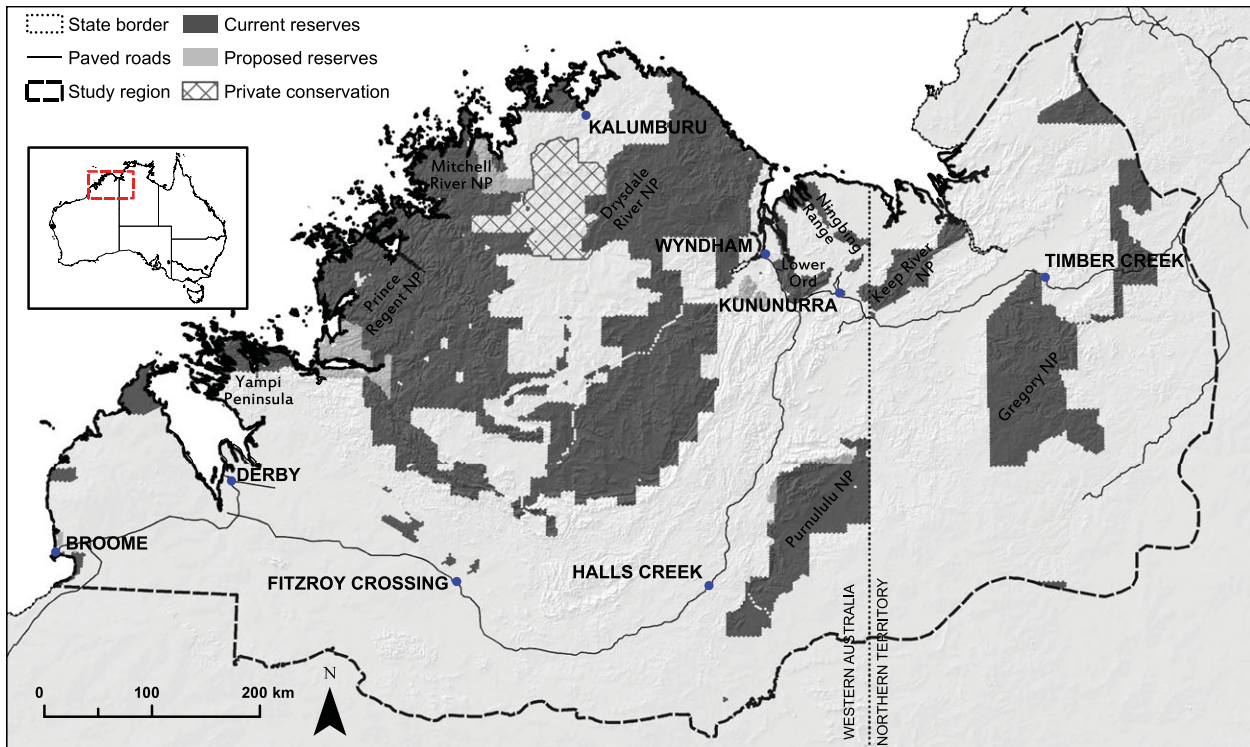


FIGURE 1 Overview of the Kimberley study region, spanning parts of Western Australia and the Northern Territory. One quarter of the region is already within reserves (IUCN categories 1–6, CAPAD database 2014)

to representing evolutionary diversity in lands managed for conservation. We thus demonstrate the value of an approach which allows data from taxonomic groups with incomplete or unreliable taxonomy to inform conservation decisions, in a system primed for its practical application.

2 | MATERIALS AND METHODS

We identified evolutionarily distinct lineages across 11 genera of lizards, modeled their distributions beyond sampled locations and then applied systematic conservation planning to identify areas that most efficiently conserve the PD, given set targets (Figure 2).

2.1 | Biological data

This conservation analysis builds on an extensive, comparative phylogeographic analysis for 46 recognized species from 11 genera of skink and gecko lizards across the AMT (Table 1). The spatial data and phylogenies central to this work, were based on 4,290 specimens from field surveys (2012 to 2015) and existing biological collections (Rosauer et al., 2016). Mitochondrial DNA (mtDNA) from each specimen was used to infer the phylogenetic relationships within each genus, and to identify 171 evolutionarily distinct lineages, defined by a minimum 6% pairwise sequence diver-

gence (Rosauer et al., 2016) from their closest relatives. While mtDNA was used for consistency across a broad range of taxa, similar relationships were recovered when phylogenies were inferred for several groups using from eight to hundreds of nuclear loci (Afonso Silva et al., 2017; Moritz et al., 2016; Potter et al. 2016). A separate phylogenetic tree was inferred for each genus, except for the closely-related skink genera *Eremiascincus* and *Glaphyromorphus* that were analyzed together. The methods for genetic sampling and phylogenetic inference are described in Rosauer et al. (2016), and biological data for the study region are summarized in Table 1.

A lineage distribution model (LDM; method in Rosauer et al., 2015) for each lineage (as prepared for Rosauer et al., 2016) predicted its distribution beyond sampled occurrences. The LDM method fits a distribution model for each species based on its occurrence in environmental space, and then partitions that model between parapatric lineages which comprise that species, based on distance and connectivity to known locations of the lineage. The resulting 171 models represent each lineage as a 0.01 degree (~1.1 km) grid with pixel values (0 to 1) indicating relative likelihood of occurrence.

2.2 | Data structure for conservation planning

The planning units (PU) for the study were a lattice of 86,439 hexagons, of area 5 km². Hexagons were chosen due to their advantages over other regular shapes such as squares, when

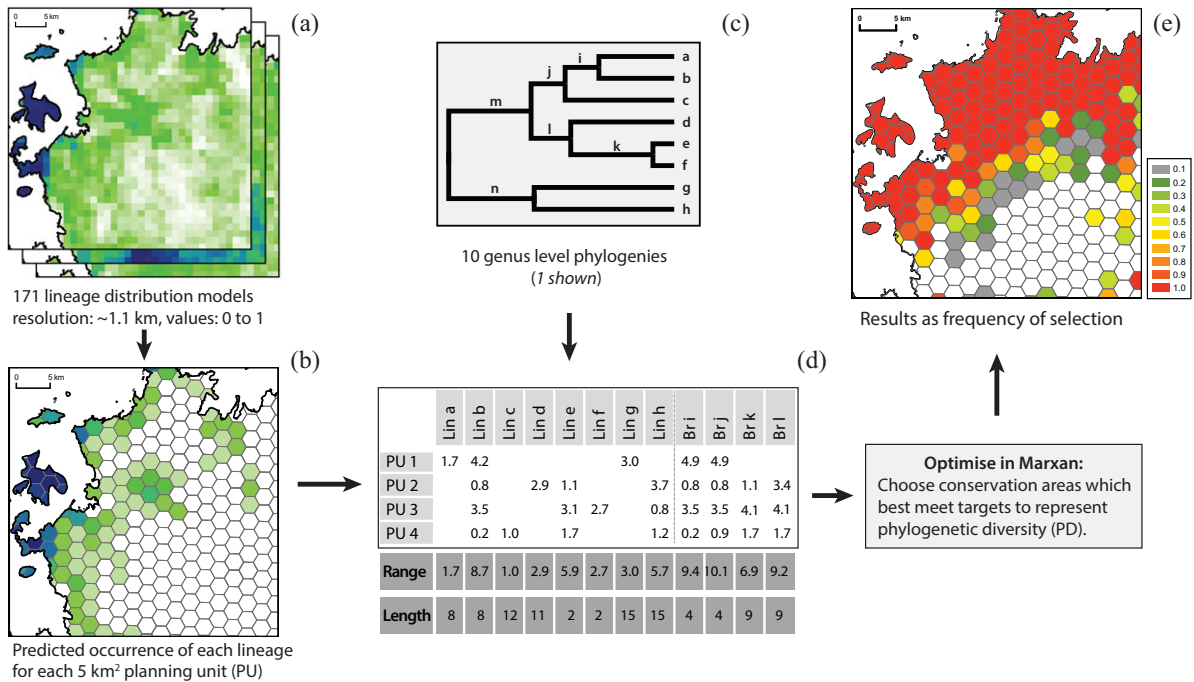


FIGURE 2 Overview of the methods in this study. LDMs (a) are combined with genus level phylogenies (c) to infer the distribution of each tip and internal branch. The model pixel values for each branch are summed within each PU (b) to record the predicted occurrence of each branch in each PU (d). Rows in (d) each represent a single hexagonal PU and columns represent phylogenetic branches. For each conservation scenario, 100 reserve solutions are generated, and results shown (e) as the frequency with which each PU was chosen

TABLE 1 Summary of lizard taxa and samples in this study. Numbers of individuals, recognized species and mitochondrial lineages (Sp/Lin) within the Kimberley and the broader AMT data set

Group	Genus	Kimberley		Whole AMT		Published sources
		Samples	Sp/Lin	Samples	Sp/Lin	
Skinks	<i>Carlia</i>	351	6/15	624	6/23	Afonso Silva et al. (2017); Potter et al. (2016)
	<i>Cryptoblepharus</i>	150	2/14	215	2/18	Blom et al. (2016)
	<i>Ctenotus</i>	243	14/16	1,007	24/31	
	<i>Eremiascincus & Glaphyromorphus</i>	83	3/8	185	5/17	
	<i>Morethia</i>	69	2/8	321	2/9	
Geckos	<i>Crenadactylus</i>	41	2/9	41	2/9	Doughty et al. (2016)
	<i>Gehyra</i>	661	10/47	1,055	12/69	Oliver et al. (2016, 2017)
	<i>Heteronotia</i>	299	2/29	694	2/58	Moritz et al. (2016)
	<i>Oedura</i>	92	4/22	153	6/27	Laver et al. (2017); Oliver and Doughty (2016)
	<i>Pseudotothecadactylus</i>	21	1/3	95	3/7	Oliver, Laver, Smith, and Bauer (2014)
Total		2,010	46/171	4,390	64/268	

boundary length is used as an indicator of spatial cohesion (Rosauer, 2000). We clipped coastal PUs to include only land, and lacking fine resolution data on costs of land acquisition and management, used the land area of each PU as a surrogate for cost of conservation. Cost per unit area was thus constant. Each PU with >50% in current reserves was set as “reserved”. While large areas of the Kimberley have been modified, especially by grazing and changed fire regimes (Ziembicki, Woinarski, & Webb, 2015), few areas have lost their cover

of native vegetation entirely. The 110 PUs with <50% native vegetation were set as unavailable for conservation.

We followed recent studies (Asmyhr et al., 2014; Carvalho et al., 2017; Pollock et al., 2015; Pollock, Thuiller, & Jetz, 2017; Rosauer et al., 2017) that used mainstream conservation planning software, *Marxan* and *Zonation* (Ball, Possingham, & Watts, 2009; Moilanen, 2007), to select areas to efficiently capture the PD of a region. Each branch on the phylogeny was a separate conservation feature analogous

TABLE 2 Settings and results for four conservation scenarios. BLM is the boundary length modifier used in Marxan to favor solutions with larger, less fragmented reserves

Scenario	Limit	Max area km ²	%	BLM	Question	Variant	Area km ²	Targets met
Current	No change	109,177	25.9		How much PD do current reserves capture?	Actual reserves	109,177	62.7%
A. Ignore existing tenure – no spatial configuration objective	Area of current reserves	109,177	25.9	0	Given the same area as now reserved, where should management be targeted?	Scattered reserves	67,965	99.0%
B. Ignore existing tenure – prefer cohesive reserves	Area of current reserves	109,177	25.9	4		Cohesive reserves	79,931	99.2%
C. Extent from existing reserves	Area of current reserves + 5%	114,636	27.2	6	How could a further 5% expansion in Western Australia best be located?		114,639	71.7%
D. Extent from existing reserves – <i>named species not PD</i>	Area of current reserves + 5%	114,636	27.2	6	How could a further 5% expansion in Western Australia best be located to represent <i>named species</i> ?		114,639	97.7% ^a

^aNote that the targets met in *scenario D* are for species. The result for PD (comparable to the other targets met) was 69.6%.

to a species, with a geographic range defined as the union of the ranges of its descendent tips. This approach assigns each branch a weighting proportional to its length, to define its importance for conservation, in this case using Marxan's Species Penalty Factor. Because the occurrence of each lineage was represented on a 0 to 1 scale, LDMs for the tips were used to calculate occurrence of each internal branch via Faith's (2008) probabilistic PD framework, to produce a distribution model for each branch.

For each PU, we recorded occurrence of each branch as the sum of the modeled occurrence values for the pixels intersecting the PU. Modeled distributions were thus transferred to PUs without the loss of information that results from converting model predictions to binary presence/absence.

Thus, we prepared a data set for conservation planning, with the occurrence of each lineage and internal branch in each PU, along with a weighting proportional to branch length, and the cost (area) and boundary lengths of each PU. Scripts are available at github.com/DanRosauer/phylospatial.

2.3 | Conservation scenarios

Reservation targets were set to protect 15% (Kirkpatrick, 1998) of the modeled occurrence of each branch based on the sum of the model values in each PU, so areas with a high model prediction for a branch would contribute more to meeting its target. To avoid loss of habitat for restricted elements

of the lizard biota, and to avoid allocating limited resources to widespread elements, a floor and ceiling were placed on targets. New government reserves, which are planned and approved, were treated as current reserves. We used *Marxan* (Ball et al., 2009) to identify sets of PUs that would maximize PD captured in reserves while limiting the total area reserved and addressing spatial configuration objectives, under four scenarios (Table 2).

Scenario A: Meet the reservation targets without exceeding the area of current reserves, ignoring current land tenure and the size and cohesiveness of potential reserves. This scenario directly reflects locations of features of conservation value, to help target management actions across land tenures.

Scenario B: Similar to A, but uses *Marxan*'s boundary length modifier (BLM) to favor solutions with larger, less fragmented reserves.

Scenario C: Existing reserves are “locked in” as reserved, with a 5% expansion allowed. This accounts for biodiversity in existing reserves across the Kimberley region, but for management relevance, only allows new conservation areas within Western Australia. This scenario is most informative for real-world management as it asks; given what we know about the distribution of PD in our sample of lizards, which areas offer greatest benefit for a small expansion of the Kimberley's multisector conservation system?

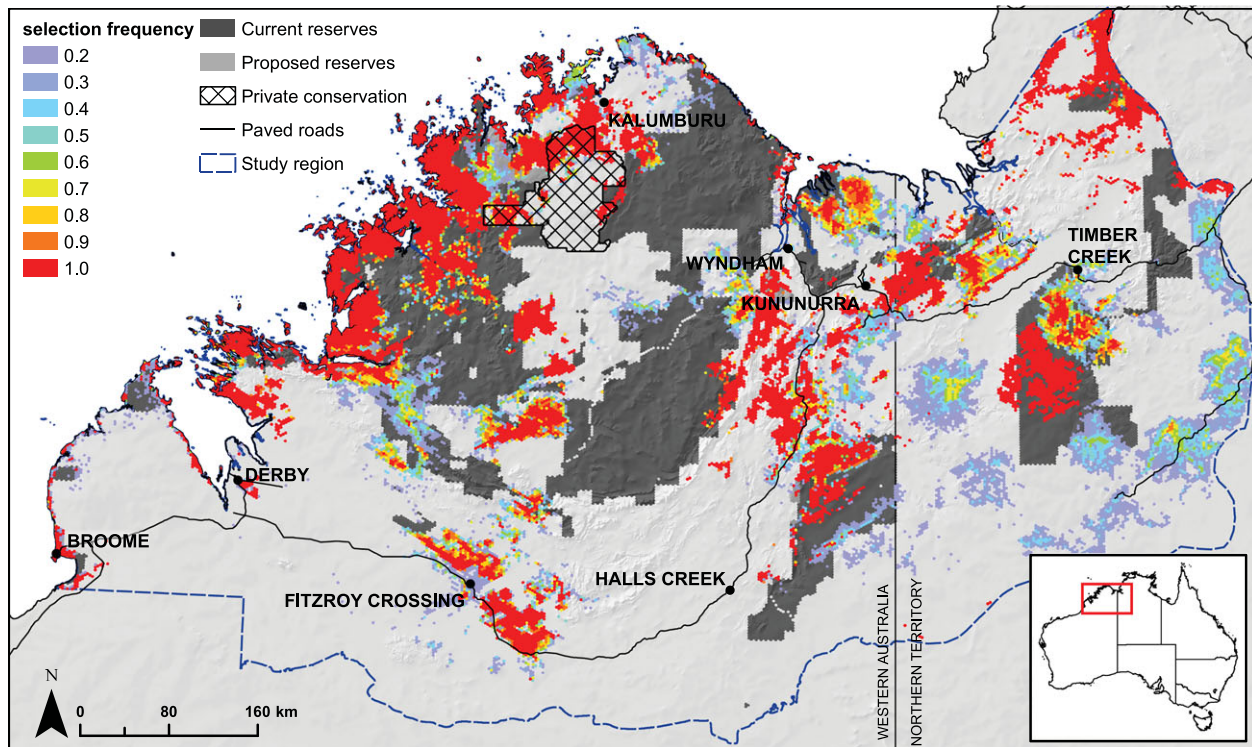


FIGURE 3 Priorities for conservation in the Kimberley based on PD in 11 genera of lizards, unconstrained by existing land tenure or spatial cohesiveness (scenario A). The blue to red color ramp indicates the frequency with which each PU was selected. Red areas were highly irreplaceable

Finally, to check how much difference our approach based on PD would make to the choice of areas, compared to species-based conservation planning, we ran *scenario D*. This used the same settings as *scenario C* to add to existing protected areas, but rather than using PD, it aimed to meet representation targets for the 46 species found in our study, thus ignoring both relationships between species and the diversity within them. The same taxa and species distribution models were used, but without any splitting into units below the level of currently recognized species.

We ran the *Marxan* simulated annealing algorithm 100 times for each of the four scenarios, for 5×10^7 iterations, with the maximum area reserved for each scenario (Table 2) enforced via the *cost threshold* parameter. For *scenarios C* & *D*, currently reserved PUs were “locked in” as reserved. All settings are archived on DataDryad. The result for each scenario is the proportion of 100 runs where each PU was selected.

3 | RESULTS

Although 26% of the region is under existing or planned conservation tenure, the biodiversity captured by current reserves met the reservation target for only 63% of PD across the 11 lizard genera (Table 2). In contrast, by selecting the same amount of land without regard to existing land tenure or frag-

mentation (*scenario A*, Figure 3), the targets for PD conservation were met easily, in an area only 63% as large (16% of the Kimberley). With a greater requirement for connectivity (*scenario B*, Figure S1) the area required to meet all targets, increased to 73% the size of current reserves (19% of region). In these scenarios, highly irreplaceable areas were found in large parts of the wet northwest Kimberley between the Yampi Peninsula and Kalumburu, along with many of the adjoining coastal islands. High-priority areas for conservation were also identified in the south near Broome and Fitzroy Crossing, in the east including much of the Keep River and Gregory national parks, and the Ord Valley south of Kununurra to Purnululu NP.

Expanding the existing reserve network by 5% in Western Australia to cover 27.2% of the region (*scenario C*), delivered more limited but practical options to enhance the existing multisector conservation estate, meeting 72% of the targets for PD conservation. A trial with no area constraint met 95% of targets by reserving 34.2% of the region. The PUs most frequently selected for protection (*scenario C*, Figure 4) encompass several main areas that would be of prime importance for conservation of the evolutionary diversity of the Kimberley's lizards, including Bigge Island (1), the Kalumburu-King Edward River area (2), areas near the Ningbing Range and the Lower Ord (3), scattered sites in the Argyle to Purnululu region (4), the Devonian Reef ranges near Fitzroy Crossing (5), and parts of Yampi Peninsula (6). Small areas close to

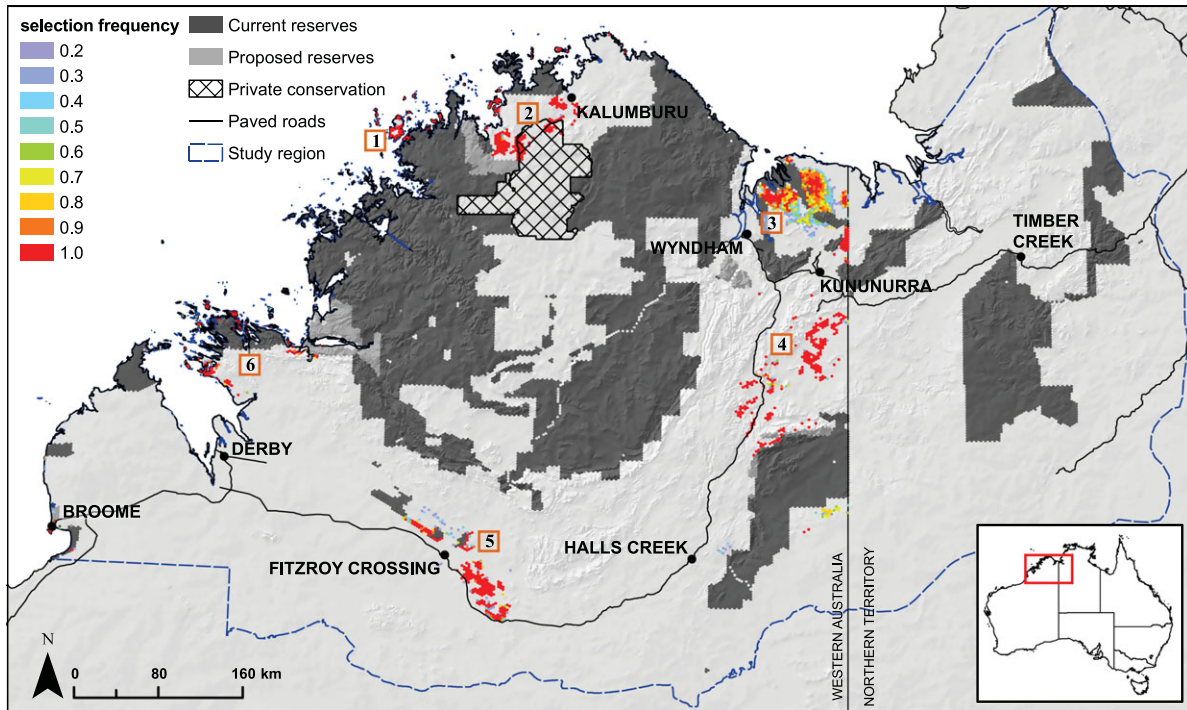


FIGURE 4 Priorities for conservation in the Kimberley based on PD in 11 genera of lizards, with a 5% expansion of reserves in the Western Australian Kimberley (scenario C). The blue to red color ramp indicates the frequency with which each PU was selected. Red areas were highly irreplaceable. The main regions with priorities for reserve expansion were: (1) Bigge Island, (2) Kalumburu - King Edward River area, (3) Ningbing Range and Lower Ord, (4) Argyle - Purnululu area, (5) Devonian Reef ranges, and (6) Yampi Peninsula

Broome and several near-shore islands were also essential to meet the conservation targets.

The species conservation result (*scenario D*, Figure S2) differed substantially from *scenario C* in its additions to the protected area network. It missed the areas found to be highly important in the West Kimberley (numbers 1, 2, and 6 in Figure 4), much of the Ningbing Range area (3) northeast of Wyndham, but agreed, however, on the importance of the ranges southeast of Fitzroy Crossing (5). This scenario met almost all species targets (97.7%) but for the same amount of land added to the existing reserve network, added far less PD (6.8% compared to 9.0% in *scenario C*). In other words, by targeting PD directly, the PD benefit of expanding the protected areas by 5% was 31% larger.

4 | DISCUSSION

Despite a firm conceptual foundation, measures of PD have so far had limited impact in on-ground conservation planning, and then only at species level and above. But here, with existing government intent to expand conservation-focused lands and to support management of those lands, we have identified priority areas to capture diversity in low dispersal vertebrates. This extends the field in two significant ways. First, along with Carvalho et al. (2017), our approach targets diver-

sity both *above and below* species level, treating evolutionary variation consistently. By working directly with phylogenetic lineages, our approach is independent of named taxa, valuing both divergence among species, and deep phylogeographic structure within species. The latter represents one important dimension of genetic diversity which is acknowledged as important in conservation policy, but rarely considered in protected area design due to the lack of appropriate metrics.

Second, our method provides a way to include in conservation planning taxonomic groups for which the taxonomy is unreliable or in flux (Brito, 2010). This requires collection and analysis of suitable, geographically-distributed genetic samples across multiple species—a common element in comparative phylogeography. Despite progress with statistical species-delimitation methods, the time required for taxonomic revisions and differences in taxonomic practice mean that there will rarely be a 1:1 match between genetically-identified lineages and named taxa. There is thus great practical value in describing the distribution and relationships of evolutionary units (Moritz et al., 2016), mapping centres of endemism (Rosauer et al., 2016) and applying these data to systematic conservation planning. Along with other recent studies (Rosauer et al., 2017), we find that planning for PD conservation alters the areas chosen and increases the total diversity captured. But independent of the ability to capture *more* diversity, we show here how to

extend conservation assessment to unnamed taxa that would otherwise lie beyond the scope of structured planning.

The priority areas which we found correspond well to areas of high diversity identified in recent studies, such as the north-west Kimberley and adjacent islands (1 in Figure 4; Gibson et al., 2017) and the limestone Devonian Reef ranges (5 in Figure 4) of the southern Kimberley, which host 11 genetically divergent lineages that appear to be endemic to that area (Oliver et al., 2017). Some of the King Edward River area (2 in Figure 4) is already actively managed for conservation by private leaseholders. Other areas highlighted in the analysis, such as the Argyle to Purnululu region (4 in Figure 4) are less surveyed, yet recent studies have revealed deeply divergent lineages (Laver et al., 2017) or entire radiations (Köhler & Criscione, 2015) in the east Kimberley. Clearly, more surveys and analysis are needed across the region.

These results provide a valid assessment of conservation priorities, but are not comprehensive in their taxonomic breadth or spatial sampling. The 11 genera of lizards sampled represent a substantial subset of the diverse lizard fauna of the Kimberley region. Further work could extend this analysis to additional taxa, including groups that may display contrasting spatial patterns of evolutionary diversity. Several groups such as mammals, frogs (Catullo et al., 2014), and land snails (Köhler & Criscione, 2015) have substantial genetic sampling for the region with potential for this type of analysis. Further work could also incorporate the effects of phylogenetic uncertainty on the choice of priority areas (Rosauer et al., 2017), noting that it is uncertainty over branch lengths which could affect results, while topological uncertainty is important only via its effect on the branch length shared between species or lineages. Uncertainty could also be reduced by sampling more of the genome, including nuclear DNA to supplement the mtDNA used to infer phylogenies in this study.







In a partnership between government, community, and private land managers, we have systematically identified the areas that would best contribute to the representation of evolutionary history across a large and diverse region, using genetic data for ecologically and taxonomically diverse lizard taxa. Importantly, our analysis does not rely on current taxonomy, which in many cases does not adequately capture the diversity in these groups. Our approach (Carvalho et al., 2017) using mainstream conservation planning software may be valuable to provide high-resolution conservation assessment for biota and regions where taxonomy is in flux, or where substantial diversity exists below the level of named taxa.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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