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SYNTHESIS

Biogeography of the Kimberley, Western Australia: a review of landscape evolution and biotic response in an ancient refugium

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ABSTRACT

Aim We review the biogeography of the Kimberley, with a particular focus on the geological and landscape history of the region. We identified broad geological and biogeographical discontinuities across the Kimberley, and propose a number of testable hypotheses concerning how the evolution of these landforms may have harboured and structured genetic diversity across the region.

Location The Kimberley region, north-western Australia.

Methods The literature available on the Kimberley is summarized, in particular regarding the evolution of Kimberley landscapes and climate. Previous genetic work was assessed in order to establish whether common patterns exist, and to identify concordance with four putative broad-scale biogeographical breaks to be tested when appropriate fine-scale genetic data become available: (1) the geological division between the Kimberley Plateau and surrounding deformation zones of the King Leopold and Halls Creek orogens; (2) the east–west geological divide between different sandstone units of the Kimberley Plateau; (3) major drainage divisions and river courses; and (4) the previously defined bioregions and subregions of the Interim Biogeographical Regionalisation for Australia (IBRA), the Northern and Central Kimberley.

Results Genetic patterns across a number of taxonomic groups in the Kimberley lend support to the four biogeographical scenarios we outline, and these now need to be tested with additional data.

Main conclusions The biogeographical patterns emerging from studies of Kimberley biota are characterized by high endemism and deep divergences. In addition, a complex relationship between the Kimberley and other monsoon tropical bioregions and the adjacent deserts suggests multiple expansions into the arid zone, and vicariance and isolation in upland refugia within the topographically complex region. Fine-scale genetic data are beginning to be accumulated for Kimberley taxa, and concordant phylogeographical patterns across disparate groups suggest that regional differences in geological structure and land-forms may have played an important role in shaping the distribution and evolutionary patterns of extant biota. Future palaeoecological, geomorphological and finer scale phylogenetic investigations based on increased sampling and emerging genetic technologies will shed more light on the evolution of the Kimberley biome amidst one of the greatest environmental changes in the Cenozoic: the widespread aridification of the Australian continent.

Keywords

Aridification, Australian Monsoon Tropics, biogeography, endemism, geological history, northern Australia, phylogeography.

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INTRODUCTION

Throughout Earth's history, the positions of continents have slowly changed. This has had a fundamental impact on biotic evolution through complex connections with different landmasses and a suite of changing climatic regimes over time. For the Australian continent, the initial breakup of Gondwana around 150 Ma and the subsequent separation at *c.* 55 Ma from Antarctica were major physiographical changes; the period of isolation that has followed has led to the evolution of a highly endemic modern fauna and flora (Udvardy, 1975). The biggest change in more recent Australian history has undoubtedly been the desertification of the continental interior, with vast inland seas and tropical ecosystems being replaced over the last 15 Myr by arid deserts and dune systems (Frakes *et al.*, 1987; Fujioka & Chappell, 2010). The impact on the evolution of biodiversity across the continent has been immense, as evidenced by the signatures of extinction, persistence, diversification and expansion etched in the genealogies of extant taxa, and the fossils and pollens laid down in the geological record (reviewed in Byrne *et al.*, 2008). The mesic fringes of northern Australia have not been immune to the influence of aridification, with palaeoenvironmental evidence suggesting much drier conditions in tropical Australia during Pleistocene glacial cycles, in conjunction with cooler temperatures, especially in lowland regions (Reeves *et al.*, 2013a).

The Kimberley, in north-western Australia, is a unique bioregion within the Australian Monsoon Tropics (AMT) biome (Fig. 1). The Kimberley lies within the seasonally dry tropics, and presently has a summer (November–April) rainfall regime originating from tropical depressions, thunderstorms and the northern Australian monsoon trough (Wende, 1997). Temperatures are high year round, with monthly averages between 25 and 35 °C (Waples, 2007). Studies of the Kimberley biota are accumulating, and emerging patterns suggest that many taxa have a deep phylogenetic history in this region, with microendemism in the herpetofauna at an intensity not exceeded anywhere else on the continent (e.g. Pepper *et al.*, 2011a; Oliver *et al.*, 2010, 2012; C. Moritz *et al.*, The Australian National University, Canberra, unpublished data). Despite a number of recent studies that have reviewed the biogeographical patterns in this region (Bowman *et al.*, 2010; Eldridge *et al.*, 2012; Potter *et al.*, 2012a; Edwards *et al.*, 2013; Catullo *et al.*, 2014a), fine-scale genetic sampling across the Kimberley is currently limited, largely because of the remote nature of the region, inaccessibility during the wet season, and large areas that are located in Aboriginal-owned lands with restricted access (Moritz *et al.*, 2013). Of particular importance, details on land-forms and the physiography and evolution of the putative biogeographical barriers have been limited.

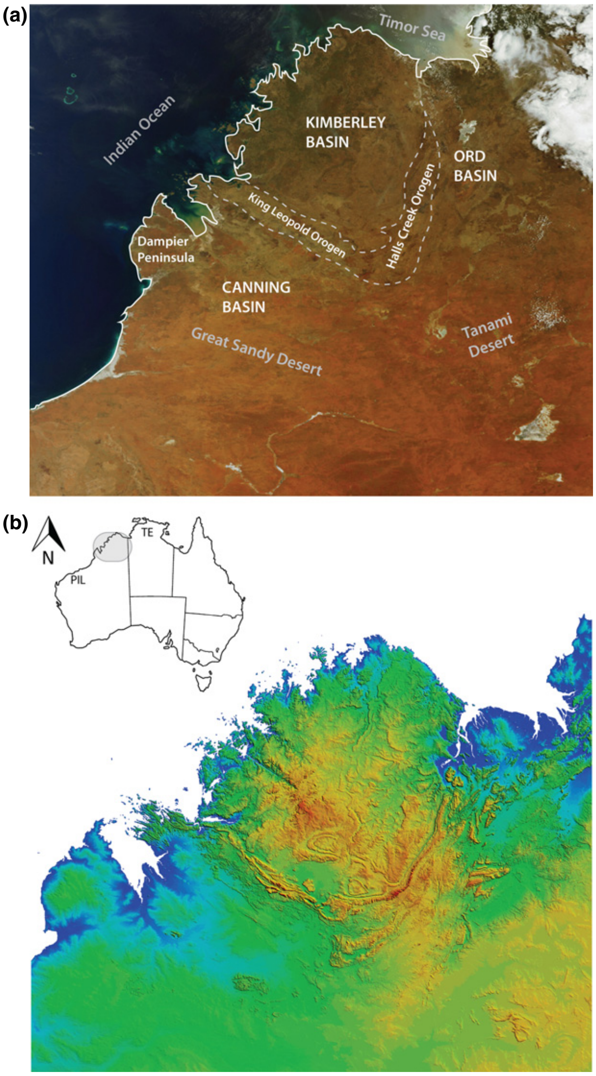

Figure 1 (a) True-colour Aqua MODIS satellite image (NASA) showing the Kimberley (Kimberley Basin + King Leopold Orogen + Halls Creek Orogen) and surrounding areas, including various places mentioned in the text (http://upload.wikimedia.org/wikipedia/commons/e/ed/Australia_satellite_plane.jpg). (b) Digital elevation model image (Shuttle Radar Topography Mission) showing the Kimberley and surrounding areas (http://dds.cr.usgs.gov/srtm/version2_1/SRTM3/Australia/). Red equates to areas of high elevation, and blue equates to areas of low elevation. The inset shows the location of the Kimberley (grey) in context with the Australian continent, including the Top End (TE) and the Pilbara (PIL).

We review the geophysical and climatic history of the Kimberley and surrounding areas to provide a much needed context within which to interpret emerging genetic data. In addition, we evaluate patterns from recently published studies of Kimberley taxa, and present hypotheses regarding how the distribution of genetic lineages may relate to major geophysical and biophysical units across the Kimberley, as well as broader biogeographical connections with neighbouring regions of the monsoon tropics and arid zone. With the rapid expansion of large-scale agricultural and industrial projects in the region, understanding the true biodiversity of the Kimberley, as well as the processes that generate and sustain it, is critical in an area increasingly recognized as an ancient centre of endemism.

DEFINING THE KIMBERLEY

The Kimberley is the general term for the northern portion of Western Australia, bound by the Timor Sea to the north, the Indian Ocean to the west, and onshore broadly by the Northern Territory state border to the east, and the Tanami and Great Sandy deserts to the south (Figs 1 & 2a). The precise region(s) encompassed by the name 'Kimberley' differs in extent and/or definition depending on the expertise and interests of the authors involved (see Ebach, 2012, for the history of different biogeographical regionalizations of Australia). For example, in geological terms, the Kimberley Block (and overlying plateau) is a broad structural division, distinct from the King Leopold and Halls Creek provinces (see below) to the south-west and south-east, respectively (Palfreyman, 1984) (Fig. 2a,b). However, these three geological entities are generally considered together as the 'Kimberley region' (Tyler *et al.*, 2012). In terms of bioregionalization [Interim Biogeographical Regionalisation for Australia (IBRA); Department of the Environment, 2012], the Kimberley is divided into the North Kimberley and Central Kimberley (Fig. 2c). These regions are defined by a number of major attributes, including climate, geology, land-form and vegetation (Thackway & Cresswell, 1995), and also correspond with the Gardner and Fitzgerald botanical districts of Beard & Sprenger (1984). Given that the boundaries of these botanical districts closely follow the geological boundary of the Kimberley Block and adjacent King Leopold and Halls Creek provinces, we define these three provinces collectively as the Kimberley. While some maps consider the Dampier Peninsula to be part of west Kimberley (i.e. Pain *et al.*, 2011), this region aligns to the Fitzroy soil-landscape province (Tille, 2006) (Fig. 2d) or the Dampier Botanical District, and is geologically and hydrologically distinct from the Kimberley (Lau *et al.*, 1987).

GEOLOGICAL SETTING

The geological history of the Kimberley is complex, largely relating to its ancient origins almost 2 billion years ago (Tyler *et al.*, 2012). The dominant geological entity of the region is the Kimberley Plateau (Fig. 2a), which comprises the uplands of the Prince Regent Plateau, Gibb Hills and the Karunjie Plateau. This region is formed mainly of generally flat-lying Palaeoproterozoic sediments of sandstone, siltstone, shale, mudstone and basalt (Tille, 2006) and is underlain by Proterozoic rocks of the Kimberley Basin (Fig. 2b). This ancient basin overlies the Precambrian Kimberley Block (also called the Kimberley Craton), which forms part of the North Australian Craton (Tyler *et al.*, 1999). Most of the rocks exposed on the Kimberley Plateau are sandstones of the Kimberley Group (Wende, 1997; Brocx & Semeniuk, 2011) and a broad east–west divide separates the geological units of the King Leopold Sandstone/Carson Volcanics to the west, and the Pentecost and Warton Sandstones to the east (Brocx & Semeniuk, 2011) (Fig. 2e). In terms of structural geology and its influence on land-form, most of the complexity in the Kimberley exists along the south-western and south-eastern margins, where intense deformation and associated fault activity, metamorphism and volcanic intrusions have produced zones of extensively folded rocks of the King Leopold Orogen to the south-west and the Halls Creek Orogen to the south-east. These tectonic belts (in places more than 100 km wide) comprise deformed and metamorphosed granites, quartzo-feldspathic volcanic rocks and schist (Griffin & Myers, 1988), and together form a 'V' shape around the central Kimberley Plateau (Fig. 2b). A concise summary of the Palaeoproterozoic origins of the Kimberley and the series of events leading to the formation of the various tectonic units of this region can be found in Tyler *et al.* (2012) and references therein. A fuller account of the geological terranes of the Kimberley region can be found in Wende (1997), Brocx & Semeniuk (2011) and Wilson (2013).

PHYSIOGRAPHY

Topography and mountain systems

The physiography of the Kimberley is topographically variable and largely determined by the underlying geological structure and lithology. Most of the Kimberley (the northern and central core) consists of a sandstone-capped plateau 40–600 m above sea level, reaching 854 m at the highest point (Boden & Given, 1995) (Fig. 1b). In the west, the plateau (also referred to as the Prince Regent Plateau; Wende, 1997) is a heavily dissected and rugged land surface of predominantly King Leopold Sandstone (Fig. 2e). Significant exposures of basalt also occur on the western plateau, comprising gently sloping terrain of lower local relief (Wende, 1997). In the east Kimberley Plateau (also referred to as the Karunjie Plateau; Wende, 1997), the uplands of mainly Pentecost Sandstone are less dissected, with numerous scarps and scattered mesas generally formed on gently dipping sedimentary rocks, with a clear dominance of sandstones over other lithologies (Wende, 1997). The topography associated with the King Leopold and Halls Creek orogens at the south-western and south-eastern peripheries of the Kimberley Plateau is very rugged, with intense folding and exposure of basement strata (McKenzie *et al.*, 2009). These regions, including the deformed margins either side of the tectonic belts, are characterized by spectacular steep-sided and parallel ridges of mountain systems, primarily the King Leopold Range in the south-west and the Durack Range in the south-east (Fig. 2a). In the rugged sandstone-dominated terrains, soil cover is generally thin, with an abundance of bedrock outcrops. In contrast, the soils developed on the volcanic plains are more extensive (Wende, 1997). A comprehensive and detailed review of the soil, geology and land-form descriptions for the provinces and composite landscape zones

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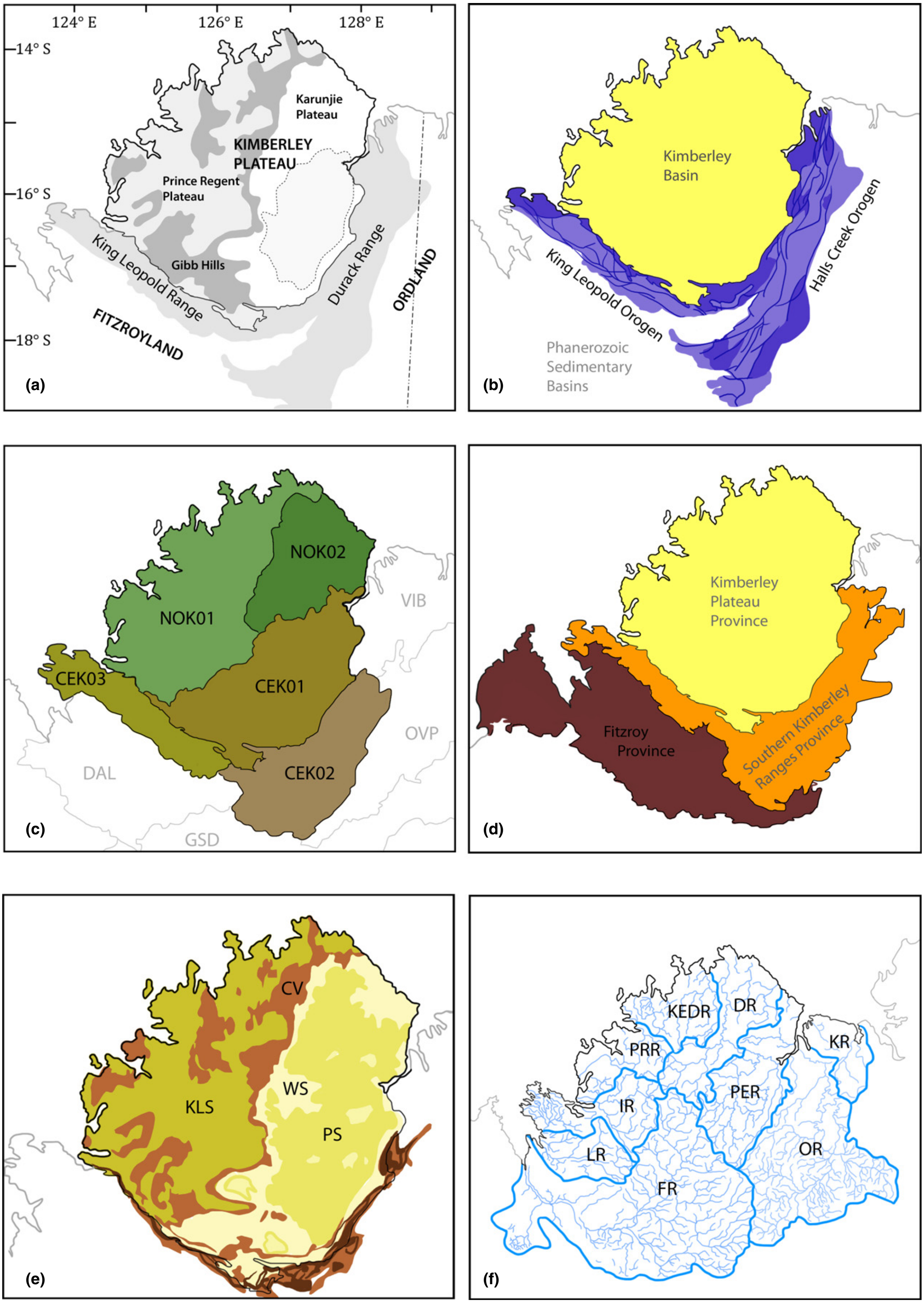
124° E
126° E
128° E
14° S
16° S
18° S
Karunjie Plateau
KIMBERLEY PLATEAU
Prince Regent Plateau
Gibb Hills
King Leopold Range
Durack Range
ORDLAND
FITZROYLAND
(a)
Kimberley Basin
Halls Creek Orogen
King Leopold Orogen
Phanerozoic Sedimentary Basins
(b)
NOK02
NOK01
VIB
CEK03
CEK01
OVP
DAL
CEK02
GSD
(c)
Kimberley Plateau Province
Fitzroy Province
Southern Kimberley Ranges Province
(d)
CV
WS
KLS
PS
(e)
KEDR
DR
PRR
KR
IR
PER
LR
OR
FR
(f)

Figure 2 (a) Physiographical divisions of the Kimberley showing the component features discussed in the text, adapted from Wende (1997). The dashed shape encloses the Durack River, Salmond River and Bindoola Creek basins. The vertical dotted line represents the state border between Western Australia and the Northern Territory. (b) Tectonic units of the Kimberley showing the component features discussed in the text, adapted from Tyler *et al.* (2012). Coloured regions denote what we consider to be the Kimberley region. Areas in purple represent the heavily metamorphosed and faulted King Leopold and Halls Creek orogens. These units relate to those we outline in biogeographical scenario 1. (c) The boundaries of the two Interim Biogeographical Regionalisation for Australia (IBRA) bioregions: North Kimberley (NOK) and Central Kimberley (CEK), along with their composite subregions (NOK01–02 and CEK01–03). These units relate to those we outline in biogeographical scenario 4. Surrounding bioregions are also shown: DAL, Dampierland; GSD, Great Sandy Desert; OVP, Ord Victoria Plain; VIB, Victoria Bonaparte. (d) Soil landscape provinces of the Kimberley, adapted from Tille (2006). (e) Simplified geological map showing various rock units of the Kimberley: PS, Petecost Sandstone; WS, Warton Sandstone; KLS, King Leopold Sandstone; CV, Carson Volcanics (adapted from Brocx & Semeniuk, 2011). These units relate to those we outline in biogeographical scenario 2. (f) Kimberley rivers and drainage basins: FR, Fitzroy River; LR, Lennard River; IR, Isdell River; PRR, Prince Regent River; KEDR, King Edward River; DR, Drysdale River; PER, Pentecost River; OR, Ord River; KR, Keep River (adapted from Geoscience Australia's river basin data, 1997 [http://www.bom.gov.au/water/about/image/basin-hi_grid.jpg], and Brocx & Semeniuk, 2011). These units relate to those we outline in biogeographical scenario 3.

within the Kimberley and surrounding regions of Western Australia can be found in Tille (2006).

Surface drainage divisions and river basins

Just like the surface topography of the Kimberley landscape, the configuration of drainage basins and their rivers, creeks and tributaries is largely controlled by lithology and the regional geology and structure. At the broadest scale, the Kimberley [along with Dampierland (Fig. 2c) and the western portion of the Top End] belongs to the Tanami–Timor Sea Coast Drainage Division, distinct from the North Western Plateau Division to the south and the Carpentaria Coast Division to the east (Bureau of Meteorology, 2012). Within the Kimberley, a number of river basins are partitioned across the landscape (Fig. 2f). The Kimberley Plateau encompasses the river basins of the Isdell, Prince Regent, King Edward, Drysdale and Pentecost, along with the northern section of the Fitzroy. The Ord and the Keep River basins flank the eastern margin. Much of the Kimberley is subject to tropical storms that are characterized by intense rainfall and high-magnitude floods, and many of the main rivers are sharply incised into the tablelands and ranges, forming deep and narrow valleys and gorges. In addition, extensive alluvial plains of the Fitzroy and Ord rivers fringe the dissected plateau (Mulcahy & Bettenay, 1972). Details of the drainage patterns are outlined in Wende (1997) and Brocx & Semeniuk (2011). The Government of Western Australia's Department of Water series has also produced a general guide for rivers of the Kimberley (Department of Water, 2008), providing information on the landscape and ecology of the 11 major rivers and their catchments.

VEGETATION AND BIOREGIONS

The richness of regional habitats and vegetation types often is a measure of geological diversity, and this is exemplified in the Kimberley. Extensive river systems and deeply excised gorges, mound springs, massive sandstones, razor-backed ridges and scarps, and alluvial plains all contribute to the heterogeneous nature of the Kimberley landscape. The availability of soil moisture is inherently linked to topography and soil type/texture, and in addition soil nutrient availability varies with topography, climate, underlying geology and soil age (Fayolle *et al.*, 2012). These complex and intertwined relationships can lead to a strong association between plant distributions and the spatial distribution of underlying geological substrates (Parker, 1991; Fayolle *et al.*, 2012).

At the regional scale, biogeographical patterns can be seen across the Kimberley that broadly reflect geological and physiographical units. Using information from a combination of geology, land-form, climate, vegetation and animal communities, the Kimberley has been divided into two geographically distinct bioregions (IBRA; Department of the Environment, 2012). The North Kimberley (NOK) is further divided into two subregions (NOK01 and NOK02), while the Central Kimberley (CEK) is divided into three subregions (CEK01–3) (Fig. 2c). The uplands of the Kimberley Plateau (NOK01, NOK02 and CEK01) generally support eucalyptus savanna woodlands with tall grasses and spinifex, with shallow stony and sandy soils characterizing the rugged sandstones, and deeper yellow sands and red loamy earths developed on the volcanic rocks (Tille, 2006). The hilly terrain of the King Leopold and Halls Creek orogens (CEK02 and CEK03) also supports eucalyptus savanna woodlands, with tall grasses and spinifex in the uplands areas, and low tree savanna over curly spinifex being the most common vegetation association elsewhere, along with minor communities of boab trees on alluvium and shale scarps (Wende, 1997).

Broad descriptions of the IBRA bioregions can be found in McKenzie *et al.* (2009). In addition, the soil landscapes (and associated vegetation) of the various landscape zones of the Kimberley have been mapped and described in detail by Tille (2006) (Fig. 2d). The bioregions surrounding the Kimberley (i.e. Dampierland to the south-west, the Ord Victoria Plain to the south, and the Victoria Bonaparte to the east; Fig. 2c) differ in climate, land-form, geology and soil, and therefore comprise different vegetation associations (McKenzie *et al.*, 2009). The southern Kimberley margin in particular denotes an obvious change in habitat, where sandplains and dunefields become common, and the floodplains of the

Fitzroy River support pindan shrublands of various acacias, with spinifex and tussock grasslands (Tille, 2006).

ARIDITY AND CHANGING CLIMATES

Global cooling of sea-surface temperatures during the Cenozoic has had a profound impact on atmospheric pressure systems and circulation, and on the Australian continent the effect of these changes has been the aridification of the continental interior (Frakes *et al.*, 1987). The climate during the Cenozoic in Australia is largely inferred using sedimentological and palaeontological data from southern marginal and inland basins (Fujioka & Chappell, 2010). A chronology of Cenozoic climate and aridification history in Australia can be found in Quilty (1994), Martin (2006), Byrne *et al.* (2008) and Fujioka & Chappell (2010). Of particular importance during this period, geological and palaeontological records from the middle Miocene (*c.* 20–10 Ma) provide evidence of the last time drainage and significant vegetation existed in central Australia (Quilty, 1994). Rapid global cooling in the late Miocene led to diminishing precipitation and increased aridification, with widespread arid conditions thought to be prevalent by the end of the late Miocene (Flower & Kennett, 1994; Fujioka & Chappell, 2010). A temporary return to warm and wet conditions is inferred in the early Pliocene (*c.* 5 Ma), associated with major sea-level rise and flooding of inland basins (Byrne *et al.*, 2008). The height of arid conditions in Australia appears to correlate with the transition from high-frequency, low-amplitude glaciations (every 40 kyr) that characterized the late Pliocene/early Pleistocene, to the low-frequency, high-amplitude glaciations (every 100 kyr) that became established in the middle Pleistocene (Huybers, 2007). This led to increasingly severe aridification and the development and subsequent expansion of the vast inland sand deserts (Fujioka *et al.*, 2009; McLaren & Wallace, 2010).

A large amount of uncertainty has surrounded the onshore palaeoclimate history of the north-west, largely because of the lack of study sites in the vicinity, the poor preservation potential of organic material (such as pollens and microbial lipids) in arid environments, and the difficulties in dating desert land-forms and obtaining chronologies beyond the late Quaternary (Fujioka & Chappell, 2011). However, our understanding of environmental change around the Last Glacial Maximum (LGM) at *c.* 25 ka, and the deglacial transition to Holocene interglacial climates, has improved substantially in recent years (Fitzsimmons *et al.*, 2013), particularly with the increase in study sites in north-western Australia (Reeves *et al.*, 2013a). Aridity in northern Australia is linked to a weakening of the monsoon, and evidence suggests that the effectiveness of the monsoon was greatly reduced during the LGM (Fitzsimmons *et al.*, 2013), creating significant aridity and causing lakes and rivers to dry, vegetation to become increasingly sparse, and sand dunes to become active (Hesse *et al.*, 2004). The drier conditions and cooler temperatures would have been particularly pronounced in lowland areas (Reeves *et al.*, 2013a), which in the Kimberley region would include areas around the Ord and Fitzroy River plains. Reactivation of the tropical monsoon is thought to have occurred *c.* 14–15 ka (Fitzsimmons *et al.*, 2013). A summary of the origin and evolution of the Australian summer monsoon in the context of the biogeography of the AMT can be found in Bowman *et al.* (2010). For a review on the nature of aridity and late Quaternary (< 400 ka to the present) climates of the Australian arid zone (including the monsoon tropics) see Hesse *et al.* (2004). In addition, syntheses of major climatic events over the last 40 kyr in arid and northern Australia can be found in Fitzsimmons *et al.* (2013) and Reeves *et al.* (2013a,b).

BIOTIC ELEMENTS OF THE KIMBERLEY

The Kimberley is one of a number of recognized centres of endemism on the Australian continent, based on congruent biogeographical patterns of fauna and flora (Cracraft, 1991; Boden & Given, 1995; Crisp *et al.*, 2001; Unmack, 2001; Slatyer *et al.*, 2007; González-Orozco *et al.*, 2011). The region supports more than 65 species of endemic fauna, including iconic species such as the scaly-tailed possum (*Wyulda squamicaudata*) and the black grasswren (*Amytornis housei*), and more than 300 species of endemic plant taxa (Carwardine *et al.*, 2011). However, the true biodiversity and endemicity of the Kimberley is likely to be vastly higher than our current understanding, as suggested by the numerous new endemic species described with every new venture into an unexplored area (Allen, 2004; Doughty & Anstis, 2007; Doughty *et al.*, 2009, 2012; Barrett & Barrett, 2011; Doughty, 2011; Köhler, 2011; Harrington *et al.*, 2012; Barrett, 2013; Maslin *et al.*, 2013). The genetic affinities of the Kimberley to adjacent areas of endemism in the AMT and the Northern Deserts has been tested in recent years using molecular data (e.g. Ladiges *et al.*, 2006; Fujita *et al.*, 2010; Melville *et al.*, 2011; Pepper *et al.*, 2011a; Smith *et al.*, 2011; Harrington *et al.*, 2012; Potter *et al.*, 2012a,b; Edwards *et al.*, 2013; Marin *et al.*, 2013; Catullo *et al.*, 2014a). These studies have revealed a complex set of relationships and show that, while the Kimberley generally harbours a deeply diverged and distinct biota, Kimberley taxa do not always share their closest relatives with a particular bioregion. At present, fine-scale genetic data across the Kimberley are limited; however, a picture of the biogeography of the Kimberley, largely in the context of the broader monsoon tropics, is beginning to emerge, with a number of similarities evident across taxonomic groups. These patterns and an explanation of the biogeographical barriers have been explored in Bowman *et al.* (2010), Eldridge *et al.* (2012) and Catullo *et al.* (2014a). In particular, these studies highlight distinct bioregions within the Kimberley (such as the Kimberley Plateau and lowlands of the Ord River basin) and demonstrate the importance of substrate type and physical environment for genetic diversification.

The evolutionary distinctiveness of Kimberley biota, as well as high levels of genetic diversity in taxa that inhabit the region, suggest that the uplands of the Kimberley may have

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provided refugia for mesic-adapted taxa during cycles of intense aridification (Byrne *et al.*, 2008; Pepper *et al.*, 2011a, b; Harrington *et al.*, 2012; Potter *et al.*, 2014). Refugia typically occur in regions with heterogeneous topography, and serve as centres of species persistence by retaining relative climatic stability during periods of unfavourable climate (Hewitt, 1999). While the refugial concept implicitly involves a reduction in population size (bottleneck) (Bennett & Provan, 2008), diversity can accumulate over time through repeated movement of populations both in and out of the refugium, as well as over elevational gradients. This results in increased genetic diversity in topographically complex regions, with taxa displaying deep coalescent histories (Hewitt, 1999). This pattern has already been detected in a number of Australian reptiles (Couper & Hoskin, 2008; Pepper *et al.*, 2011b), with species diversity in the rocky Pilbara region of Western Australia found to be exceptionally high (Pepper *et al.*, 2006, 2008, 2013). Similarly, the uplands of the Kimberley Plateau would provide a more thermally buffered environment than that of the surrounding lowlands, and species diversity is also expected to be high in this region. Indeed, the rugged and deeply dissected uplands in the high-rainfall area of north-west Kimberley has particularly high species diversity and levels of endemism compared with more topographically subdued parts of the region (Slatyer *et al.*, 2007; Doughty, 2011; González-Orozco *et al.*, 2011; Maslin *et al.*, 2013). Geological complexity is known to drive species diversification, particularly of plants. However, under the pressures of aridification, rainfall is likely to be the principal limiting factor, and moisture gradients related to topography and soil type/texture can strongly influence distributions (Parker, 1991). In the Kimberley, geological complexity is highest in the deformed zones of the King Leopold and Halls Creek orogens along the south-west and south-east margins. However, these regions receive significantly less annual rainfall (600 mm compared with 1200 mm in north-west Kimberley) and experience substantially greater annual evaporation (Wende, 1997). Nonetheless, the terrain is typically rugged, with valleys, gorges and cave systems creating microtopographical refuges that retain both moisture and soil. High diversity and endemism in camaenid snail fauna in the Napier and Oscar ranges in south-west Kimberley suggests that these regions also have provided centres of persistence during arid phases (Cameron, 1992), with stabilized linear dunes in nearby regions indicating past environments in which annual rainfall may have been as low as 200 mm (Cameron, 1992). Future surveys of these regions of the Kimberley are likely to identify high levels of species diversity and endemism in other biota.

FUTURE DIRECTIONS

The Kimberley is fast becoming recognized as a centre of mega-diversity and microendemism, with the distributions of taxa undoubtedly shaped by changing climates, landscape physiology and geological history. However, the current lack of fine-scale sampling across the Kimberley and surrounding bioregions has hindered the development of our understanding of the biogeographical history of the region. Regular flooding in the wet season means roads are closed for many months at a time, and much of the region is so topographically rugged it is only accessible by helicopter. In addition, large areas of the Kimberley are private lands managed by traditional Aboriginal owners and require special collecting permits and protocols administered by the Kimberley Land Council (KLC) on behalf of the traditional owners (Department of Families, Housing, Community Services & Indigenous Affairs, 2014) or direct negotiation with the traditional owners themselves.

Taxon sampling is often most adequate in areas around the Kimberley margin, including the north-west coast and places accessible from major roads in the south. However, a notable paucity of samples from the central and eastern portions of the Kimberley Plateau is evident (Moritz *et al.*, 2013). A number of recent phylogenetic studies of Kimberley reptiles have revealed extremely high levels of cryptic diversity unlike that seen anywhere else on the continent (Fujita *et al.*, 2010; Oliver *et al.*, 2010, 2012; Pepper *et al.*, 2011a; Moritz *et al.*, 2013). The presence of multiple lineages exhibiting greater than 10% mitochondrial (mt)DNA sequence divergence across small geographical scales further highlights the need for very fine-scale sampling in order to refine the locations of the geographical boundaries of genetic divergence. Integrating phylogenetic, phylogeographical and palaeoenvironmental data will provide further insights into the evolution of this unique monsoon biome, and help untangle its long and complex history with the arid zone. Below we outline a number of key elements that will be important in designing future studies of Kimberley biogeography.

Putative biogeographical breaks

Spatial heterogeneity within the Kimberley, along with the known landscape discontinuities with neighbouring regions, suggests numerous potential physiographical and habitat barriers that may have influenced the evolutionary history of the Kimberley biota. Based on the existing knowledge of geology and vegetation structure that is widely used in biodiversity assessment of the Kimberley, four simple biogeographical subdivisions (described below) are relevant for testing as data become available. If vicariance or local adaptation to these distinct regions within the Kimberley, and the subsequent diversification of taxa within each region, are responsible for the evolutionary diversification of Kimberley biota, then taxa should exhibit phylogeographical structuring concordant with major geophysical and/or biophysical units. Furthermore, adaptation to distinct habitats should act to reduce gene flow between habitat types, resulting in greater genetic divergence between, rather than within, habitat types.

1. *The major geological divide separating the Kimberley Plateau from the highly deformed zones of the King Leopold and Halls Creek orogens, and the separation of these orogenic belts* *from the Canning Basin to the south and the Ord Basin to the east (Fig. 2b).*

The contrasting geologies and landscapes of these different parts of the Kimberley suggest that there may also be accompanying differences in the population structure of taxa found across these regions. Indeed, evidence from a number of studies suggests that the lowlands of the Joseph Bonaparte Gulf and the Ord basin regions are associated with a break in distribution between many Kimberley and Top End taxa (e.g. Ford, 1978; Braby, 2008; Toon *et al.*, 2010; Potter *et al.*, 2012a; Catullo *et al.*, 2014a). In addition, the boundary of the southern Kimberley, where the King Leopold Ranges of the King Leopold Orogen meet the sandplains and dunes of the underlying Canning Basin, is also reflected in species distribution patterns (reviewed in Bowman *et al.*, 2010) and has been recovered using genetic analysis of *Uperoleia* toadlets (Catullo *et al.*, 2014a,b). More detailed sampling along the boundary of the Kimberley Plateau and the adjacent deformation zones, as well as between the deformation zones and adjacent bioregions, will provide a clearer picture of the influence of these landscape and habitat differences on evolutionary patterns.

2. *The geological east–west division within the Kimberley Plateau separating the eastern Pentecost and Warton Sandstones from the western King Leopold Sandstones and Carson Volcanics (Fig. 2e).*

Potter *et al.* (2012a) identified a major split between mitochondrial lineages of the rock wallaby (*Petrogale brachyotis*) (referred to as the East–West Kimberley Divide) and suggested that the large exposures of basalts along this central zone (and discontinuities in the sandstone ranges) may have restricted the dispersal of populations. Similarly, Smith *et al.* (2011) have reported a divergence between agamid lizard (*Diporiphora magna*) populations in this general region. The northern part of this divide is also reflected in the boundary between the IBRA subregions NOK01 and NOK02, and also separates the western Prince Regent Plateau and Gibb Hills from the eastern Karunjie Plateau (Wende, 1997) (Fig. 1a). More detailed sampling along this central zone is needed to clarify the distributions of genetic clades in order to assess further the effects of this putative biogeographical barrier.

3. *The major drainage divisions within the Kimberley and the geographical distributions of the major rivers (Fig. 2f).*

The structuring of genetic lineages by rivers and drainage divides is well documented in arid and semi-arid freshwater biota (e.g. Unmack, 2001; Murphy & Austin, 2004; Masci *et al.*, 2008). Based on endemism of freshwater fish fauna, Unmack (2001) divided the Kimberley Province into the West and East Kimberley (different to the geographical areas we describe here). In addition, the genetic results of Phillips *et al.* (2009) suggest that, in the Kimberley, the separation of river systems by plateaus rather than lowlands has resulted in higher genetic subdivision of the western rainbowfish (*Melanotaenia australis*). The phylogenetic structuring of terrestrial taxa by drainage divisions (Pepper *et al.*, 2011c) may relate to differences in moisture availability across the landscape, whereby dry ridgelines separating drainage divides may be the most arid parts of the landscape, which in hyperarid periods of the Pleistocene may have been substantially drier than today. Testing this hypothesis using fine-scale data of terrestrial organisms will shed more light on this intriguing association. In addition, the distribution of the major rivers in the Kimberley may create important geographical barriers to dispersal of terrestrial taxa. Rivers such as the Fitzroy in the south, the Drysdale in the north, and the Pentecost, Salmond and Chamberlain rivers to the east, are major landscape features of the Kimberley. The most recent period of stream incision and the development of deep valleys and gorges is postulated to have been in the late Tertiary, as the result of renewed uplift of the Kimberley Plateau (Wende, 1997). This timeframe is undoubtedly of relevance to studies of modern biota.

4. *The IBRA bioregions of the North Kimberley (NOK) and Central Kimberley (CEK), as well as their component subregions, delimited based on differences in vegetation communities and land-systems across the Kimberley (Fig. 2c).*

Some of these divisions correspond to those mentioned above. For example, the NOK01 and NOK02 boundary reflects the geological east–west division in the northern part of the plateau, and the CEK03 and CEK02 reflect the King Leopold and the Halls Creek orogens, respectively. The CEK01 subregion crosses a number of geological and hydrological domains (the east–west divide of scenario 2, and the major drainage division between the Fitzroy and the Pentecost of scenario 3) within the southern Kimberley. Molecular data sampled at a finer scale throughout CEK01 may reveal more complex patterns that reflect the geographical subdivisions within this subregion.

Assessing genetic patterns across disparate taxonomic groups

At present, fine-scale genetic studies across the Kimberley are rare. However, as phylogeographical studies of additional taxa accumulate, our understanding of the spatial genetic patterns and the extent to which they may have been shaped by common processes will improve. In particular, plant and burrowing invertebrate taxa, which have a more intrinsic association with geological and substrate variation, and are inherently less vagile, are likely to provide compelling insights into fine-scale patterns across the Kimberley. While the importance of the geological substrate in shaping plant distribution patterns is widely recognized (Parker, 1991; Kruckeberg, 2002; Fine *et al.*, 2005; Fayolle *et al.*, 2012), characteristics such as soil moisture gradients and texture are likely to play an important role in the persistence, distribution and diversification of other terrestrial biota, particularly in regions affected by aridification. Collecting data to quantify these environmental variables, along

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with fine-scale genetic sampling, will be a fruitful area for future study.

Harnessing the power of improved molecular sampling and geopalaeontological data

Incorporating information from multiple loci into estimates of population and species diversification is standard practice in contemporary phylogeographical and phylogenetic studies (Hickerson *et al.*, 2010). Until now, a major hindrance has been a lack of suitable nuclear and chloroplast DNA markers for intraspecific genetic studies, particularly of non-model organisms. The transition to next-generation sequencing (NGS) will bring about the ability to target hundreds to thousands of loci to assess genetic diversity, and evolutionary and population history. In particular, the growing pool of genomic reference species (Ekblom & Galindo, 2011) is rapidly making these types of approaches feasible for non-model taxa, and will facilitate a greater understanding of deep histories and speciation processes (McCormack *et al.*, 2013). Combining this kind of genomic data with detailed mtDNA coverage across the Kimberley, to capture fine-scale variation across landscape and habitat boundaries, will offer a powerful method to test hypotheses and understand better the biogeographical and evolutionary processes shaping species diversity in this region.

Importantly, advances in palaeoenvironmental climate reconstruction for north-western Australia will make a significant contribution to our understanding of Kimberley biogeography. Recent progress includes an increase in study sites in and adjacent to the Kimberley, improved chronological control, and a wide range of climate proxy data that incorporates deep-sea core, coral, speleothem, pollen, charcoal and terrestrial sediments (Reeves *et al.*, 2013a,b). Excellent reviews summarizing the palaeoenvironmental change in tropical Australasia since the last glaciation can be found in the Australasian-Intimate Project special volume of *Quaternary Science Reviews* (Reeves *et al.*, 2013c). In addition, the ability to date arid zone land-forms with improved precision will revolutionize studies of biogeography in xeric systems that are inherently problematic. Advances in luminescence methodologies for dating dunefields (Telfer & Hesse, 2013) and *in situ* cosmogenic nuclides to determine exposure ages and erosion rates (Fujioka *et al.*, 2009) allows much more accurate reconstruction of arid zone chronology, not only of the late Quaternary but also into the Miocene (Fujioka & Chappell, 2011). Combining this Earth sciences information with dated molecular genetic datasets will illuminate the links between desert landscapes, late Cenozoic climate change and speciation processes. In particular, a greater understanding of events, such as when the lowlands of the Ord Basin were hyperarid, or the timing of channel incision and peak periods of fluvial activity, would allow explicit vicariance hypotheses and biogeographical scenarios to be tested (Hickerson *et al.*, 2010; Crisp *et al.*, 2011).

Incorporating conservation planning

Information emerging from molecular studies of Kimberley taxa also has significant implications for diversity assessment and conservation management in a region heavily impacted by human development. The Kimberley has unique geological resources, endowed with oil, gas and rich mineral deposits of bauxite, lead, zinc, nickel and diamonds (Mudd, 2007; Tyler *et al.*, 2012). The adverse impacts of current and proposed mining operations, as well as additional environmental threats, including broad-scale agricultural industrialization, introduced domestic and feral herbivores, altered fire regimes, and the arrival of the cane toad (*Rhinella marina*) and other feral animals and plants, present an ever-increasing challenge for conserving biodiversity in the Kimberley (Carwardine *et al.*, 2011). Indeed, the Kimberley is listed as a National Biodiversity Hotspot (Department of the Environment, 2014) and a major Western Australia state government programme, *The Kimberley Science and Conservation Strategy* (Department of Parks & Wildlife, 2011), has been developed and implemented to conserve the region's natural and cultural values. However, biologists surveying the Kimberley are grappling with extreme levels of cryptic and undescribed diversity across many taxonomic groups. With so little known of the distribution and partitioning of genetic diversity across this remote region, we hope that this review will provide a framework for future research aimed at understanding the evolutionary and biogeographical processes that have shaped the floral and faunal composition of this biodiversity hotspot. Mounting evidence of the Kimberley as a historical and ancient centre of refugia warrants high priority from scientists, government, conservation agencies, indigenous landholders and local communities to protect and conserve its unique biota, and the processes responsible for generating and sustaining it.

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