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SYNTHESIS

Geodiversity and endemism in the iconic Australian Pilbara region: a review of landscape evolution and biotic response in an ancient refugium

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ABSTRACT

Aim We review the biogeography of the Pilbara, synthesize information on the geological and landscape history of this region and surrounds, and assess fine-scale genetic structure across multiple taxa to examine hypotheses concerning the distribution of genetic lineages. We use this to provide a baseline for future biological studies in an ancient area of endemism.

Location The Pilbara region, Western Australia.

Methods Literature is summarized, including the history of Pilbara landscapes and climate, and previous biogeographical work. We used mitochondrial DNA phylogenetic datasets of seven co-distributed gecko (diplodactyline and gekkonine) lineages to assess the monophyly of Pilbara lineages, and concordance with geological and habitat divisions.

Results The Pilbara harbours taxa genetically distinct from their non-Pilbara relatives, despite close geographical proximity of populations. This is emphasized at the eastern and southern margins of the Pilbara, where habitat gradients are pronounced. In contrast, the northern margin, where sandy substrates of the Pilbara meet the dunes of the northern deserts, exhibits little genetic differentiation. Within the Pilbara, diversification patterns are idiosyncratic and may reflect species-specific ecological differences. However, a repeated north/south partitioning of genetic diversity is evident across taxa. An additional emerging pattern is an east/west genetic division in the northern Pilbara, which may relate to major drainage divides and geological discontinuities associated with east and west Pilbara terrains.

Main conclusions The Pilbara is an area of exceptionally high biotic diversity and endemism. The broader biogeographical patterns revealed in our molecular analyses are consistent with those recently identified using species richness patterns of invertebrates. Future studies of additional taxa using multiple molecular markers will provide the means to test and refine the biogeographical hypotheses presented here. Understanding the biogeography of the Pilbara and the partitioning of genetic diversity across the ancient and heterogeneous landscape is of paramount importance in the face of rapidly expanding economic and developmental pressures.

Keywords

Arid zone, biogeography, desert, Diplodactylidae, gecko, Gekkonidae, geology, phylogeography, Pilbara, Western Australia.

INTRODUCTION

Australia is an old and weathered continent, with subdued topography and few major physical barriers. Since the early Eocene, global climatic shifts associated with polar ice-sheet growth and decay have dramatically changed the landscapes and biomes across the continent (Fujioka & Chappell, 2010). Tropical forests that dominated the central interior have long

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since disappeared, replaced by vast deserts of an arid regime established in the mid- to late Miocene, and reaching its peak during the glacial cycles of the Pleistocene (Flower & Kennett, 1994). Much like the spread of ice sheets across the Northern Hemisphere, desertification of the Australian interior would have resulted in significant geographical displacement of temperate-adapted taxa, and undoubtedly had a profound effect on the composition and diversification of the Australian biota (reviewed in Byrne *et al.*, 2008).

The Australian landmass is dominated by a relatively homogeneous central arid zone surrounded by a periphery of wetter biomes that often are separated by arid corridors. The historical fragmentation and isolation of these biomes had important evolutionary consequences, and recognition of a distinctive fauna and flora has led to the delimitation of a number of areas of endemism across Australia (e.g. Cracraft, 1991; Unmack, 2001). While fine-scale patterns of diversity and evolutionary history have been well studied in areas such as the rain forests of north-eastern Queensland (e.g. Bell *et al.*, 2010), and the temperate forests of south-western (e.g. Kay & Keogh, 2012) and south-eastern Australia (e.g. Chapple *et al.*, 2011), other regions, particularly arid parts of the continent, have received comparatively little attention (Byrne *et al.*, 2008).

The Pilbara region in remote north-western Western Australia is one of the oldest land surfaces on Earth (Pillans, 2007). Bound by the Indian Ocean to the west, vast sand deserts to the north and east, and highly metamorphosed rocks to the south, it has long been regarded as one of Australia's centres of biological endemism (Cracraft, 1991), and has a landscape so different from surrounding regions it can be identified from space (Fig. 1a). Situated in what is presently part of Australia's vast arid zone, the Pilbara has preserved in its unique and ancient sediments a rich and complex history: marine structures in the form of a 3.43 billion-year-old stromatolite reef (Allwood *et al.*, 2007); immense glacial scarring from the Permo-Carboniferous ice age (Gale, 1992); numerous palaeochannels reflecting past, wetter hydrological regimes (Macphail & Stone, 2004); and the richest concentration of indigenous rock art in the world (Environmental Protection Authority, 1995).

While the Pilbara is well known to harbour a unique biota (Cracraft, 1991; Unmack, 2001), comparatively little is known of the evolutionary history of the flora and fauna that inhabit the region. Inadequate fine-scale sampling in the remote area has limited phylogeography-based studies, and existing phylogenies typically use only a small number of Pilbara samples to place the broader Pilbara region in context with other areas of endemism. However, a recent comprehensive survey of biodiversity has collected and catalogued a wealth of biological material, along with detailed records of habitat and physical landscape across the entire region (McKenzie *et al.*, 2009). The enormous potential of these data for future work warrants an assessment of what is currently known about the Pilbara. Here we review the geophysical and climate history of the region to lay the foundations upon which hypotheses regarding the evolution of the unique Pilbara fauna can be outlined, refined and tested. We evaluate patterns emerging from previous studies of Pilbara biota, both in the broader context of the arid zone, and also how they relate to the distribution of major geo- and biophysical units across the Pilbara itself. We then assess alternative biogeographical scenarios using a molecular phylogenetic approach based on multiple gecko taxa, to shed light on the relationship between biotic diversification and the evolution of the Pilbara landscape.

Defining the Pilbara region

The precise region(s) encompassed by the name 'Pilbara' differ in extent and/or definition depending on the expertise and interests of the authors involved. For example, the 'Pilbara district' refers to the broad area generally known as the 'north-west', and lies north of latitude 25°00′ S and west of longitude 121°30′ E, including the coastline from Shark Bay to Eighty-Mile Beach (Beard, 1975). More specifically, the 'Pilbara biogeographical region' is defined by a number of major attributes including climate, geology, landform and vegetation (Thackway & Cresswell, 1995) and corresponds with the 'Fortescue botanical district' of the Eremaean Province (Beard, 1990). For geologists, the 'Pilbara craton' refers to the ovoid, plateaued and rugged region distinguished by surface outcrops of ancient rocks (see below). Given that the boundaries of the Pilbara biogeographical region and the Fortescue botanical district closely follow the geological boundary of the Pilbara craton, this particular region specifically will be referred to as the 'Pilbara', as differentiated from the broader 'Pilbara district'.

Geological setting

The Pilbara is a distinct geological entity, so different from surrounding regions that it is visible in satellite imagery. The region is defined by underlying sedimentary and igneous rocks of the Pilbara craton ranging up to 3.72 billion years (Ga) in age, and is overlain by one of the most ancient erosion surfaces on Earth (Geological Survey of Western Australia, 1990; Myers & Hocking, 1998). The craton can be divided into two parts; heavily weathered Archaean (3.72–2.85 Ga) granites and metamorphosed volcanic rocks ('greenstones') forming undulating hills and plains in the north, and stratigraphically overlying these rocks in the south is a group of younger (2.77 to 2.40 Ga) Archaean to Proterozoic basalts, and iron-rich sedimentary rocks deposited in the Hamersley Basin (Van Kranendonk *et al.*, 2002) (formally named the Mount Bruce supergroup; Trendall, 1995; Fig. 1b). A comprehensive summary of the different geological formations and their landform expression can be found in Beard's (1975) description of the Pilbara's natural regions. For more detailed information on the structure and tectonic development of the craton see Myers (1993), Trendall (1995) and Van Kranendonk *et al.* (2002).

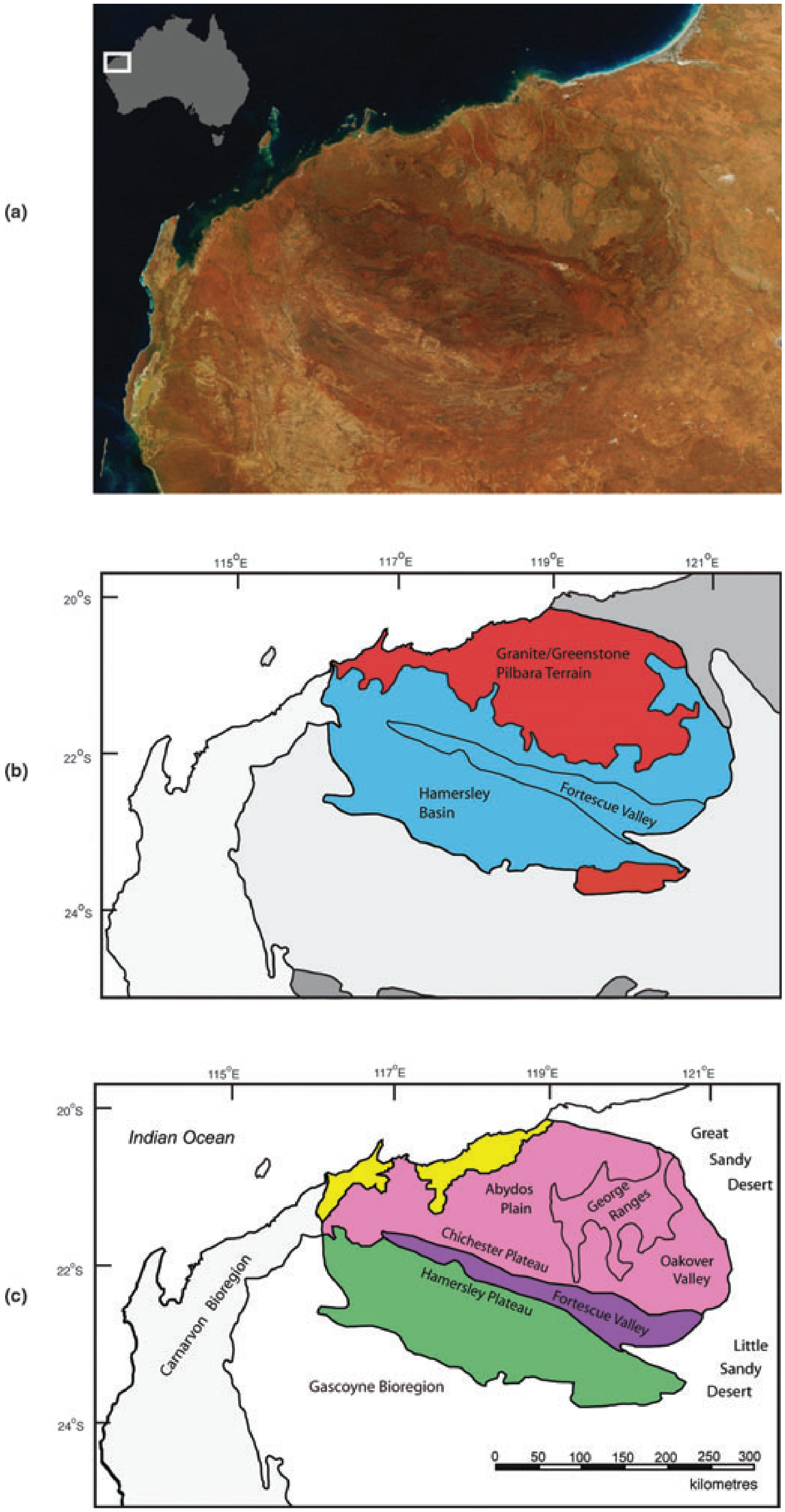

Figure 1 (a) True-color Aqua MODIS satellite image (NASA) showing the Pilbara craton and surrounds. (b) Simplified geological basement map of the Pilbara showing component features discussed in the text. The geology is adapted from the Australian Crustal Elements map (Shaw *et al.*, 1996). (c) Boundaries of the four IBRA (Interim Biogeographic Regionalisation for Australia) subregions – Chichester (pink), Hamersley (green), Fortescue Plains (purple) and Roebourne (yellow) – overlain with Beard's (1975) physiographical units. Surrounding the Pilbara are other bioregions discussed in the text.

Much younger terrains of unmetamorphosed sedimentary rocks surround the Pilbara craton to the north and east, and these are overlain by topographically homogeneous sand deserts that dominate the arid interior of Australia. To the south, however, the rocky terrains of the Pilbara extend into rocky landscapes of the geological entity known as the Capricorn Orogen (and associated Gascoyne Complex). This region is composed of folded, faulted and highly metamorphosed rocks, and reflects the ancient collision and amalgamation of the Pilbara and adjacent Yilgarn craton (Myers, 1993).

Physiography

The Pilbara landscape is topographically variable and largely determined by underlying geological structures. The rugged ranges of the Pilbara comprise ridges and mountains that generally are associated with the rocks of the Hamersley Basin in the southern part of the craton. The most noticeable topographical elements of this region are the plateaus of the iron-rich Hamersley and basaltic Chichester Ranges that traverse the craton roughly east–west, and reach elevations of around 900 (and up to 1250) and 600 m a.s.l., respectively. In addition, the Fortescue River valley dissects the Hamersley Basin east to west, and consists of alluvial plains in the east, and deeply incised gorge systems in the central and western parts of the drainage. This formidable land feature not only divides the rocky landscapes on either side of the river valley, but provides a distinct habitat itself based on the sand/clay/silt substrates of the valley floor (McKenzie *et al.*, 2009). The northern part of the craton is much more topographically subdued, due to the highly weathered nature of the granite/greenstone terrains. This region is characterized by low hills and alluvial plains, which are traversed by numerous flood channels of the Oakover, DeGrey, Coonan, Shaw, Yule and Turner rivers (see Reeves *et al.*, 2007). The northern part of the craton can be divided into a number of distinct landforms represented in the 'natural regions' of Beard (1975), and these appear to correlate with distinct structural elements of the underlying geology (see Van Kranendonk *et al.*, 2006; and Allwood *et al.*, 2007). For example, there is a strong east–west division separating the Abydos Plain of Beard (1975) (correlating with the underlying De Grey Superbasin; Van Kranendonk *et al.*, 2006), and the Oakover Valley (and associated underlying East Pilbara Terrain). A gently sloping coastal plain has developed along the north-western Pilbara. For a detailed review of the physiography of the region, see Beard (1975) and Johnson (2004).

Although geologically distinct, some of the landscapes surrounding the Pilbara craton are similar to those found within the Pilbara. For example, sandy areas of the coastal plain resemble those of the adjacent Great Sandy and Little Sandy deserts, and also the Carnarvon coastal plain to the south of the craton. Furthermore, rocky substrates like those that characterize the southern Pilbara are also found throughout the Capricorn Orogen to the south, although here they are less extensive than within the craton.

Vegetation and bioregions

The richness of regional habitats and vegetation types often is a measure of geological diversity, and this is exemplified in the Pilbara. The extensive river systems and deeply excised gorges, aquifer-fed springs and wetlands, flat coastal plains and razor-backed ridges all contribute to the heterogeneous nature of the Pilbara landscape that, as mentioned above, is shaped to a large degree by underlying geological substrate. At the regional scale, biogeographical patterns can be seen across the Pilbara that broadly reflect the geological and physiographical units of the craton. Using information from a combination of geology, landform, climate, vegetation and animal communities, the Pilbara has been divided into four geographically distinct subregions [Interim Biogeographic Regionalisation for Australia (IBRA); Environment Australia, 2008] (Fig. 1c). The Hamersley subregion comprises the southernmost portion of the Hamersley Basin and encompasses the Hamersley Range. This region is characterized by skeletal soils developed on the iron-rich sedimentary rocks, and generally consists of spinifex grassland with mulga and snappy gum (tree steppe) (Beard, 1975). The Chichester subregion encompasses the granite/greenstone terrains of the northern craton but also includes the Chichester Plateau of the Hamersley Basin. Beard (1975) defined a number of subdivisions within the northern craton (see above), reflecting substantial landscape heterogeneity across this broad area. While the broader Chichester subregion is characterized by deeply weathered regolith and is dominated by spinifex (*Triodia* spp.) grassland with irregularly scattered shrubs (shrub steppe), the Chichester Plateau (bordering the northern side of the Fortescue Valley) more closely reflects the soil landscape and vegetation of the Hamersley Plateau (Tille, 2006). The Fortescue Plains subregion is delineated by the Fortescue River valley, which cuts through the sedimentary rocks of the Hamersley Basin. This region consists of salt marshes, mulga-bunch and short grass communities, with eucalyptus (*Eucalyptus* spp.) woodlands along the permanent springs. Finally, the Roebourne subregion encompasses the mudflats and low dunes of the coastal plain and is composed largely of alluvial and aeolian sediments, often with a cover of grasses and soft spinifex. Detailed descriptions of the subregions can be found in McKenzie *et al.* (2009) and are summarized in Guthrie *et al.* (2010). In addition, the soil landscapes of the Pilbara have been mapped and described in detail by Tille (2006).

The IBRA bioregions surrounding the Pilbara (i.e. Carnarvon to the south-west, Gascoyne to the south, and the Great Sandy and Little Sandy deserts to the east) differ in climate, landform, geology and soil, and therefore comprise different vegetation associations (Beard, 1969, 1975, 1990).

A stable refuge amidst changing climates

The landscapes of the Pilbara have been subaerially exposed since the Pre-Cambrian (> 540 Ma) (Pillans, 2007). During this time, vastly different climatic regimes have come and gone, and the region has been greatly modified, with extensive glaciers during the Permo-Carboniferous ice age carving valleys into the Pilbara plateau, and aiding the erosion of more than 700 m from the mountains (Taylor, 1994). During its more recent history, and the timeframe of relevance to studies of the modern biota, vast changes have occurred across areas surrounding the Pilbara. However, largely due to its topographical heterogeneity and proximity to the coast, the Pilbara (or more likely, localized regions within the Pilbara) would have sustained more thermally buffered environments compared to the lower-lying, homogeneous landscapes that comprise much of the arid zone (Macphail & Stone, 2004; Byrne *et al.*, 2008), allowing the persistence of mesic-adapted taxa (Oliver *et al.*, 2010; Pepper *et al.*, 2011a,b,c).

Excellent descriptions of the palaeohistory of landforms in Australia, including the Pilbara, can be found in Wasson (1982) and Taylor (1994), therefore below we present a brief summary of events that have contributed to the isolation of the Pilbara in more recent times. The mid-Cretaceous (*c.* 100 Ma) saw the chain of basins to the east of the Pilbara inundated by shallow oceans, separating the Archaean rocks of the Pilbara craton from their exposures in the Kimberley and central Australia. Sea-level transgressions and regressions during the Cretaceous saw the basins oscillate between non-marine and open-water conditions, and would have had a significant impact on spatial and habitat diversity in the area (Wasson, 1982). Changes in sea level along the continental shelf also periodically connected offshore islands such as those in the Dampier Archipelago, most recently during the Last Glacial Maximum (Yokoyama *et al.*, 2001). As well as encompassing physical changes to the environment, global oscillations in sea level reflect large-scale variations in climate regimes. Global cooling of sea surface temperatures during the Cenozoic had a profound impact on atmospheric pressure systems and circulation, and on the Australian continent the effect of these changes was the aridification of the continental interior (Frakes *et al.*, 1987). Climate during the Cenozoic in Australia is largely inferred using sedimentological and palaeontological data from southern marginal and inland basins (Fujioka & Chappell, 2010), and a large amount of uncertainty surrounds the onshore palaeoclimate history of the north-west. 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 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 increasing aridification, with widespread arid conditions thought to be prevalent by the late Miocene (Flower & Kennett, 1994; Fujioka & Chappell, 2010). A temporary return to warm and wet conditions is inferred in the early Pliocene, associated with major sea level rise and basin flooding (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 of the vast inland sand deserts (Fujioka *et al.*, 2009; McLaren & Wallace, 2010). While a lack of chronological data from Western Australia precludes an accurate age estimate of the Great Sandy, Gibson and Great Victoria deserts, dated playas and dunes in central Australia indicate they probably formed < 1 Ma (Fujioka *et al.*, 2009; Fujioka & Chappell, 2010). The recent development of these vast sand deserts entirely isolated the Pilbara from rocky exposures in central and northern Australia with hundreds of kilometres of dune fields and sand plains.

Biotic elements of the Pilbara

The antiquity and complex geological and climatic history of the Pilbara and surrounds has undoubtedly had a profound influence on the evolutionary history of the flora and fauna that inhabit these regions. Indeed, the distinctive biota has led to recognition of the Pilbara as one of Australia's regional centres of endemism (Cracraft, 1991; Unmack, 2001; Ladiges *et al.*, 2006). A number of studies have attempted to put the Pilbara in context with other areas of endemism, in particular that of Cracraft (1991), who used cladistic biogeographical analyses of a number of vertebrate groups to conclude that, although the precise affinity of the Pilbara to other regions of endemism was uncertain, a close association with the western and eastern deserts was evident. This relationship has been supported by a number of subsequent molecular studies on both plants and animals (Edwards, 2003; Ladiges *et al.*, 2006; Pepper *et al.*, 2006, 2011a,b; Oliver *et al.*, 2010; Catullo *et al.*, 2011; Melville *et al.*, 2011).

While detailed molecular studies of Pilbara biota are in their infancy, the Pilbara appears to be a region of high species diversity, due in part to its long history as a mesic refugium (Oliver *et al.*, 2010; Pepper *et al.*, 2011a,c). In particular, a growing literature is emerging on subterranean invertebrate fauna (Humphreys, 2001; Finston & Johnson, 2004; Eberhard *et al.*, 2005; Karanovic, 2007; Harvey *et al.*, 2008; Finston *et al.*, 2009). These studies suggest that vicariant isolation and divergence due to surface aridification, coupled with underlying geological complexity, have generated astonishing levels of extremely localized diversity, highlighting the Pilbara as a region of global significance (Eberhard *et al.*, 2005). High diversity has also been found in snails (Johnson *et al.*, 2006), and preliminary results from the Pilbara Biodiversity Survey indicate a substantial undescribed flora and terrestrial invertebrate fauna. For example, Guthrie *et al.* (2010) reports that 68% of beetles collected could not be assigned to recognized species, and Volschenk *et al.* (2010) could not classify 83% of scorpion morphotypes to described species.

The Pilbara is known to harbour a suite of endemic vertebrates (How & Cooper, 2002; How & Dell, 2004; Gibson & McKenzie, 2009; Doughty *et al.*, 2011a), with studies of widespread arid zone taxa typically revealing morphologically and genetically divergent Pilbara populations (e.g. Baverstock *et al.*, 1983; Painter *et al.*, 1995; Aplin & Donnellan, 1999; Blacket *et al.*, 2000; Pepper *et al.*, 2006; Ford & Johnson, 2007; Oliver *et al.*, 2010; Doughty & Oliver, 2011; Melville *et al.*, 2011). In addition, emerging results from fine-scale molecular studies of terrestrial vertebrates suggest substantial cryptic diversity and complex genetic patterns across the Pilbara landscape (Pepper *et al.*, 2008, 2011a; Shoo *et al.*, 2008; Doughty *et al.*, 2010, 2011b; Catullo *et al.*, 2011).

Biogeographical hypotheses

Spatial heterogeneity within the Pilbara, along with the extensive surrounding deserts, suggests numerous potential physiographical and habitat barriers that may have influenced the evolutionary history of the terrestrial biota. Certainly species richness patterns of both invertebrates and vertebrate fauna have shown a strong correlation with surface type (Durrant *et al.*, 2010; Guthrie *et al.*, 2010; Doughty *et al.*, 2011a). Using comparative, independent datasets of multiple taxa distributed both within and outside the Pilbara, it is possible to assess fine-scale patterns of genetic structuring in relation to the distribution of major landscape types and geodiversity, and in doing so identify potential barriers to dispersal and other abiotic factors associated with diversification.

Hypothesis 1. *Pilbara populations are monophyletic with respect to populations/species outside the Pilbara.*

The vastly dissimilar climate and landforms surrounding the Pilbara are likely to have isolated habitat-specialized fauna following the development of the deserts. For example, the distributions of widespread saxicolous taxa across western, northern and central Australia are often disjunct, reflecting the presence of vast, intervening sand dunes (Ford & Johnson, 2007; Shoo *et al.*, 2008; Oliver *et al.*, 2010; Doughty *et al.*, 2011b; Pepper *et al.*, 2011c). However, arid-adapted taxa distributed throughout the deserts as well as in the Pilbara also exhibit genetic differentiation across the Pilbara margin (Pepper *et al.*, 2006). This suggests potential vicariant isolation, or alternatively diversification driven by habitat specialization (Pianka, 1969; James & Shine, 2000). Sampling other widespread taxa that occur both in the Pilbara and surrounds provides the opportunity to assess whether habitat specificity and/or vicariance has played a role in the differentiation of Pilbara biota on a larger scale. Because some areas of the Pilbara comprise habitats similar to those outside the craton (i.e. the sands of the Pilbara Roebourne coastal plain and those of the adjacent Great Sandy Desert, or the rocks of the Pilbara Hamersley Basin and those of the Gascoyne Bioregion) we might expect taxa with specific habitat preferences to span both regions. However, if multiple taxa exhibit genetic breaks concordant with the boundary of the Pilbara craton irrespective of these largely continuous habitats, it is possible that vicariant isolation and subsequent diversification in response to a presently absent physical barrier (such as ephemeral river systems) were responsible.

Hypothesis 2. *The phylogeographical structure of populations/species within the Pilbara reflects the distribution of recognized geographical subdivisions.*

Little is known of intraspecific genetic structure of Pilbara vertebrates. Variations in geology, topography and associated habitats are, to varying degrees depending on the taxon, expected to influence the partitioning of genetic diversity across the Pilbara. We assess phylogenetic concordance to broad geographical subdivisions within the Pilbara in order to lay foundations for future studies. Based on existing knowledge of geology and vegetation structure that is widely used in biodiversity assessment of the Pilbara, three simple biogeographical subdivisions are relevant:

Scenario A. The major geological divide separating the northern granite/greenstone terrain (Fig. 1b, red) from the southern Hamersley Basin (Fig. 1b, blue). The results of Pepper *et al.* (2008) suggested a possible correlation between genetic patterns and underlying geological substrate.

Scenario B. The four IBRA subregions – Chichester (Fig. 1c, pink), Hamersley (Fig. 1c, green), Roebourne (Fig. 1c, yellow) and Fortescue (Fig. 1c, purple) – delimited based on differences in vegetation communities and landsystems across the Pilbara. Importantly, the Chichester Plateau (comprising a major mountain range in the Pilbara), aligned *geologically* with the southern geological unit of the Hamersley Basin (see scenario A), is considered here as part of the broad northern Chichester subregion in the IBRA regionalization. A number of recent studies have examined invertebrate species compositional patterns in light of these subregions (Durrant *et al.*, 2010; Guthrie *et al.*, 2010; Pinder *et al.*, 2010), as well as vertebrates (Gibson & McKenzie, 2009; Doughty *et al.*, 2011a).

Scenario C. Implicit in the above scenario B is the subdivision north and south of the Fortescue River valley. The Fortescue Valley is known to harbour a unique assemblage of invertebrate taxa (e.g. Durrant *et al.*, 2010); however, there is potential for this substantial topographical discontinuity to act as a barrier to dispersal for small terrestrial vertebrates. In this case, we might expect to see stronger genetic divergence between taxa on either side of the central valley where there is a more pronounced topographical divide, whereas the flat and marshy headwaters in the east, and estuarine areas in the west, with their associated poorly defined channels, may facilitate movement of organisms into adjacent regions.

If local adaptation to distinct regions within the Pilbara, and the subsequent diversification of taxa within each region (scenarios A or B), or vicariance (scenario C) are responsible for the diversification of Pilbara 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.

To assess the above predictions, we build on previous results with new and published molecular datasets to generate phylogenies for seven co-distributed gecko lineages. Specifically, we use this genetic information to address the following questions.

1. Do taxa exhibit genetically differentiated populations across the Pilbara craton boundary?

2. Within the Pilbara, is genetic diversity concordant with previously hypothesized regions (A, B or C, above), and is there congruence across taxa?

The timing of our study is significant. The Pilbara also has unique geological resources, endowed with rich deposits of minerals, oil and gas, and is the location for some of the world's largest mining operations for manganese and iron ore. The large-scale exploitation of these natural resources presents an ever-increasing challenge for conserving biodiversity in the region (Lloyd *et al.*, 2002), and has been publicly acknowledged for short-range endemic invertebrate fauna in particular (Majer, 2009; Tomlinson & Boulton, 2010). With so little known of the distribution and partitioning of genetic diversity of low-vagility terrestrial vertebrates across the region, the potential for short-range endemism, particularly of habitat specialists, requires immediate attention.

MATERIALS AND METHODS

Taxonomic sampling and DNA methods

We chose gecko taxa representing both Pilbara endemics and more widespread species to assess the Pilbara in a broader biogeographical context. *Diplodactylus conspicillatus* Lucas and Frost, 1897, is a habitat generalist widespread through arid and tropical northern Australia. Previous genetic work on this species in other parts of its range has identified multiple cryptic species (Oliver *et al.*, 2009). *Lucasium stenodactylum* Boulenger, 1896, is also widespread throughout the arid zone, with substantial genetic diversity across its distribution (Pepper *et al.*, 2006, 2008). *Gehyra pilbara* Mitchell, 1965, is distributed throughout the north-western and central arid zone and inhabits termite mounds, while *Gehyra punctata* Fry, 1914, is a rock-adapted specialist distributed throughout rocky hills of central and northern Western Australia (Wilson & Swan, 2003). The genus *Gehyra* is known to represent a taxonomic predicament, with substantial cryptic diversity and a high misidentification rate hampering efforts to resolve the species complexes (C. Moritz, The Australian National University, Canberra, and M. Sistrom, Yale University, New Haven, pers. comm.). *Heteronotia spelea* Kluge, 1963, *Lucasium wombeyi* Storr, 1978, *Diplodactylus savagei* Kluge, 1963, and *Diplodactylus galaxias* Doughty, Pepper and Keogh, 2010, are rock/stony-soil specialists and are endemic to the Pilbara (see Pepper *et al.*, 2011c for a detailed assessment of *H. spelea,* and Doughty *et al.*, 2010 for *D. galaxias*).

We use previously published material for *L. stenodactylum* (Pepper *et al.*, 2006, 2008), *D. savagei* and its sister taxon *D. galaxias* (Doughty *et al.*, 2010), and *H. spelea* (Pepper *et al.*, 2011c). Our sampling for *D. conspicillatus*, *L. wombeyi*, *G. pilbara* and *G. punctata* represents new material. For all new samples we followed the protocol of Pepper *et al.* (2006), targeting a *c.* 1200 base pair fragment of the mitochondrial gene NADH dehydrogenase subunit II (*ND2*). Sequence data were edited using Sequencher 4.1 (Gene Codes Corporation, Ann Arbor, MI, USA). Alignment of sequences was performed automatically using the software muscle 3.6 (Edgar, 2004), then refined by eye in Se-Al (Rambaut, 1996). Protein-coding regions were translated into amino acid sequences using the vertebrate mitochondrial genetic code and were checked for internal stop codons and frame-shift mutations. Museum and GenBank accession numbers, and collection localities, are given in Appendix S1 in Supporting Information.

Outgroup selection

For the diplodactyline geckos, appropriate outgroups were chosen based on higher-level phylogenetic studies of Pepper *et al.* (2006) and Oliver *et al.* (2007). *Diplodactylus klugei*, *D. pulcher* and *D. savagei* were used as outgroups for *D. conspicillatus. Diplodactylus klugei*, *D. pulcher* and *D. conspicillatus* were used as outgroups for *D. savagei* and *D. galaxias*. *Lucasium squarrosum* and *L. stenodactylum* were used as outgroups for *L. wombeyi*. *Lucasium squarrosum* and *L. wombeyi* were used as outgroups for *L. stenodactylum*. For the gekkonine geckos *G. pilbara* and *G. punctata*, *Cyrtodactylus marmoratus* was used as the outgroup. For *H. spelea*, *Dixonius vietnamensis* and the other members of the genus *Heteronotia* (*H. binoei* and *H. planiceps*; Pepper *et al.*, 2011c) were used as outgroups.

Phylogenetic analyses

Each edited alignment comprised 1053 characters. Maximum likelihood (ML) estimation of the phylogeny of each dataset was performed in RAxML 7.0.4 (Stamatakis, 2006). The data were partitioned by codon position, and analysed under the generalized time reversible model of sequence evolution (variable base frequencies, and a symmetrical substitution matrix) and with across site rate variation modelled to a Gamma distribution (GTR+Γ). Ten runs with different starting trees were performed, and the most likely tree chosen from this set. Support values were estimated from 100 bootstrap replicates using the '–f i' search function. We chose to combine our datasets for *G. pilbara* and *G. punctata* because initial analyses suggested a high degree of paraphyly.

RESULTS AND DISCUSSION

Our phylogenies are characterized by generally well-supported clades near the tips of the trees (Fig. 2; Appendix S2: Figs S1–

S5), and for *L. stenodactylum* and *H. spelea* this is supported by a number of additional nuclear DNA loci (Pepper *et al.*, 2006, 2011c). For each newly sequenced taxon, substantial intraspecific diversity was uncovered that in many instances is equal to or exceeds species-level differences in closely related taxa (Oliver *et al.*, 2009). This is particularly evident in the two *Gehyra* species where deep genetic structure and paraphyly of currently recognized species is clearly indicative of multiple species complexes. The taxonomic assessment of the taxa represented here is beyond the scope of this paper, (and in the case of *Gehyra* is being prepared elsewhere; P. Doughty *et al.*, in prep.), and for the purpose of identifying broad patterns is largely irrelevant. We therefore assign the mitochondrial DNA (mtDNA) genetic groups to geographical regions independent of putative species boundaries.

Do taxa exhibit genetically differentiated populations across the Pilbara craton boundary?

All taxa we examined have populations distributed outside the Pilbara craton, including the Pilbara 'endemics' *L. wombeyi*, *D. savagei* and *H. spelea*, which also comprise samples from the Gascoyne bioregion to the south of the craton (Fig. 1c).

The distributions of saxicolous taxa are limited by the sand dunes at the northern and eastern craton margin. However, rocky substrates are continuous into the Gascoyne. With the exception of *L. wombeyi* (where no differentiation between Pilbara and Gascoyne individuals is apparent; see Fig. 2), our results show that *Gehyra* Clade 1, *H. spelea* and *H. savagei* exhibit genetically differentiated populations along the southern craton margin at the boundary with the Gascoyne bioregion (Appendix S2: Figs S1–S3). For the not strictly saxicolous taxa, including *Gehyra* Clade 2 and *D. conspicillatus*, there is still a genetic distinction between populations within versus outside the craton margin (Appendix S2: Figs S1 & S4). In a study of the gecko *L. stenodactylum*, a widespread species complex from the arid zone, Pepper *et al.* (2008) also found that within the Pilbara 'group' of *L. stenodactylum*, populations south and east of the Pilbara craton were genetically divergent across the craton boundary, despite extremely close geographical proximity to individuals within the craton. Similarly, a recent revision of the spiny-tailed skinks *Egernia* Gray, 1839, also reports the genetic distinctiveness of taxa along the southern Pilbara margin (Doughty *et al.*, 2011b).

This pattern, repeated across taxa, suggests some level of habitat specialization and/or climate or landscape-induced

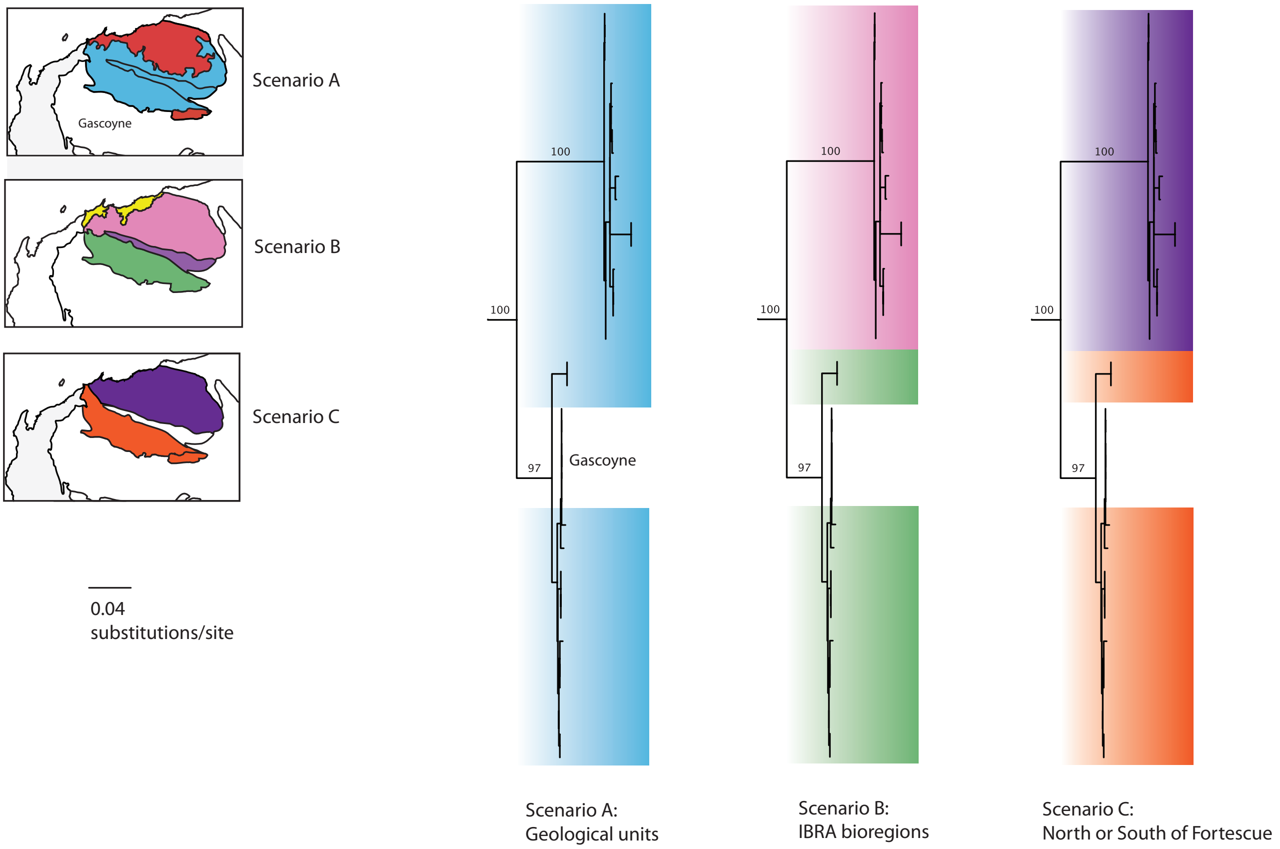

Figure 2 Phylogenetic results of *Lucasium wombeyi* based on a maximum likelihood analysis in RAxML. Only individuals found within the boundaries of the Pilbara craton are coloured on the trees. Clades are colour-coded according to their distribution in relation to three biogeographical scenarios (A to C). For the phylogenetic results of other taxa in this study see Appendix S2: Figs S1–S5.

vicariance. Certainly, major differences in vegetation, topography and substrate exist in the Carnarvon and Gascoyne bioregions (Beard, 1975; Tille, 2006; Environment Australia, 2008). Similarly, the topographical, substrate and vegetation differences between the eastern Pilbara craton boundary and the adjacent dunes of the Great Sandy and Little Sandy deserts are also pronounced in this area.

In addition to the habitat gradient across the craton boundary, hydrological divisions and the distribution of river systems are likely to have influenced the evolution of modern taxa. For example the north, east and southern margins of the craton are traversed by river channels and tributaries of the De Grey and Ashburton rivers. Despite the often ephemeral existence of these arid zone rivers, the size of their channels and floodplains appear as large scars across the landscape on satellite imagery (GOOGLE EARTH), indicating their immense presence under historically wetter climates (Martin, 2006), and would have periodically isolated the Pilbara from surrounding regions. The distinctiveness of taxa from the Gascoyne may be explained by the distribution of the Ashburton River, located just south of the Pilbara craton, in the northern Gascoyne. Areas to the south of the Ashburton River (including the majority of the Gascoyne bioregion) are located in a separate drainage division (see Pinder *et al.*, 2010).

Within the Pilbara, does genetic diversity correlate with previously hypothesized biogeographical regions (scenarios A, B or C, above), and is there congruence across taxa?

We found a substantial amount of genetic diversity within populations of *D. conspicillatus*, *G. pilbara*, *G. punctata* and *L. wombeyi* in the Pilbara. When added to what is already known about genetic patterns in *H. spelea*, *D. savagei* and *L. stenodactylum*, it is clear the Pilbara has had a dynamic evolutionary history, resulting in high species diversity and endemism. Because little is known about the partitioning of genetic diversity across the Pilbara for terrestrial vertebrates, we assessed genetic patterns against three simple biogeographical scenarios based on the delimitation of the Pilbara into sub-bioregions, and also the distribution of major geological units and landforms (Fig. 2, Appendix S2: Figs S1–S5).

Scenario A. The major geological divide separating the northern granite/greenstone terrain from the southern Hamersley Basin

Some taxon patterns suggest a broad distinction between these two geological domains. This is most obvious in the phylogenies for *D. conspicillatus* Clade 2 and *L. stenodactylum* (Appendix S2: Figs S4–S5). *Lucasium wombeyi*, *H. spelea* and *D. savagei* are almost entirely restricted in their range by the distribution of rocks of the Hamersley Basin (Fig. 2; Appendix S2: Figs S2 & S3). Examination of patterns in other taxa reveals this same geological unit harbours the majority of genetic diversity. In *Gehyra* in particular, many of the genetic lineages found in this region comprise numerous geographically overlapping clades, and may reflect narrow range endemism.

Scenario B. The four IBRA biogeographical subregions

Depending on the taxon, and at what level of the genealogical hierarchy patterns are examined, there are varying degrees of support for the IBRA subregions. For example, the phylogenies of *L. wombeyi*, *H. spelea* and *D. savagei* broadly reflect the Hamersley, Chichester and Roebourne subregions (Fig. 2; Appendix S2: Figs S2 & S3), while *L. stenodactylum* shows no clear pattern (Appendix S2: Fig. S5). Only two of the taxa examined comprise individuals collected from within the Fortescue subregion. Our phylogeny for *D. conspicillatus* revealed a highly divergent Fortescue clade distributed in the wider, eastern extent of the valley (Appendix S2: Fig. S4). In contrast, individuals of *L. stenodactylum* from throughout the Fortescue subregion show no genetic association (Appendix S2: Fig. S5). There appears to be a close association between the two northern subregions, the Roebourne and the Chichester. In particular, *D. conspicillatus*, *Gehyra* Clade 1 and *L. stenodactylum* each comprise clades confined to the Roebourne and western Chichester, while *D. savagei* and *L. wombeyi* have clades restricted to the eastern Chichester.

Scenario C. North and south of the Fortescue River valley

Lucasium wombeyi, *D. savagei* and *D. galaxias* comprise major clades distributed on opposite sides of the Fortescue River. However, the level of complexity within the phylogenies for *Gehyra*, *L. stenodactylum* and *D. conspicillatus* preclude us from examining this pattern in any detail. As is the case with the previous hypotheses, at finer scales of genetic subdivision, there is some level of distinction between clades north and south of the valley.

None of our biogeographical scenarios clearly match the genetic partitions observed in our datasets, but the high degree of intraspecific diversity and unclear taxonomic boundaries, species-specific ecological differences and difficulties in assigning individuals to specific geographical regions at boundary edges, make it difficult to delineate patterns at the finer scale. Despite this, broad biogeographical patterns are emerging that appear to be repeated across taxonomic groups (summarized in Fig. 3). The most consistent feature of our results is a north/south genetic differentiation across the Pilbara craton.

Our data illustrate that interpreting patterns in the western Pilbara is particularly vexing. In this region, the distribution of genetic clades show little correlation with the IBRA subregions, and while not apparent in the level of detail shown in our phylogenetic results, individuals from the south-western Chichester subregion show closer affinities to the broader Hamersley subregion than to the northern Chichester. In this

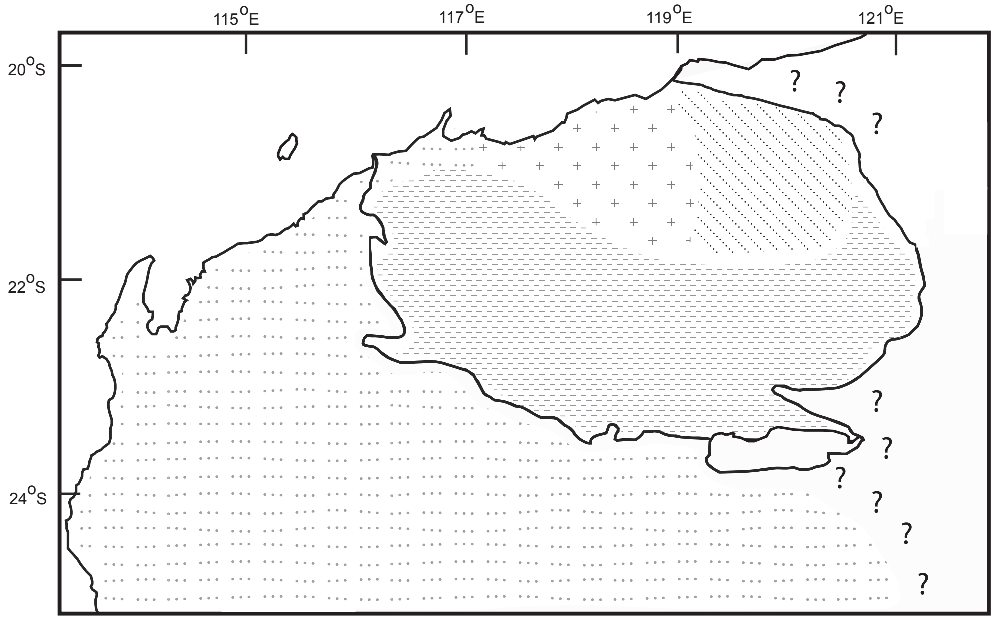

Figure 3 Simplified map illustrating the broad phylogeographical patterns emerging from the current as well as previous studies assessing fine-scale genetic structure across multiple taxa in the Pilbara. Genetic diversity is usually partitioned to either side of the southern craton boundary (as indicated by the vertical dots) with the exception of the coastal region. Within the craton, genetic diversity is typically partitioned into the south (dashed lines), the north-east (diagonal dots) and the north-west (crosses). Further sampling in the central desert regions is required to understand patterns of divergence across the eastern and northern craton margins.

same area, individuals also show little, if any, differentiation across the Fortescue River. This pattern is better explained by the distribution of the Hamersley Basin geological unit, which encompasses a portion of the Chichester subregion and both sides of the Fortescue River valley in this part of the Pilbara. While the Fortescue River may have played a role in vicariance-induced diversification of Pilbara taxa sometime in the past, the distribution of closely related individuals on either side of the river valley suggests recent connectivity across this topographical divide. This connectivity appears to be associated with the far eastern and western bounds of the river valley, where topographical variation is less pronounced. The ephemeral nature of this arid zone river could potentially lead to a weakening of this geographical barrier over time.

The patterns identified in our study are largely consistent with previous taxonomic work. In particular, a signal of north–south differentiation across the Pilbara has been found in patterns of species composition of spiders (Durrant *et al.*, 2010), beetles (Guthrie *et al.*, 2010) and ostracods (Reeves *et al.*, 2007). Examination of the published literature reveals similar genetic patterns reflected in a number of other reptiles, including pebble-mimic dragons (Shoo *et al.*, 2008), and pygmy spiny-tailed skinks (Doughty *et al.*, 2011b). This same north/south pattern is also observed in gecko taxa of the *Heteronotia binoei* species complex (C. Moritz *et al.*, unpublished data) and *Ctenotus* skinks (D. Rabosky, University of Michigan, Ann Arbor, pers. comm.).

There is also evidence for an east–west pattern across the northern Pilbara. In particular, the genetic distinctiveness of taxa in the north-western Pilbara (Beard's Abydos Plain; Beard, 1975) compared with the north-east Pilbara (Beard's Oakover Valley; Beard, 1975) is apparent (Fig. 1c). Based on our results, we agree with Guthrie *et al.* (2010) and conclude that the classification of the Chichester subregion into a single unit is too simplistic, and Beard's (1975) physiogeographical subdivisions within this subregion better explain genetic variation across the northern Pilbara. In addition to substantial geological differences between the east and west portions of the northern craton, a major drainage divide between systems associated with the De Grey and Oakover rivers in the east versus the western river systems (Pinder *et al.*, 2010) may also have influenced this genetic pattern.

A blueprint for future research in the Pilbara

A tantalizing picture is emerging on the biogeographical history of the Pilbara. Our results suggest that regional habitat differences as well as vicariant processes have probably played an important role in the evolutionary history and genetic cohesiveness of the gecko taxa. In addition, substantial genetic differentiation within taxa in the Pilbara appears to support previous conjectures of Pilbara uplands providing important refugia following Miocene aridification (Byrne *et al.*, 2008; Pepper *et al.*, 2008, 2011a; Oliver *et al.*, 2010) in contrast to desert-dwelling taxa that have been shown to exhibit much lower levels of diversity (Fujita *et al.*, 2010; Pepper *et al.*, 2011a,b).

The future for scientific discovery in this remote region looks bright following the Pilbara Biodiversity Survey through access to comprehensive biological collections across a suite of plant and animal groups, coupled with detailed geo/biophysical data associated with all collection localities. The availability of these data, along with ever-improving analytical techniques, will facilitate detailed tests of diversification history in this arid region, and provide much needed insights into the evolutionary consequences of the most severe climate change in recent geological history in Australia. We outline below a number of key elements that will be important in designing future studies of the Pilbara.

Improved sampling

Widespread and detailed sampling (which should be achievable for many taxa using Pilbara Biodiversity Survey collections) across the Pilbara will help delineate centres of diversity with greater precision (see McKenzie *et al.*, 2009, for quadrat sampling locations). Furthermore, using well-resolved phylogenies and having a clear idea of putative species boundaries a priori will be useful for selecting an appropriate sampling strategy. Additional sampling that targets the boundaries of geographical units will be important to facilitate tests of the biogeographical scenarios outlined above, particularly across the central Pilbara where landscape features such as the Fortescue Valley and major geological differences occur. In addition, obtaining genetic material from the greatly under-sampled desert regions to the east and north of the Pilbara craton (the Little Sandy and Great Sandy deserts) will be paramount for assessing levels of divergence across this interface, and shedding light on the importance and timing of the Pilbara as a mesic refuge, especially for non-saxicolous taxa. Finally, including widespread or closely related taxa that also occur in the Kimberley, central Australia and the sandy deserts will not only help reconcile area relationships of the Pilbara to other arid zone regions, but will be of central importance for understanding the nature and timing of the evolution of the Australian arid zone biota. While we did not attempt to date lineages in our study due to the limited power of a single mtDNA locus (Edwards & Beerli, 2000), the substantial genetic differentiation of Kimberley populations suggest that it is unlikely that divergence was the result of the recent isolation of the Pilbara and Kimberley by the development of the sand deserts < 1 Ma. Indeed, Pepper *et al.* (2011c) inferred that the split between Kimberley and Pilbara/central Australian *Heteronotia* geckos occurred at least 4 Ma, divergence of Pilbara and Kimberley *Livistona* plants was estimated to have occurred between 5 and 7 Ma (Crisp *et al.*, 2010), while Oliver *et al.* (2010) estimated that divergences between Kimberley, Pilbara and central Australian *Crenadactylus* geckos occurred prior to 10 Ma.

Assessing genetic patterns across disparate taxonomic groups

With the exception of the subterranean fauna, fine-scale genetic studies across the Pilbara are rare. However, as phylogeographical studies of additional taxa accumulate, our understanding of spatial patterns of genetic divergence and the extent to which they may have been shaped by common processes will improve. In particular, plant and terrestrial invertebrate taxa that have a more direct association with geological and substrate variation, and are inherently less vagile, are likely to provide compelling insights into fine-scale patterns across the Pilbara.

Better integration of geological, habitat and climate data

Collaboration with researchers in the fields of geomorphology and palaeoclimatology will be important to gain access to better geological dates and more accurate historical climate reconstructions. In particular, the novel application of cosmogenic isotope dating methods, which have much longer age ranges than traditional luminescence dating (Fujioka *et al.*, 2009; Fujioka & Chappell, 2010), offers a powerful approach for future studies of arid environments. Dates such as the formation of the Fortescue Valley and peak periods of hydrological activity would allow explicit vicariance hypotheses and biogeographical scenarios to be tested (Hickerson *et al.*, 2010; Crisp *et al.*, 2011).

Harnessing the power of improved molecular sampling and analysis

The use of mtDNA or chloroplast DNA will be important for initial assessment of genetic patterns. However, the addition of multiple nuclear loci will dramatically improve the performance of coalescent-based analytical methods, and enable robust estimation of parameters of demographic history and dating of divergence events (Brito & Edwards, 2009). The application of emerging model-based analytical methods to infer parameters and compare models (reviewed in Hickerson *et al.*, 2010) will provide a powerful means for statistically testing complex and competing biogeographical hypotheses, including the vicariance versus ecological scenarios presented here. Methods for model-based comparative phylogeographical inference such as approximate Bayesian computation (ABC) can be used to test for simultaneous divergence times (Leaché *et al.*, 2007) or congruence in biogeographical scenarios across co-distributed taxa (Carnaval *et al.*, 2009).

Incorporating new species delimitation measures to improve taxonomic understanding

Species discovery in a biologically diverse and poorly explored region such as the Pilbara will be a natural outcome from future genetic studies. With an emphasis on demographic and evolutionary processes responsible for lineage diversification, it will be valuable to utilize an 'integrative taxonomy' framework (Padial *et al.*, 2010) for improved species delimitation and taxonomic understanding. The advantage of coalescent-based approaches is that they have clear and objective underpinnings. When such approaches are combined with more traditional phylogenetic inference methods, as well as with detailed morphological, geographical and ecological data, they will provide more complete and robust information on species distributions and boundaries.

Incorporating conservation planning

The information emerging from fine-scale molecular studies such as ours have significant implications for diversity assessment and conservation management in a region heavily impacted by human development. It is now well known that short-range endemic invertebrates are particularly vulnerable to the impacts of mining and industrial development in the Pilbara, and have received considerable attention from conservation agencies and mining companies (Johnson, 2004; Majer, 2009). While short-range endemism in much of the subterranean invertebrate fauna is of a finer scale than for terrestrial vertebrates, an alarming discovery from our study concerns the number of evolutionarily distinct gecko lineages that appear to have extremely restricted distributions, particularly in the geological unit of the Hamersley Basin, the region comprising the unique iron-rich rocks at the core of Australia's iron-ore mining industry. While further sampling may extend the known distributions of these lineages in the Pilbara, the low-dispersal capability of small terrestrial vertebrates suggests that there may be negative consequences for failing to recognize how genetic diversity is partitioned across the region. Emerging views of the Pilbara as an historical and ancient centre of refugia (Oliver *et al.*, 2010; Pepper *et al.*, 2011a,c) warrants high priority from government and conservation agencies to protect and conserve its unique biota.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Museum and GenBank accession numbers and collection locality information.

Appendix S2 Phylogenetic results based on maximum likelihood analyses (Figs S1–S5).

BIOSKETCHES

Mitzy Pepper is a postdoctoral researcher in Scott Keogh's lab, and this work was completed as part of her PhD. Her interests concern the landscape and climate evolution of the Australian arid zone, and the associated genetic impacts on arid zone biota.

Paul Doughty is a systematist who specializes in Western Australian reptiles and amphibians and is the Curator of Terrestrial Vertebrates at the Western Australian Museum.

J. Scott Keogh is a molecular systematist, biogeographer and professor in evolutionary biology.

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