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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 eleven 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 prioritised for ecological management, and also areas that would provide the greatest benefit if added to the multi-sector conservation estate. We provide a rigorous and effective approach to represent the spectrum of genetic and species diversity in conservation planning.

## Introduction

In the face of rapid biodiversity loss, the use of phylogenetic diversity (PD; Faith 1992) in conservation assessments holds the promise of better prioritising investment for biodiversity conservation (Carvalho *et al.* 2017; Forest *et al.* 2007; Pollock *et al.* 2015; Rosauer *et al.* 2017) including genetic and species diversity. Conserving evolutionary diversity contributes to ecosystem stability (Cadotte *et al.* 2012) and the adaptability of species (Sgrò *et al.* 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 *et al.* 2014; Rosauer *et al.* 2016; Thomassen *et al.* 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 *et al.* 2007). Second, divergent evolutionary lineages, sometimes referred to as evolutionarily significant units (Moritz 1994) are often nested within species. Third, in many taxa, even amongst well-known vertebrates, taxonomy is in flux or does not adequately represent the phylogenetic diversity. 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 *et al.* 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 organisations, 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 to building and managing a multi-sector conservation estate (Kimberley Science & Conservation Strategy; Government of Western Australia 2011).

The Kimberley region comprises the western portion of Australia's monsoonal tropics (AMT; Fig. 1) covering 421 000 km<sup>2</sup>. It is a major centre of species diversity and endemism (Bowman *et al.* 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

unrecognised lineage diversity (Afonso Silva *et al.* 2017; Laver *et al.* 2017; Moritz *et al.* 2016; Oliver *et al.* 2017; Potter *et al.* 2016; Potter *et al.* 2012) and sometimes misconstrued species boundaries (Catullo *et al.* 2014; Rabosky *et al.* 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 (NRS). 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 (i) have highest priority for ecological management, irrespective of tenure, and (ii) given a 5% expansion target, make the greatest additional contribution 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.

FIGURE 1 NEAR HERE

## Materials and Methods

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

FIGURE 2 NEAR HERE

## Biological data

This conservation analysis builds on an extensive, comparative phylogeographic analysis for 43 recognised 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 4290 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 divergence (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 analysed together. The methods for genetic sampling and phylogenetic inference are described in Rosauer *et al.* (2016), and biological data for the study region are summarised 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.

**TABLE 1 NEAR HERE**

### **Data structure for conservation planning**

The planning units (PU) for the study were a lattice of 86 439 hexagons, of area 5km<sup>2</sup>. Hexagons were chosen due to their advantages over other regular shapes such as squares, when 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 *et al.* 2015), few areas have lost their cover of native vegetation entirely. The 110 PU 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, 2017; Rosauer *et al.* 2017) that used mainstream conservation planning software, *Marxan* and *Zonation* (Ball *et al.* 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 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 modelled occurrence values for the pixels intersecting the PU. Modelled 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 dataset 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](https://github.com/DanRosauer/phylospatial).

### **Conservation scenarios**

Reservation targets were set to protect 15% (Kirkpatrick 1998) of the modelled 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 favour 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 multi-sector conservation system?

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 43 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 recognised species.

#### TABLE 2 NEAR HERE

We ran the *Marxan* simulated annealing algorithm 100 times for each of the four scenarios, for  $5 \times 10^7$  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.

## 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 fragmentation (*scenario A*, Fig. 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, Fig. 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.

### FIGURE 3 NEAR HERE

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 multi-sector 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*, Fig. 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, the Kalumburu - King Edward River area, areas near the Ningbing Range and the Lower Ord, scattered sites in the Argyle to Purnululu region, the Devonian Reef ranges near Fitzroy Crossing and parts of Yampi Peninsula. Small areas close to Broome, and several nearshore islands were also essential to meet the conservation targets.

### FIGURE 4 NEAR HERE

The species conservation result (*scenario D*, Fig. 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 Fig. 4), much of the Ningbing Range area (3) northeast of Wyndham, but agreed however, on the importance of the ranges south-east 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.

## 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-focussed 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 diversity 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 (e.g. 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 northwest Kimberley and adjacent islands (1 in Fig. 3B; Gibson *et al.* 2017) and the limestone Devonian Reef ranges (5 in Fig. 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 Fig. 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 Fig. 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 eleven 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 (and see 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

**Figure S1.** Priorities for conservation in the Kimberley under scenario B, unconstrained by existing land tenure but with a requirement for spatial cohesiveness.

**Figure S2.** Scenario D – priorities for conservation in the Kimberley based current species in eleven genera of lizards, with a 5% expansion of reserves in the Western Australian Kimberley.

Data, code and configuration files are available from DataDryad at [dryad url]

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## Tables

### Table 1

**Table 1 – Summary of lizard taxa and samples in this study.** Numbers of individuals, recognised species and mitochondrial lineages (Sp/Lin) within the Kimberley and the broader AMT dataset.

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 <i>et al.</i> 2017; Potter <i>et al.</i> 2016)
	<i>Cryptoblepharus</i>	150	2/14	215	2/18	(Blom <i>et al.</i> 2016)
	<i>Ctenotus</i>	243	14/16	1007	24/31	
	<i>Eremiascincus</i> & <i>Glaphyromorphus</i>	83	3/8	185	5/17	
	<i>Morethia</i>	69	2/8	321	2/9	
Geckoes	<i>Crenadactylus</i>	41	2/9	41	2/9	(Doughty <i>et al.</i> 2016)
	<i>Gehyra</i>	661	10/47	1055	12/69	(Oliver <i>et al.</i> 2012, 2017)
	<i>Heteronotia</i>	299	2/29	694	2/58	(Moritz <i>et al.</i> 2016)
	<i>Oedura</i>	92	4/22	153	6/27	(Laver <i>et al.</i> 2017)
	<i>Pseudothecadactylus</i>	21	1/3	95	3/7	(Oliver <i>et al.</i> 2014)
	<b>TOTALS</b>	<b>2010</b>	<b>44/171</b>	<b>4290</b>	<b>59/259</b>	

## Table 2

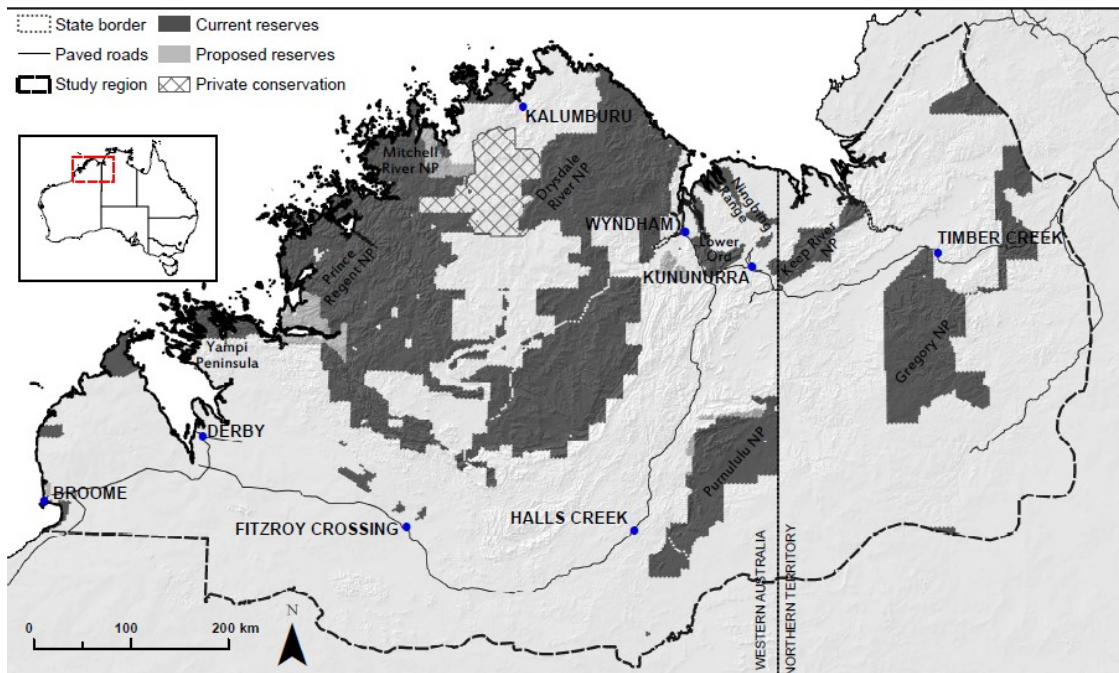
**Table 2:** Settings and results for four conservation scenarios.

Scenario	Limit	Max area km <sup>2</sup>	%	BLM	Question	Area km <sup>2</sup>	Targets met
Current	no change	109 177	25.9		How much PD do current reserves capture?	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?	67 965	99.0%
B. Ignore existing tenure – prefer cohesive reserves	area of current reserves	109 177	25.9	4		79 931	99.2%
C. Extend 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. Extend 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*

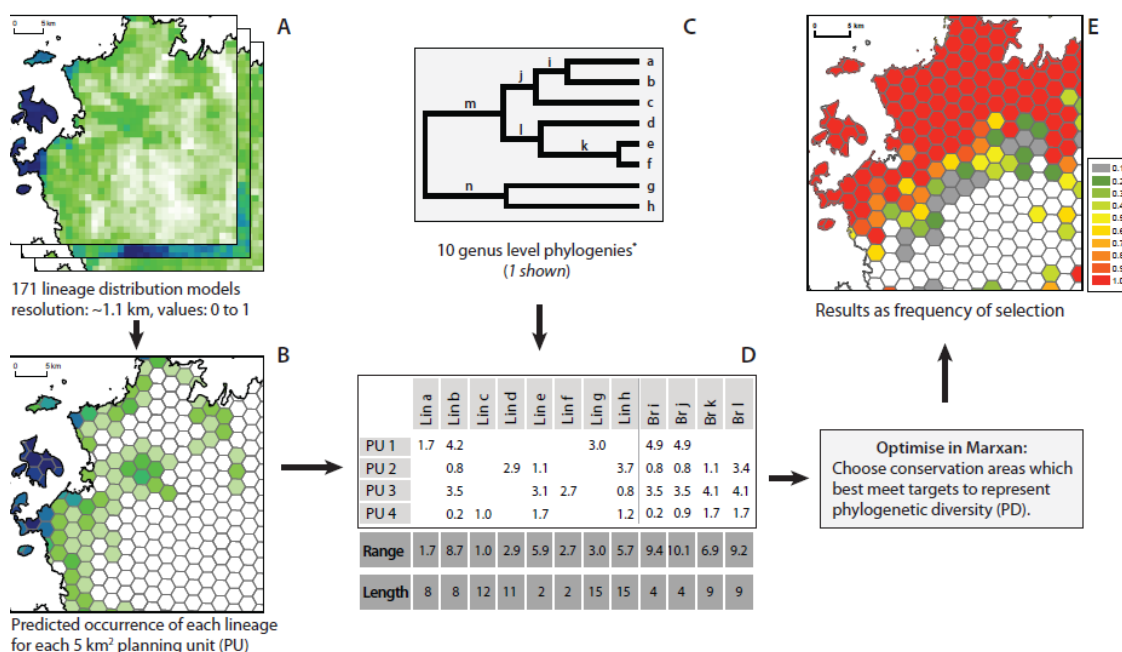
\* Note that the targets met in *scenario D* are for species. The result for PD (comparable to the other targets met) was 69.6%.

## Figure legends

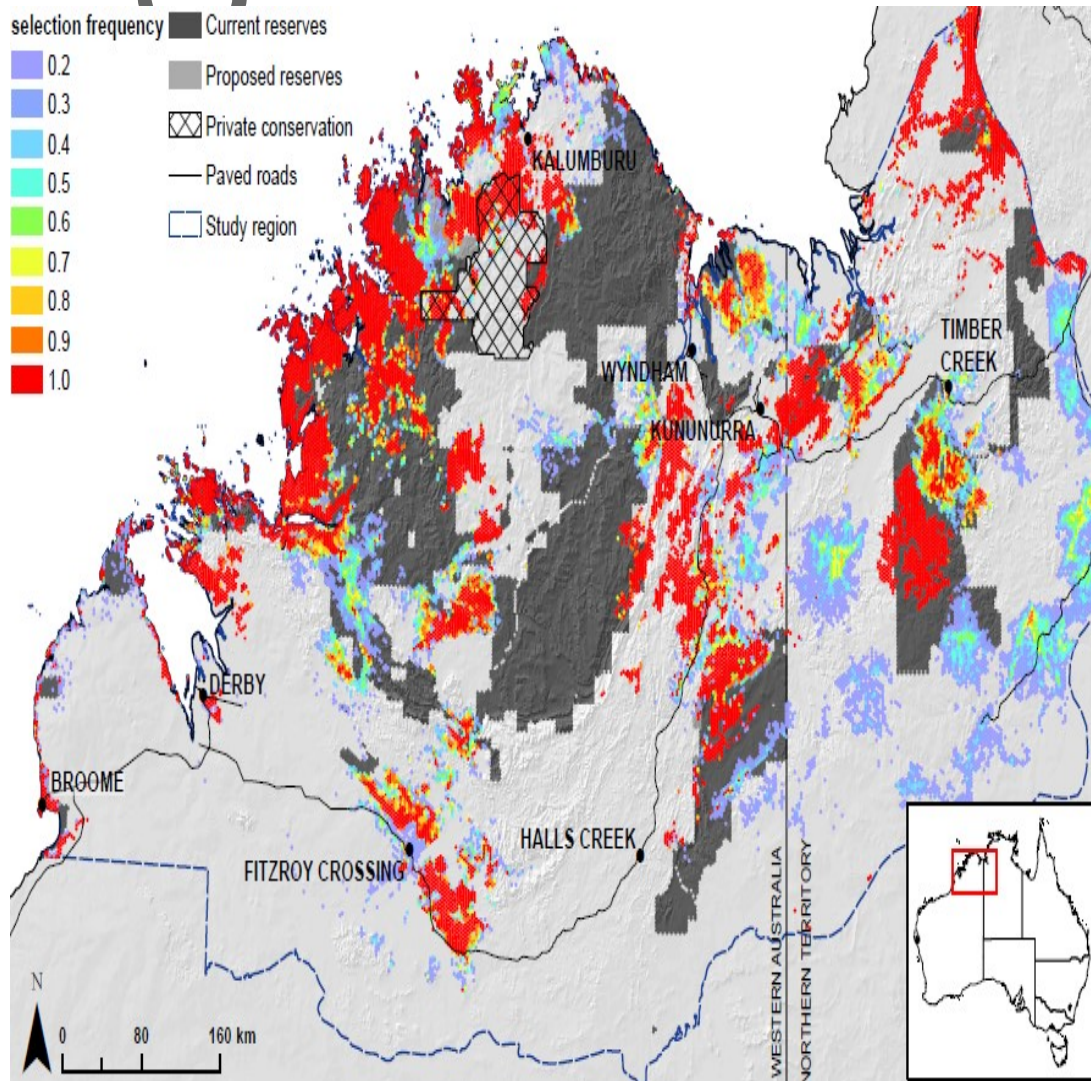
**Figure 1.** Overview of the Kimberley study region, spanning parts of Western Australia and the Northern Territory. One quarter of the region is already within reserves (IUCN categories 1-6, CAPAD database 2014).



**Figure 2.** Overview of the methods in this study. Lineage distribution models (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 planning unit (PU) (B) to record the predicted occurrence of each branch in each PU (D). Rows in D each represent a single hexagonal planning unit 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.



**Figure 3.** Priorities for conservation in the Kimberley based on phylogenetic diversity in eleven genera of lizards, unconstrained by existing land tenure or spatial cohesiveness (scenario A). The blue to red colour ramp indicates the frequency with which each planning unit was selected. Red areas were highly irreplaceable.





**Figure 4.** Priorities for conservation in the Kimberley based on phylogenetic diversity in eleven genera of lizards, with a 5% expansion of reserves in the Western Australian Kimberley (scenario C). The blue to red colour ramp indicates the frequency with which each planning unit 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.

