Hans Lambers *Editor*

On the Ecology of Australia's Arid Zone

Springer

On the Ecology of Australia’s Arid Zone

Hans Lambers
Editor

On the Ecology of Australia's Arid Zone

Springer

Editor
Hans Lambers
School of Biological Sciences
The University of Western Australia
Crawley, WA, Australia

ISBN 978-3-319-93942-1 ISBN 978-3-319-93943-8 (eBook)
https://doi.org/10.1007/978-3-319-93943-8

Library of Congress Control Number: 2018951778

© Springer International Publishing AG, part of Springer Nature 2018
This work is subject to copyright. All rights are reserved by the Publisher, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other physical way, and transmission or information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed.
The use of general descriptive names, registered names, trademarks, service marks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.
The publisher, the authors, and the editors are safe to assume that the advice and information in this book are believed to be true and accurate at the date of publication. Neither the publisher nor the authors or the editors give a warranty, express or implied, with respect to the material contained herein or for any errors or omissions that may have been made. The publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

This Springer imprint is published by the registered company Springer Nature Switzerland AG.
The registered company address is: Gewerbestrasse 11, 6330 Cham, Switzerland

Contents

Introduction

Hans Lambers

Australia is the flattest and driest vegetated continent on Earth. More than two-thirds of the land is considered arid, and half is desert, which supports an amazingly adapted flora and fauna (White 1994). The iconic Red Centre of Australia broadly corresponds with the driest part of the continent, the Australian Arid Zone, suggesting that redness is related to aridity. However, the history of redness in Central Australia is longer than that of the Australian Arid Zone (Pillans 2018). The arid zone is Australia's largest biome, occupying approximately 70% of the entire continent. It hosts a variety of vegetation types from shrub woodlands, acacia and mallee eucalypt shrublands, spinifex grasslands, tussock and hummock grasslands and chenopod shrublands, with a complex evolutionary history in both plants and animals (Byrne et al. 2018).

Australia's arid zone has an amazing flora and fauna. The plants not only have to cope with low and erratic rainfall (Grigg et al. 2008a, b) but also with nutrient-impoverished soils (He et al. 2018). The suite of marsupials now found inhabiting the arid zone is nowhere near what the first European settlers in the late eighteenth and early nineteenth centuries would have seen (Woinarski et al. 2015). Early explorers of the arid zone described how they needed to erect barriers around their tents to prevent marauding 'rat kangaroos' from raiding their stores of biscuits and other provisions. The situation is vastly different today. In the Little Sandy Desert in Western Australia, for example, there were 43 mammal species present at the time of European settlement. Of those, 19 are still present, but a further 19 marsupial species and six rodents once collected there are now regionally extinct (Bradshaw 2018). The arid zone may seem an unusual location for frogs, but to date, 52 species have been recorded (Roberts and Edwards 2018). It has a reptilian fauna that is at least three times as rich in number of species as that of other desert regions of the world. Yet, their ecophysiology has been little studied, and we only

---

H. Lambers (✉)
School of Biological Sciences, University of Western Australia, Perth, Australia
e-mail: hans.lambers@uwa.edu.au

H. Lambers (ed.), *On the Ecology of Australia's Arid Zone*,
https://doi.org/10.1007/978-3-319-93943-8_1

have speculations and hypotheses to account for reptile abundance and diversity (Bradshaw 2018).

The Australian terrestrial invertebrate fauna is highly diverse, with many immense radiations as well as archaic, relictual elements. However, the arid zone fauna has arguably received considerably less attention, and many discoveries can still be made in this area (Majer et al. 2018). A remarkable component of the invertebrate fauna lives belowground, either aquatic in groundwater or air-breathing in the unsaturated zone from depths of a metre or so below the ground surface down to the water table (Halse 2018).

Although fire is widespread and a major ecosystem disturbance throughout Australia, it is a relatively rare event in much of the arid lands, because rainfall and, therefore, productivity are generally too low to support the dense vegetation needed to sustain fires (van Etten and Burrows 2018). However, landscapes dominated by xerophytic perennial grasses, where infrequent periods with above-average rainfall can result in exceptional grass and herb growth, may experience fire more frequently. Climate change and increased atmospheric CO_2 concentrations have also been linked to increased fire activity in arid zones (van Etten and Burrows 2018).

A book on Australia's arid zone is not complete without a chapter on its archaeology, given the very long time humans have occupied this part of Australia. First occupation occurs between 51,100 and 46,200 years ago (Veth et al. 2017). The archaeological evidence for animal depictions from the North West arid zone reveals a long figurative tradition, which spans the Last Glacial Maximum and continues throughout the Holocene. Species depicted include large-range fauna, species outside their current distributions or extinct, e.g., bandicoot and thylacine. While depictions may have been executed to inform dietary, regenerative, totemic and mythological narratives, there is a precision in anatomical detail in some classes which allows attribution to genus and species levels. The painting and engraving traditions of the North West arid zone clearly have a significant naturalistic component, which is significant for studies of human and natural ecology (Veth et al. 2018).

The book ends with three chapters discussing the threats to Australia's arid zone. These include weeds, over 400 alien plant species making up less than 9.7% of the flora, depending on the region. Most of these introductions are not genuinely invasive species, and only a small proportion have a negative impact on their local ecosystem. However, the negative impacts that do occur are far-ranging and difficult to manage, because of the distances and remoteness of the area, a lack of economic incentives for control and contention regarding the economic, environmental and social benefits and costs of some species. Management will need to respond to changes in climate with research required into adaptive responses (Scott et al. 2018). Following European settlement, Australia also experienced an invasion of exotic animals, either deliberately introduced for transport, livestock, as companion animals or for recreational hunting. Many of these became feral pests and quickly spread across the continent, occupying a diversity of habitats including the semiarid and arid regions. In an environment naïve to their ecology, they have caused and continue to cause substantial adverse economic and environmental damage. The extent of damage is largely a function of the density of the feral animal species. In order to manage feral animals in a cost-effective manner that reduces impact on values, it is necessary to understand and quantify the relationships between densities of feral animals and the damage they cause (Burrows 2018). A third threat is climate change. There is very high confidence in projections that average, maximum and minimum temperatures will continue to increase to the end of the century. Average annual temperature and average maximum and minimum temperatures across central Australia are projected to increase by 0.6–1.4 °C by 2030 under intermediate- and high-emission scenarios, compared with average conditions from 1986 to 2005. We can gain some appreciation of the significance of these changes from comparison with the change in temperature already observed. Mean annual temperature has increased by about 1 °C over the past 100 years, while the middle of the range for intermediate emissions is 1 °C by 2030. That represents a fivefold increase in the rate of warming (i.e. 0.1 °C per decade since 1910 compared with 0.5 °C per decade to 2030) (Foster 2018).

We dedicate this book to the memory of Alan Louey Yen (1950–2017). After completing his PhD at LaTrobe University and a postdoctoral research post at Monash University, he joined the National Museum of Victoria (now Museums Victoria) in 1981 where he served as Curator of Invertebrate Survey for two decades. Alan then held a joint appointment with the Victorian Department of Economic Development, Jobs, Transport and Resources at AgriBio and La Trobe University in Melbourne, holding the position of Research Leader for Invertebrate Sciences. Alan's research focussed on insects and other terrestrial invertebrates, especially regarding their conservation and biosecurity (Yen 2015). He was also passionate on humans using insects as a food resource (Yen 2012). He published several books and peer-reviewed papers and made a contribution to the chapter on terrestrial invertebrates in this volume (Majer et al. 2018). We will sorely miss his humour, wit and unpretentious attitude to life.

References

Bradshaw SD (2018) Ecophysiology of Australian arid-zone marsupials. In: Lambers H (ed) On the ecology of Australia's arid zone. Springer, Dordrecht

Burrows NE (2018) Feral animals in the semi-arid and arid regions of Australia; origins, impacts and control. In: Lambers H (ed) On the ecology of Australia's arid zone. Springer, Dordrecht

Byrne M, Joseph L, Yeates D, Roberts JD, Edwards D (2018) Evolutionary history. In: Lambers H (ed) On the ecology of Australia's arid zone. Springer, Dordrecht

Foster I (2018) Climate change. In: Lambers H (ed) On the ecology of Australia's arid zone. Springer, Dordrecht

Grigg AM, Veneklaas EJ, Lambers H (2008a) Water relations and mineral nutrition of closely related woody plant species on desert dunes and interdunes. Aust J Bot 56:27–43

Grigg AM, Veneklaas EJ, Lambers H (2008b) Water relations and mineral nutrition of *Triodia* grasses on desert dunes and interdunes. Aust J Bot 56:408–421

Halse SA (2018) Subterranean fauna of the arid zone. In: Lambers H (ed) On the ecology of Australia's arid zone. Springer, Dordrecht

He H, Eldridge DJ, Lambers H (2018) Mineral nutrition of plants in Australia's arid zone. In: Lambers H (ed) On the ecology of Australia's arid zone. Springer, Dordrecht

Majer JD, Harvey MS, Humphreys WF, Davis JA, Yen AL (2018) Terrestrial invertebrates of the Australian arid zone. In: Lambers H (ed) On the ecology of Australia's arid zone. Springer, Dordrecht

Pillans BJ (2018) Seeing red: some aspects of the geological and climatic history of the Australian arid zone. In: Lambers H (ed) On the ecology of Australia's arid zone. Springer, Dordrecht

Roberts JD, Edwards DL (2018) The evolution, physiology, and ecology of the Australian arid zone frog fauna. In: Lambers H (ed) On the ecology of Australia's arid zone. Springer, Dordrecht

Scott JK, Friedel MH, Grice AC, Webber BL (2018) Weeds in Australian arid regions. In: Lambers H (ed) On the ecology of Australia's arid zone. Springer, Dordrecht

van Etten EJB, Burrows ND (2018) Fire regimes and ecology of arid Australia. In: Lambers H (ed) On the ecology of Australia's arid zone. Springer, Dordrecht

Veth P, McDonald J, de Koning S (2018) Archaeology and rock art of the north-west arid zone with a focus on animals. In: Lambers H (ed) On the ecology of Australia's arid zone. Springer, Dordrecht

Veth P, Ward I, Manne T, Ulm S, Ditchfield K, Dortch J, Hook F, Petchey F, Hogg A, Questiaux D, Demuro M, Arnold L, Spooner N, Levchenko V, Skippington J, Byrne C, Basgall M, Zeanah D, Belton D, Helmholz P, Bajkan S, Bailey R, Placzek C, Kendrick P (2017) Early human occupation of a maritime desert, Barrow Island, North-West Australia. Q Sci Rev 168:19–29

White ME (1994) After the greening: the browning of Australia. Kangaroo Press, Sydney

Woinarski JCZ, Burbidge AA, Harrison PL (2015) Ongoing unraveling of a continental fauna: decline and extinction of Australian mammals since European settlement. Proc Natl Acad Sci U S A 112:4531–4540

Yen AL (2012) Edible insects and management of country. Ecol Manage Restor 13:97–99

Yen AL (2015) Conservation of Lepidoptera used as human food and medicine. Curr Opin Insect Sci 12:102–108

Seeing Red: Some Aspects of the Geological and Climatic History of the Australian Arid Zone

Brad J. Pillans

Introduction

"Old, flat and red" is how the Australian landscape has been described by Pain et al. (2012). In this chapter, I will focus on the last of these three descriptors – red – in the context of the geological and climatic history of the Australian arid zone. This narrative of redness is not a standard geological history, describing events in each geological period. Rather, it seeks to examine the major boundary conditions or controls on the evolution of the Australian arid zone and some of its defining features. Of necessity, this requires reference to events that occurred millions, and sometimes billions of years ago, and to refer to periods of time that are named as part of the international geological timescale (see Fig. 1).

Let's start with "old". As I have previously pointed out (Pillans 2007), based on palaeogeographic reconstructions, parts of the Australian continent may have been subaerially exposed for hundreds of millions of years (Fig. 2). A similar conclusion had been reached almost 100 hundred years earlier, by Jutson (1914, p.92), when he stated that "the land surface of Western Australia is one of the oldest land surfaces on the globe, and that it has not been below the sea for many geological ages". In contrast, for much of the twentieth century, the prevailing view of many northern hemisphere geomorphologists was that little of the Earth's topography was older than the Cenozoic and most was no older than Pleistocene (e.g. Thornbury 1954). Such a view was based on the conclusion that ongoing erosional processes ensure the destruction of ancient landforms, perhaps unsurprising given that large areas of the Northern Hemisphere had been overrun and reshaped by Pleistocene ice sheets and glaciers. In contrast, mainland Australia was little affected by Pleistocene glaciation, except for a small area around Mt. Kosciuszko (Barrows et al. 2001). Thus, we might expect ancient landforms to be preserved in Australia.

B. J. Pillans (✉)
Research School of Earth Sciences, Australian National University, Canberra, Australia
e-mail: brad.pillans@anu.edu.au

H. Lambers (ed.), *On the Ecology of Australia's Arid Zone*,
https://doi.org/10.1007/978-3-319-93943-8_2

Fig. 1 Geological timescale (after Gradstein et al. 2012). There are numerous named epochs in pre-Cenozoic periods which are not shown for simplicity. Basal ages of major units are given in millions of years ago (Ma)

EON	ERA		PERIOD	EPOCH	Age (Ma)
Phanerozoic	Cenozoic		Quaternary	Holocene	0.0117
				Pleistocene	2.58
		Tertiary	Neogene	Pliocene	5.33
				Miocene	23.0
			Paleogene	Oligocene	33.9
				Eocene	56.0
				Paleocene	66.0
	Mesozoic		Cretaceous		145
			Jurassic		201
			Triassic		252
	Paleozoic		Permian		299
			Carboniferous		359
			Devonian		419
			Silurian		444
			Ordovician		485
			Cambrian		541
Precambrian	Neo-Proterozoic		Ediacaran		635
			Cryogenian		720
			Tonian		1000
	Meso-Proterozoic		Stenian		1200
			Ectasian		1400
			Calymmian		1600
	Paleo-Proterozoic		Statherian		1800
			Orosirian		2050
			Rhyacian		2300
			Siderian		2500
	Archean		Neoarchean		2800
			Mesoarchean		3200
			Paleoarchean		3600
			Eoarchean		4000
	Hadean				4600

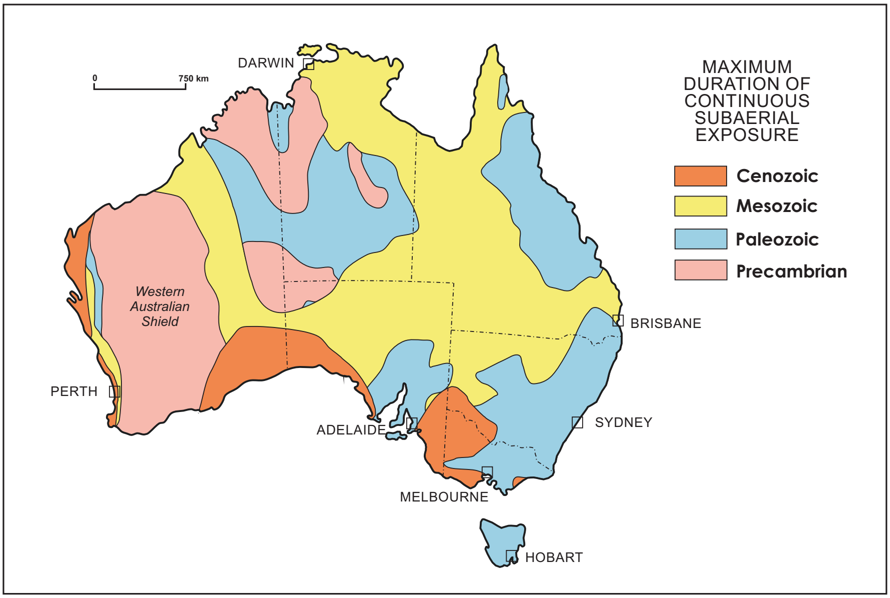


Fig. 2 Duration of subaerial exposure based on palaeogeographic reconstructions. (After Pillans 2007)

Now we turn to "flat". Australia is the flattest and lowest continent, with an average elevation of only 325 m (Pain et al. 2012). Overall, the continent is bowl-shaped – low in the centre (as low as −16 m elevation in Lake Eyre) and high around the edges (up to 2228 m on Mt. Kosciuszko) – a function of having three rifted passive margins (west, south and east coasts) and being located in the centre of a lithospheric plate, remote from active plate margins. The Australian plate is moving north at a rate of 6–7 cm year^{-1} (fingernails grow at about the same rate!), and tilting downwards to the north, perhaps by as much as 300 m since the Miocene (Sandiford 2007) – not enough to have a major effect on the flatness of the continent. With no major orogenic events in the last 250 million years, coupled with low rates of long-term erosion, flatness has been perpetuated!

Then there is "red", which will be the major narrative thread of this chapter. The Australian arid zone or major parts thereof are variously referred to as the "The Red Centre", "The Outback", "Central Australia", "The Back of Bourke", etc. The town of Alice Springs is close to the centre of Australia, regardless of how it is measured [there are several ways, including calculating the centre of gravity of Australia's irregular continental shape or measuring the maximum distance from the sea]. The area stretching some 250 km west and south of Alice Springs to Uluru is usually described as the Red Centre in tourist information brochures and includes iconic red landforms such as Uluru, Kata Tjuta, the West MacDonnell Ranges and Kings Canyon. However, equally iconic red landforms are much more widespread, includ-

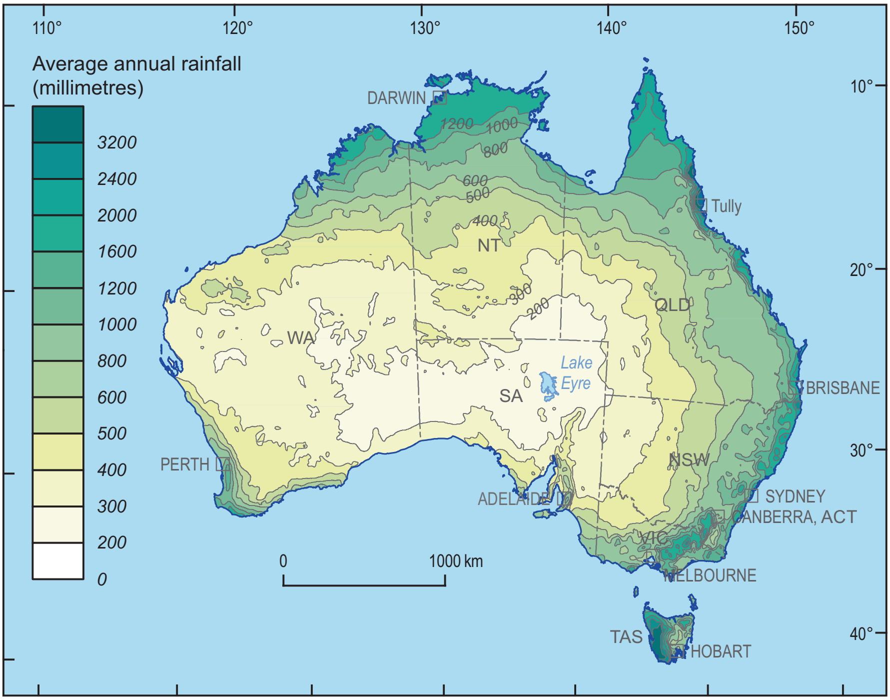


Fig. 3 Modern mean annual rainfall. (Bureau of Meteorology & Geoscience Australia; Blewett 2012, Fig. 1.8, p.29)

ing the sand dunes of the Simpson Desert and the gorges of Karijini National Park in Western Australia.

Why is the central core of Australia red? The red colour primarily comes from the iron oxide hematite (Fe_2O_3), formed by the oxidation of ferrous (Fe^{2+}) iron. The Red Centre is broadly encompassed by the modern-day 500 mm mean annual rainfall isohyet (Fig. 3), suggesting that redness is related to aridity. However, as we will see, aridity came late to Central Australia, and some of the red pigmentation was formed, by weathering, at much earlier times when the climate was significantly wetter than present (Pain et al. 2012). The history of atmospheric oxygen is also an important factor influencing the red colours that occur in rocks, soils and sediments of Central Australia, and this will be discussed to highlight the long history of "redness".

Modern Setting

Byrne et al. (2008) defined the Australian arid zone as the region of Australia having a moisture index of less than 0.4 (mean annual rainfall divided by evaporation). With an area comprising some 40% of the Australian continent, it is one of the

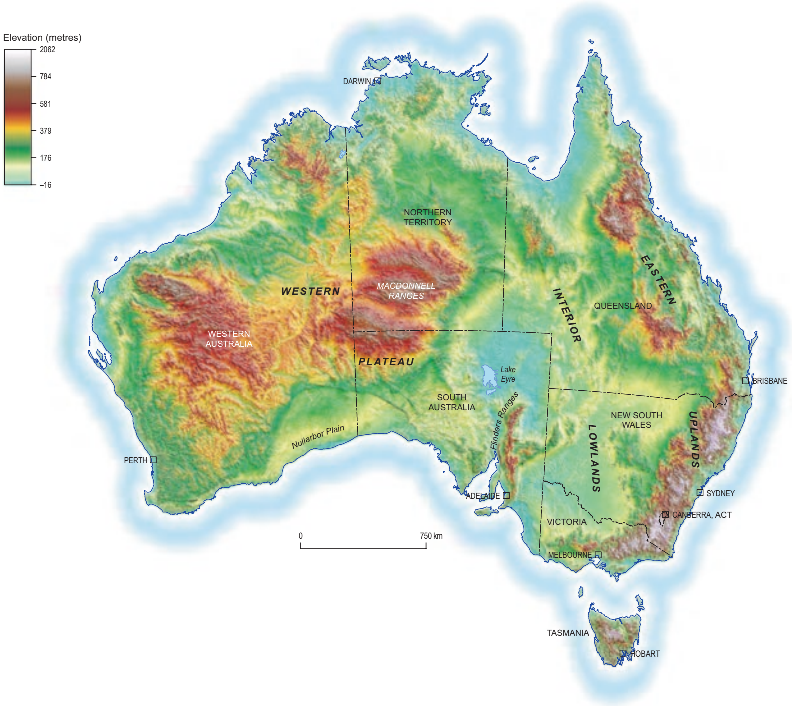


Fig. 4 Digital elevation model of Australia showing the major physiographic features. (Blewett 2012, Fig. 1.5, p.15)

largest deserts in the world. The Australian arid zone stretches from the northwest coast of Western Australia, through the southern half of the Northern Territory and northern and central South Australia, to western New South Wales and Queensland in the east (Fig. 4).

Jennings and Mabbutt (1967) recognised three major physiographic regions in Australia – the Eastern Uplands, Interior Lowlands and Western Plateau, the latter two of which include the Australian arid zone. These regions are well expressed in the digital elevation model (DEM) shown in Fig. 4. They are also broadly coincident with the three major geological subdivisions of Australia – the eastern fold belts, central basins and western shields.

The geological history of the Australian arid zone is both long and complex, with many different kinds of rocks being represented in the modern landscape. The western and northern parts are dominated by Archean and Proterozoic igneous and metamorphic rocks, while the eastern and southern parts are dominated by Mesozoic and Cenozoic sedimentary rocks (Fig. 5).

A striking feature of the Australian continent, which sets it apart from all other continents, is the large percentage of its land surface that is internally draining, i.e. drainage basins with no outlet to the sea (Fig. 6). The Lake Eyre Basin is the largest

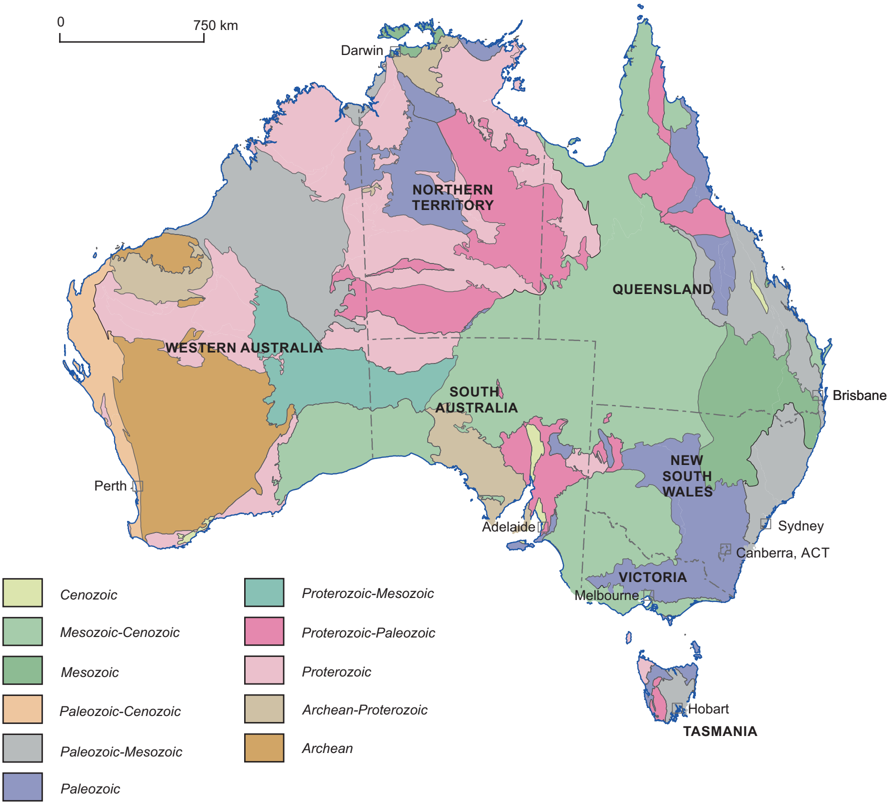


Fig. 5 Major geological regions of Australia. (Simplified from Blewett 2012, Fig. 2.8, p. 70)

of these, comprising about 1.2 million km^2 or some 16% of the continent. Only on the western margin of the Australian arid zone do rivers reach the coast today, and most of these only do so seasonally. In contrast, in the early Cenozoic, large southward-flowing rivers drained into the Great Australian Bight and westwards to the west coast of Western Australia (Hou et al. 2008; Bell et al. 2012), so internal drainage came late in our geological history, a consequence of increasing aridity (the rivers dried up) and northward tilting (rivers don't flow uphill).

The red colour of the Australian arid zone which is clearly seen in satellite imagery (Fig. 7) comes from the regolith. The term "regolith" describes the weathered skin of the Earth's crust – everything from fresh air to fresh rock – including what we refer to as soil. Australian regolith, particularly in the Australian arid zone, is often described as old, highly weathered and nutrient-poor (McKenzie et al. 2004), all the result of the long history of subaerial exposure to weathering processes that have acted in a low-relief landscape. In large open pit mines, the depth to fresh rock may be more than 100 m, and the red colour of surface regolith can be seen to extend many metres below the present ground surface (Fig. 8).

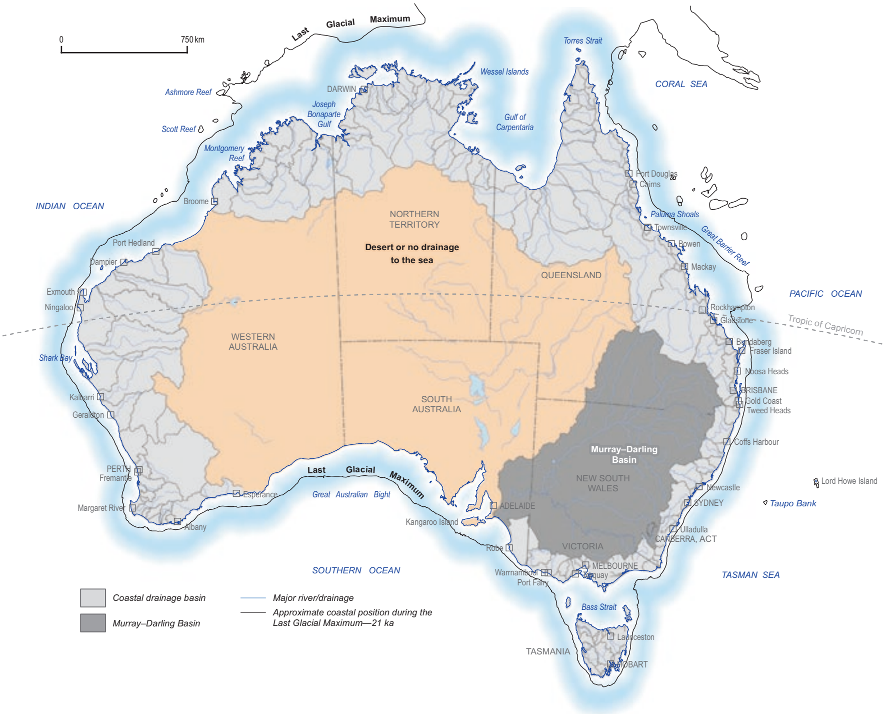


Fig. 6 Major drainage systems of Australia. Much of the Australian arid zone has no drainage to the sea. (Blewett 2012, Fig. 6.2, p. 283)

Two major categories of regolith can be recognised:

1. Transported regolith includes detrital (fragmented) and dissolved materials that have been carried varying distances from their source, including by water, wind, ice and gravity. Typical deposits include sand dunes, river and lake sediments. Linear sand dunes, salt lakes, ephemeral streams and stony plateaus characterise much of the Australian arid zone (Fig. 9)
2. In situ regolith forms by weathering of the rocks immediately beneath – the material that remains in place after losses from weathering and erosional transport. The deeply weathered rocks that are exposed in mine pits are in situ regolith, called saprolite. Sometimes, when deep saprolite is eroded, residual masses of less weathered and more resistant rock remain – the Devil's Marbles near Tennant Creek are residual granite corestones formed in this way (Fig. 10).

Wilford (2012) developed a weathering intensity index across the Australian continent, at a 100 m resolution, based on regression models of airborne gamma-ray spectrometry imagery and elevation data from the Shuttle Radar Topography Mission (SRTM) – see Fig. 11. Intensely weathered regolith is typical of landscapes that have been exposed to weathering for long periods of time which is particularly

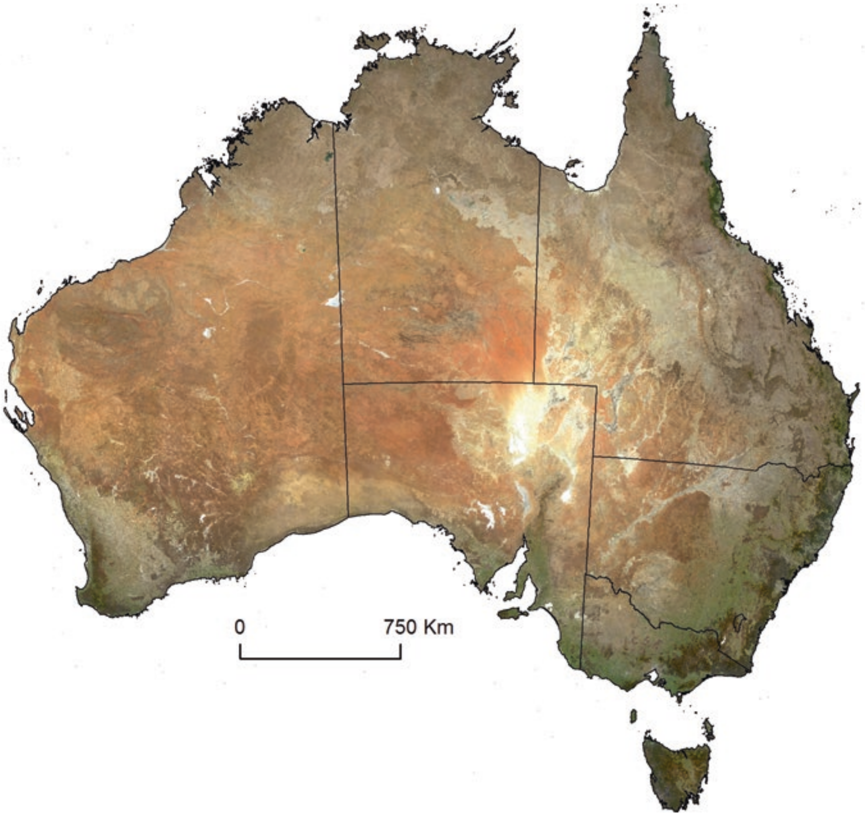


Fig. 7 Composite cloud-free Landsat 8 satellite image with bands 4, 3, 2 (RGB), showing reddish surface colours dominating Central Australia. (Source – NASA: Geoscience Australia, courtesy of John Wilford)

true of many low-relief regions in Central Australia. In these areas, intensely weathered regolith is characterised by residual elements such as Fe and Al (ferricretes and bauxitic profiles, respectively), often occurring as erosion-resistant caps on mesas, such as at Balgo in the far north of Western Australia (Fig. 12). In contrast, in higher-relief areas, erosion rates are faster, and both the depth and intensity of bedrock weathering are lower, although regolith redness can persist (e.g. Pilbara region).

Measuring Redness

The measurement and significance of redness has been the subject of much research (and debate) in the earth sciences. There are two main ways of measuring regolith colour, either qualitatively, by visual comparison with standard colour charts (e.g.

Fig. 8 Deep oxidation of regolith, western Tanami Desert, Northern Territory; exposure is 50 m deep. (Pillans photo)

Munsell Color Company 1975), or by quantitatively measuring spectral reflectance (Bullard and White 2002; Viscarra Rossel et al. 2006).

The redness of regolith is largely a function of iron oxide mineralogy, which varies with environmental conditions such as pH, Eh, temperature and moisture. In particular, red colours are associated with hematite. Viscarra Rossel et al. (2010) measured the reflectance spectra of more than 4000 surface soil samples from across Australia to generate RGB true colours that could be converted to Munsell parameters of hue, value and chroma (spectral colour, lightness and brightness, respectively). Mapped according to hue, Fig. 13 shows that the Australian arid zone is indeed dominated by "red" hues.

Actually, not all hematite looks red – coarsely crystalline hematite is often a dark-grey metallic colour. Geologists have long used what is called the "streak test" to distinguish hematite from other, similar looking minerals which involves scratching a white, unglazed porcelain surface – the resulting powder scratch or streak is characteristically red for hematite, suggesting that, in part, the red colour is dependent on the presence of fine particles, which the streak test creates. Similar links between fine-grained (<2 μm) hematite and its red colour have been noted in a range of geological studies (e.g. McBride 1974; Walker 1979; Morris et al. 1985; Blodgett 1988). Laboratory studies have also demonstrated a link between magnetic properties and redness (Morris et al. 1985; Rossman 1996).

Fig. 9 Distribution of Australia's stony and sandy deserts. (Blewett 2012, Fig. 5.1, p.228)

Fig. 10 Devils Marbles, Northern Territory – granite core stones exhumed by regional denudation. (Pillans photo)

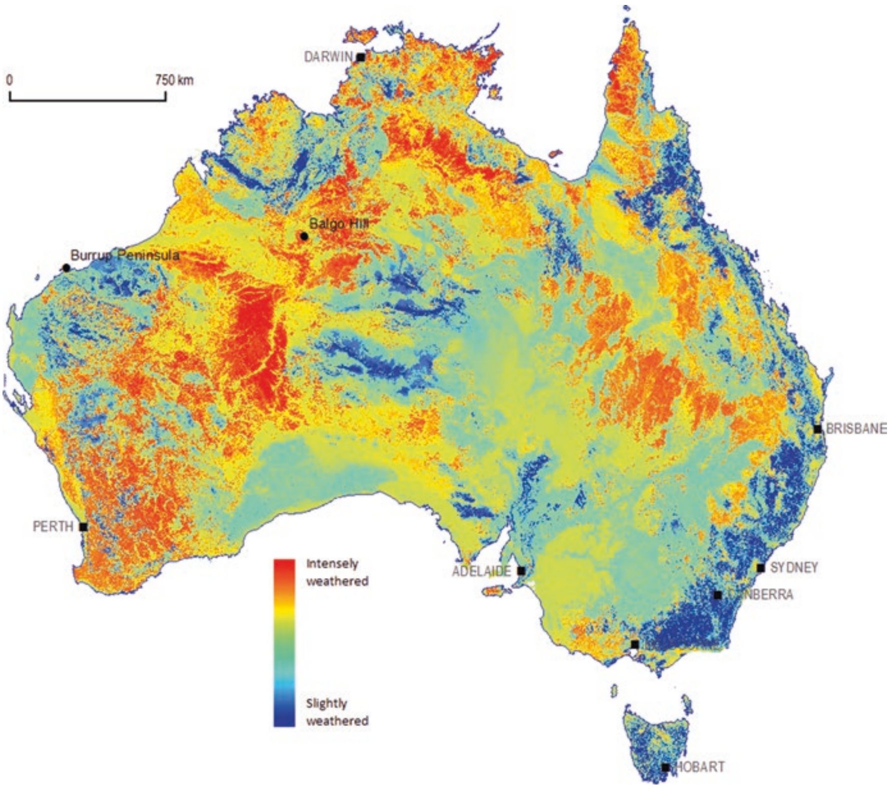


Fig. 11 Weathering intensity map of Australia (Courtesy of John Wilford). Balgo Hill (high) and Burrup Peninsula (low) have contrasting weathering intensity indices but are both dominated by red weathered rocks (see also Figs. 11 and 16)

Atmospheric Oxygen

Formation of red-pigmenting hematite requires free oxygen, the primary source of which is photosynthesis. Oxygen forms some 21% of the modern atmosphere, but for much of Earth history, it was very much lower – low enough to inhibit oxidation of Fe to form hematite (Fig. 14).

Atmospheric oxygen levels during the Archean (4–2.5 billion years ago) were extremely low, probably less than 0.001% of the present atmospheric level, as evidenced by the widespread occurrence of redox-sensitive detrital siderite ($FeCO_3$), pyrite (Fe_2S) and uraninite (UO_2) in Archean sediments (Catling and Claire 2005). In Archean fluvial sediments from the Pilbara region in Western Australia, these detrital minerals show evidence of rounding consistent with prolonged transport in well-aerated waters and with very low atmospheric oxygen concentrations (Rasmussen and Buick 1999). Such minerals are very rare to absent in modern river sediments, because modern atmospheric oxygen levels ensure their complete oxidative destruction.

Fig. 12 Intensely weathered terrain at Balgo, western Tanami Desert, Northern Territory (Pillans photo)

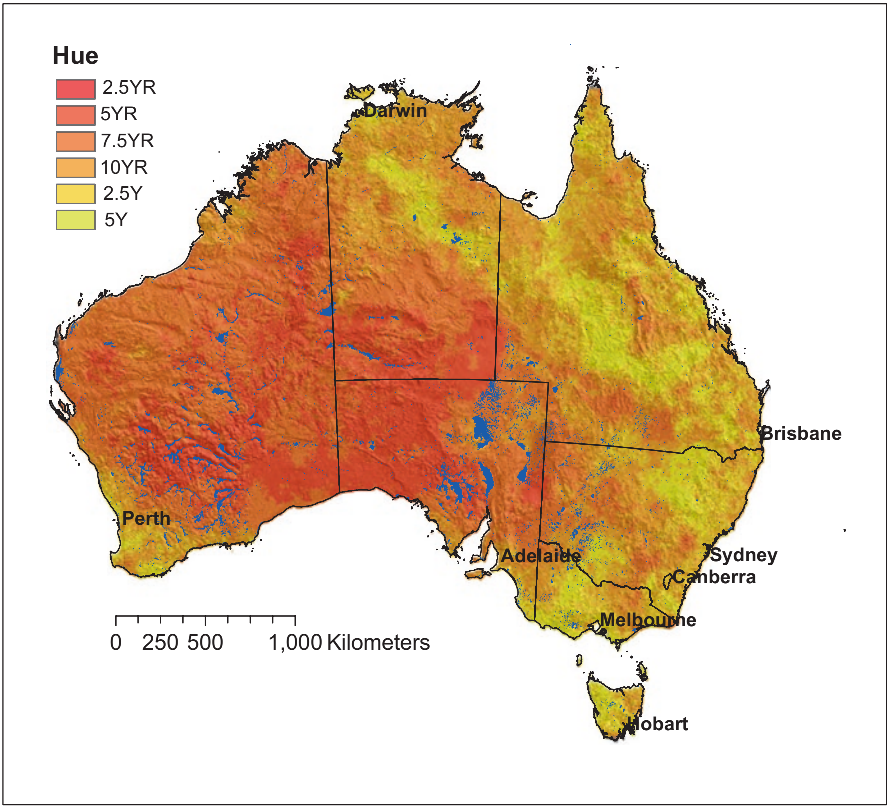


Fig. 13 Spectral hue of Australian soils. (Viscarra Rossel et al. 2010)

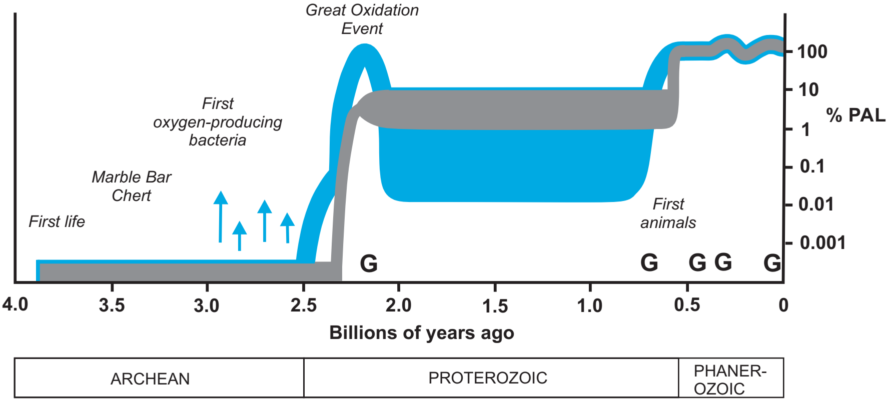


Fig. 14 History of atmospheric oxygen (Modified after Lyons et al. 2014). Grey curve shows the classic two-step view of atmospheric oxygen evolution. Blue curve is an another model, with blue arrows indicating possible "whiffs" of oxygen in the late Archean. Right axis (%PAL) indicates percentage of oxygen relative to present atmospheric level. G = major glacial episodes

Between 2.4 and 2.1 billion years ago, atmospheric oxygen appears to have increased dramatically – usually referred to as the Great Oxygenation Event. Red weathered sediments (red beds) appear in the geological record, detrital pyrite disappears, and atmospheric oxygen probably rose to around 1–3% of the present atmospheric level (Catling and Claire 2005). The Great Oxygenation Event could have been a response to emergence and proliferation of photosynthetic organisms, the earliest of which were probably cyanobacteria. However, fossil evidence suggests that cyanobacteria may have arisen before 3.5 billion years ago, perhaps as early as 3.7 billion years ago (Nutman et al. 2016), so why the billion-year delay to the Great Oxygenation Event? Opinions vary, but it may have been a balance between oxygen sources and oxygen sinks (e.g. carbon, sulphur and iron compounds) that took time to overcome (Lyons et al. 2014).

During the Proterozoic, atmospheric oxygen likely remained well below modern levels, until it increased to approximately modern levels about 600 million years ago, coeval with the rise of animals (Canfield et al. 2007; Chen et al. 2015; Brocks et al. 2017). Subsequently, atmospheric oxygen has fluctuated between about 0.75 and 1.75 of the present atmospheric level (between 15% and 35% oxygen in the atmosphere, respectively), which is the so called "fire window", constrained by the occurrence of fossil charcoal since the latest Silurian, 419 million years ago (Glasspool and Scott 2010).

Early History (Precambrian)

Some of the oldest rocks on Earth occur in Western Australia, including the world's oldest known minerals – zircons dated to 4.4 billion years (Valley et al. 2014). Indeed, large areas of Western Australia comprise rocks from 4 to 2.5 billion years old, belonging to the Archean Eon (Fig. 1). Evidence of some of the earliest life forms also comes from these rocks – laminated carbonate structures known as stromatolites (e.g. Hofmann et al. 1999; Allwood et al. 2006). Although there has been a long debate about whether Archean stromatolites are of microbial (biogenic) origin or whether they are abiogenic, Allwood et al. (2006) have demonstrated that stromatolites in the 3.43 billion-year-old Strelley Pool Chert in the Pilbara region are "most plausibly interpreted" as microbially formed structures – very similar to living examples in Shark Bay, Western Australia, today. Stromatolites are aptly described as "living fossils", because they were known from the fossil record before living examples were recognised, for the first time, in Shark Bay in 1954 (Playford et al. 2013).

Spectacular banded red rocks, of similar antiquity to the Strelley Pool Chert, occur as a prominent rock bar across the Coongan River at Marble Bar, in Western Australia (Fig. 15). The rock bar gave its name to the nearby town of Marble Bar, but, despite the name, the rock is not marble, it is a type of jasper or chert. The Marble Bar Chert consists of alternating layers of silica and hematite, interpreted by

Fig. 15 Marble Bar Chert outcrop on the Coongan River, Marble Bar, Western Australia. (Pillans photo)

Hoashi et al. (2009) to have been deposited in partly oxygenated ocean water 3.46 billion years ago. They suggested that the hematite crystals formed from hydrothermal fluids, rich in ferrous iron, at temperatures greater than 60 °C. According to Hoashi et al. (2009), the hematite is detrital, meaning that it was deposited as sedimentary particles, not formed by post-depositional weathering – in other words, it was red from the start. If correct, this represents the oldest known occurrence of red rocks in Australia, and probably the world. Subsequently, Rasmussen et al. (2014a) undertook a detailed petrographic study of the Marble Bar Chert and concluded that the hematite was not primary, but rather it formed after sediment deposition. Key observations supporting a secondary origin of the hematite included the presence of magnetite cores in some hematite grains, lateral transitions in mineralogy within individual sediment layers and the occurrence of hematite in fractures and veins. In contrast, Hoashi et al. (2009) observed hematite crystals in the cores of many magnetite crystals, but not on the outside, indicating that the magnetite formed later than the hematite. Perhaps some of the hematite is primary, and there was a whiff of oxygen 3.46 billion years ago!

The spectacular red gorges of Karijini National Park (Fig. 16), in the Pilbara region of Western Australia, are cut through red rocks including Banded Iron Formations (BIFs) – sedimentary rocks comprising alternating layers of iron-rich and silica-rich minerals that were deposited from anoxic, iron-rich sea water during the Archean. With the rise of atmospheric oxygen around 2.4 billion years ago, ocean waters became more oxygenated, and Banded Iron Formations became much

Fig. 16 Spectacular red gorges in Karijini National Park, Pilbara region, Western Australia. (Photo courtesy Brent Alloway)

less common (Rasmussen et al. 2012). However, like the Marble Bar Chert, the Banded Iron Formations contain significant amounts of hematite which is inconsistent with formation in an anoxic environment. Rasmussen et al. (2014b) concluded that the hematite was formed as a secondary mineral after deposition of the BIFs, perhaps as a distal signature of the processes that formed the giant iron ore deposits in the Pilbara – which involved hematite replacement in unmineralised Banded Iron Formations, via deep infiltration of oxygenated meteoric fluids.

Palaeomagnetic studies of Banded Iron Formations and associated sediments (Schmidt and Clark 1994; Abrajevitch et al. 2014; Schmidt and Williams 2017) indicate several episodes of iron mineralisation, from the Paleoproterozoic through to the Cenozoic. Multiple episodes of hematite formation are also confirmed by U/Pb dating of xenotime (YPO_4) and monazite ($CePO_4$) that formed concurrently with the hematite (Rasmussen et al. 2007; Sheppard et al. 2017). Thus, if the hematite in Banded Iron Formations came later, they were not red from birth but acquired their red colouration at various times subsequent to the Great Oxygenation Event.

Burrup Peninsula, near Karratha, is a landscape dominated by red boulder-covered ridges and rocky hills (Fig. 17a). It is also home to the world's largest gallery of rock art (Bird and Hallam 2006). The rocks are mostly Archean granophyre (2.7 billion years old), and while the red colour would appear to be pervasive, it is actually only "skin deep". Broken rocks reveal an outer weathered zone, no more than about 1 cm thick (called a weathering rind), which contains the red colour, whereas the interior is a dark grey colour (Fig. 17b). Many rock surfaces also have a thin layer of ferruginous rock varnish, overlying the weathering rind. How long the rocks have been red is uncertain, but clearly not from birth. Long-term surface

Fig. 17a Red rocky outcrops on Burrup Peninsula, near Dampier, Western Australia. (Pillans photo)

Fig. 17b Broken clast of granophyre, Burrup Peninsula, showing the limited depth of red weathering, to about 1 cm. (Pillans photo)

erosion rates, as measured by cosmogenic nuclides, are in the range 0.15–1 mm per 1000 years (Brad and Keith Fifield 2013), which would remove a 1-cm-thick weathering rind in less than 60,000 years, so the red colour that we see today must be younger than that. Of course, chemical weathering processes continue to act on the rock surfaces and a balance is reached between surface erosion and inwards movement of the weathering front. Just how many centimetres of weathering have been removed in this way is unknown, so we cannot really say how long the rocks have looked red on the Burrup.

Summary: From the three examples above, we can conclude that while the rocks are very old (2.5–3.5 billion years), much of their red colour has likely been acquired at various times since the Great Oxidation Event around 2.4–2.1 billion years ago.

Middle History (Palaeozoic and Mesozoic)

Uluru, a 348-m-high inselberg (Fig. 18) and one of the most famous landforms in Australia, lies close to the centre of the Australian arid zone. It is a massive outcrop of red sandstone of latest Proterozoic to earliest Cambrian age – 550–540 million years (Sweet et al. 2012). Some 30 km west of Uluru is Kata Tjuta (Fig. 19), an equally impressive outcrop of red conglomerate of similar age to Uluru. The sandstone and conglomerate were originally deposited as alluvium by rivers that drained

Fig. 18 Uluru, a large inselberg of red weathered Cambrian sandstone, stands some 348 m above the surrounding sand plain. (Pillans photo)

from rapidly eroding mountains in the area of the modern-day Petermann Ranges. The sandstone is rich in feldspar, and is called an arkose sandstone, but this is not why Uluru is red. As with the older rocks, described above, the red colour comes from iron oxides that were formed much more recently. Just how recently is open to conjecture. Beneath the sand plain between Uluru and Kata Tjuta, there are sediments containing fossil spores and pollen of Late Cretaceous age (Harris and Twidale 1991). Thus, by the late Cretaceous, Uluru and Kata Tjuta must already have been high points in the landscape, though ongoing weathering and erosion has changed their size and shape since that time. The red colour of Uluru and Kata Tjuta is a surface weathering feature, much like the rocks on Burrup Peninsula (see above). Within caves around the base of Uluru, fresh rock (of grey colour) is exposed. Similarly, exposures at Kata Tjuta reveal that the unweathered conglomerate is a pale colour.

Kings Canyon (Fig. 20), some 300 km southwest of Alice Springs, is a spectacular 100-m-deep gorge, cut through red weathered Palaeozoic sediments within the Amadeus Basin (Bagas 1988). The upper gorge walls are formed of Mereenie Sandstone, deposited in shallow marine conditions sometime during the Silurian to Devonian Periods (the age is uncertain). Like Uluru, the red colour is a surface weathering feature, much of which must have been acquired after the gorge was cut – iron oxides coat the surface but the unweathered sandstone is pale coloured.

Fig. 19 Kata Tjuta, 30 km southwest of Uluru, composed of red weathered Cambrian conglomerate. (Pillans photo)

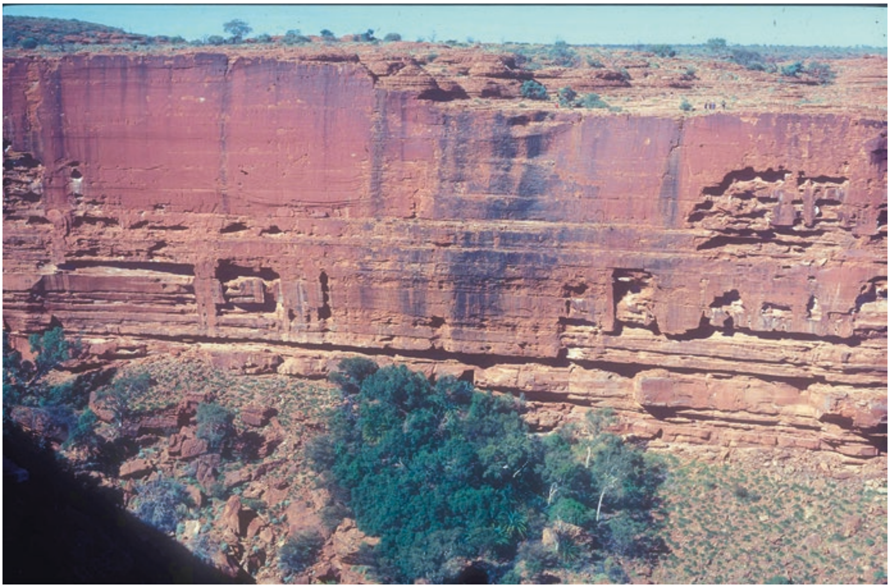


Fig. 20 Red weathered Mereenie Sandstone, South Wall, Kings Canyon, Northern Territory. (Pillans photo)

Fig. 21 Marla mesa, in northern South Australia, is an example of inverted relief. It is capped by iron-cemented fluvial sand and gravel, palaeomagnetically dated to ~60 million years. (Pillans photo)

During the late Carboniferous and Early Permian (c. 320–280 million years ago), Australia was part of the Gondwana supercontinent, which also included India, Africa, South America, New Zealand and Antarctica. Gondwana was situated at high southern latitudes, and much of the continent was affected by glaciation. Indeed, a large continental ice sheet, several kilometres thick, may have covered the Yilgarn Craton in Western Australia (Crowell and Frakes 1971). Along the eastern margin of the Yilgarn Craton, there are glacial landforms and sediments consistent with glacial meltwater discharge eastwards into the Officer Basin (Eyles and de Broekert 2001). At Lancefield, glacial till is red weathered and yields a palaeomagnetic pole consistent with oxidation during the Late Carboniferous. This was also a period of increased atmospheric oxygen, perhaps 50% higher than present (Berner et al. 2003). Thus, the combination of deep regolith oxidation and extensive ice sheets may have no modern analogue (Pillans 2007).

During the Cretaceous Period, much of Central Australia was flooded by a series of marine transgressions, the most extensive of which (between 120 and 110 million years ago) covered some 40% of the Australian continent (Frakes et al. 1987). The sediments that were deposited during that time have undergone little subsequent deformation and remain relatively flat-lying to this day, producing a characteristic landscape dominated by extensive plains and low plateaus (Fig. 21). Although the Cretaceous is generally regarded as a period of extended global warmth, the Australian continent lay at high southern latitudes, and the world's only known Cretaceous glacial deposits are recorded at the northern end of the Flinders Ranges (Alley and Frakes 2003). There are also glacially rafted dropstones in Cretaceous marine sediments in the southern Eromanga Basin. Much of the area covered by Cretaceous seas in the eastern Australian arid zone is in the area now known as the

Great Artesian Basin. Australia's world-famous opal deposits are also located within this area, likely formed by acidic oxidative weathering during the period 100–60 million years ago (Rey 2013).

From Greenhouse to Icehouse in the Cenozoic

Major river systems characterised the Australian arid zone in the Cenozoic, preserved as large interconnected paleovalleys that are buried beneath the modern arid landscape (Fig. 22). These paleovalley systems, which are important groundwater aquifers today, formed under a humid temperate climate, with higher rainfall, lower evaporation and a temperate rainforest vegetation (English et al. 2012).

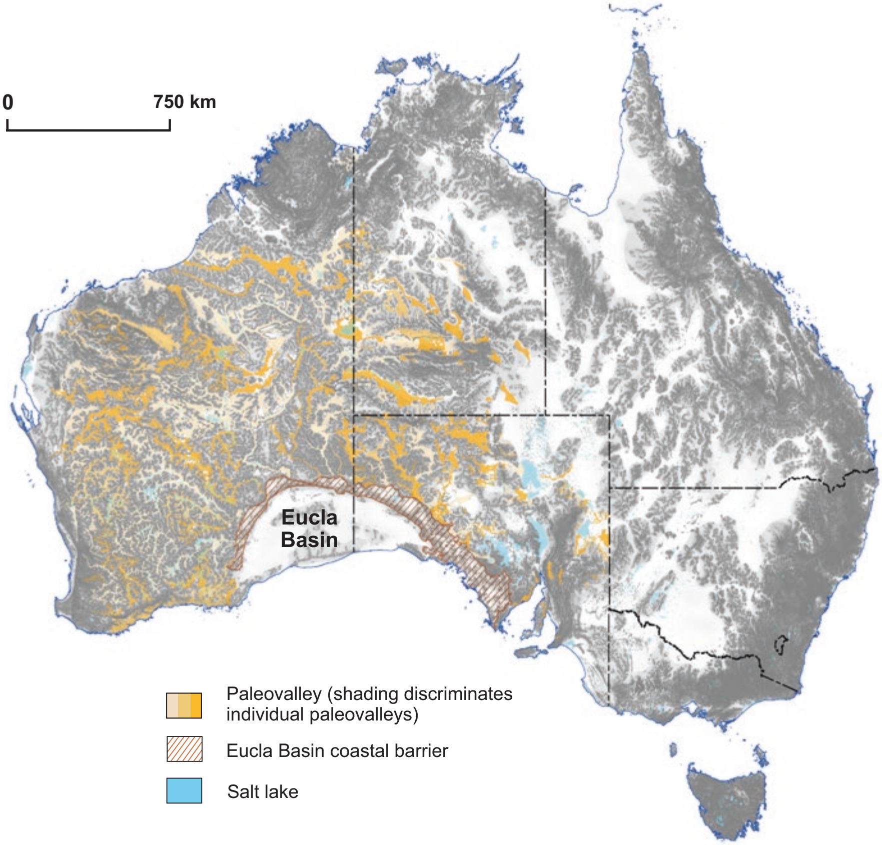


Fig. 22 Paleovalley systems (yellow), mostly last active during the Paleogene, are a testament to the major arid shift in climate during the Neogene. (Bell et al. 2012)

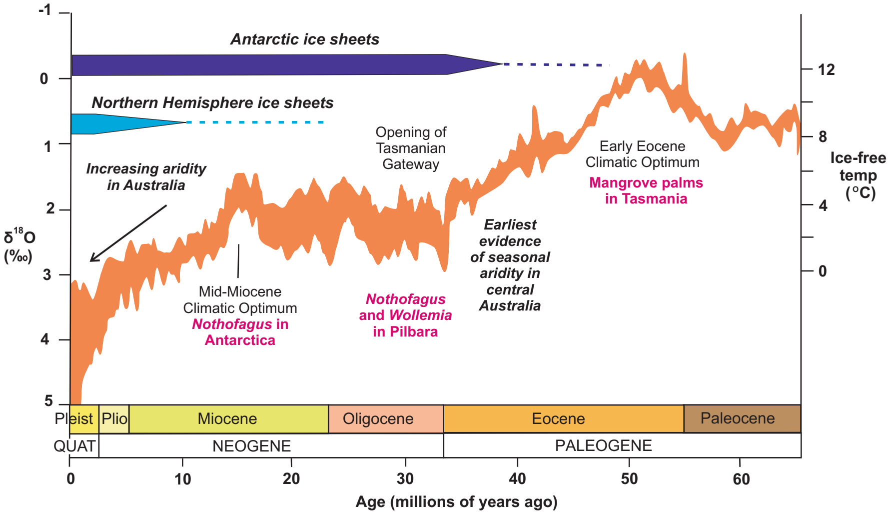


Fig. 23 Evolution of global climate over the last 65 million years. (After Zachos et al. 2008)

To understand the dramatic change from humid to arid climate in Central Australia during the Cenozoic, we need to look at global climatic changes – in particular the build-up of the Antarctic ice sheet since the Oligocene (Fig. 23). From about 55 million years ago, the Southern Ocean began forming as Australia separated from Antarctica and the Australian continent has moved some 30 degrees north since that time. With opening of the Tasmanian Gateway, which connects the Indian and Pacific Oceans, and the opening of Drake Passage between the Atlantic and Pacific Oceans, the Antarctic Circumpolar Current was established around 30 million years ago (Lawver and Gahagan 2003; Lagabrielle et al. 2009; Scher et al. 2015). Onset of the Antarctic Circumpolar Current thermally isolated Antarctica, preparing the way for growth of the Antarctic ice sheet (Zachos et al. 2001, 2008). It was also associated with major changes in the global ocean circulation system and may have contributed to subsequent lower levels of atmospheric carbon dioxide (Scher et al. 2015).

During the Palaeocene and Eocene Epochs (65–35 million years ago), Earth was essentially ice-free, with global warmth reaching a peak around 50–55 million years ago (Early Eocene Climatic Optimum). Atmospheric CO_2 was probably significantly higher than today (Zachos et al. 2008). Warm to cool temperate rainforest covered much of Australia (Martin 2006), including *Nothofagus* (southern beech), which is today restricted to high-rainfall areas in southeast Australia, New Zealand, New Caledonia, New Guinea and southern South America. Near-tropical warmth was experienced in Tasmania, with mangrove palms (*Nypa*) growing at 65 °S (Pole and Macphail 1996; Carpenter et al. 2012). The spectacular paleovalley systems (Fig. 22) were active, with major rivers feeding water and sediment to the Eucla Basin, where massive coastal sand barriers formed, during the middle Eocene (38–34 million years ago), containing heavy mineral deposits that are mined today (Hou et al. 2008). Palaeomagnetic dating indicates that extensive deep weathering of regolith also occurred in the Palaeocene, including mobilisation of Fe to form ferricretes (Idnurm and Senior 1978; Smith et al. 2009).

Middle Eocene pollen and macrofossil assemblages from the southern Lake Eyre Basin (Alley et al. 1996; Greenwood 1996) indicate a dominance of Casuarinaceae (*Casuarina* and *Gymnostoma*), rather than *Nothofagus*, but including some taxa with monsoon forest affinities. The evidence suggests a mosaic of riverine rainforests and interfluve sclerophyllous plant communities, with seasonal rainfall. The macrofossils are preserved in silcrete (silica-cemented sediment), with silicification occurring soon after the plant remains were deposited. Further evidence of a significant sclerophyll component in Eocene vegetation comes from paleovalleys in southern Western Australia, including the diverse presence of members of the Proteaceae and Myrtaceae (Carpenter and Pole 1995; Carpenter et al. 2014; Mack and Milne 2015).

Palaeoenvironmental evidence from the Oligocene Epoch (34–23 million years ago) is scarce in Central Australia. In the Lake Eyre Basin, the interval appears to have been one of prolonged weathering, erosion and silicification (Alley and Pledge 2000). Vertebrate faunas preserved in the lowest part of the Etadunna Formation may be latest Oligocene in age, around 24–25 million years ago, based on magneto and biostratigraphy (Woodburne et al. 1994), with ages adjusted to the latest Oligocene timescale (Gradstein et al. 2012). The faunas include numerous birds, including the giant flamingo, *Phoeniconotius eyrensis,* and many aquatic species (fish, crocodiles, turtles, and dolphins), indicating substantial permanent lakes. Fossils of terrestrial taxa also include browsing marsupials and arboreal animals (Woodburne et al. 1994; Alley and Pledge 2000).

Three other sites that have yielded silicified leaf fossils in Central Australia, Stuart Creek (northern South Australia), Glen Helen (Northern Territory) and Lightning Ridge (New South Wales), are poorly dated but likely to be late Oligocene to Miocene in age (Greenwood et al. 2001; Carpenter et al. 2011). The sites are significant, because they contain leaf impressions of banksias (Proteaceae), consistent with drier climates than in the Eocene (but still significantly wetter than today). At two of the sites (Stuart Creek and Glen Helen), there are also taxa, which are closely comparable to extant *Brachychiton* and are broadly indicative of a seasonally-wet tropical to subtropical climate. Based on the floral assemblage at Stuart Creek, mean annual rainfall may have been around 1000 mm (Greenwood et al. 2001).

By the early to mid-Miocene (23–12 million years ago), regular flows in the paleovalley systems in Western Australia had ceased, and rainforest was probably restricted to small pockets (Martin 2006). Rainfall was still significantly higher than today, but the first major step towards aridity had been taken.

The period from 17 to 14 million years ago was globally the warmest part of the Neogene and is usually referred to as the Miocene Climatic Optimum (Fig. 23), with woody vegetation growing in Antarctica (Ashworth and Cantrill 2004). From around 14 million years ago, the Antarctic ice sheet expanded rapidly, with global cooling and drying in the Late Miocene eventually culminating in the Pleistocene ice ages. Recent U/Pb dating of spectacular fossil sites in the Riversleigh World

Heritage Area, in north Queensland (Woodhead et al. 2016), provides a precise chronology for palaeoecological reconstructions in the range 18.2–13.5 million years ago (early to middle Miocene). The diverse faunal assemblages at Riversleigh are indicative of temperate lowland closed forest habitats in the early and middle Miocene, with more open forest habitat in the late Oligocene and late Miocene (Travouillon et al. 2009; Woodhead et al. 2016).

Ferricrete and silcrete are more resistant to erosion than most other regolith materials, and they therefore occur as cappings on mesas and plateaus throughout the Australian arid zone. A common type of ferricrete is Fe-cemented alluvial sediment, that originally formed in valley floors, but subsequent stream incision has lowered the surrounding landscape to create what is often termed "inverted relief" (Pain and Ollier 1995), resulting in alluvium in high parts of the landscape (Fig. 21). In the Pilbara region of Western Australia, a major source of iron ore is Channel Iron Deposits, which infill large meandering paleochannels, now preserved as inverted relief (Ramanaidou et al. 2003). The Channel Iron Deposits are typically composed of pedogenically derived pisoliths with hematite nuclei and goethite cortices, as well as abundant mineralised charcoal/wood fragments cemented by goethite-rich matrix (Morris and Ramanaidou 2007). Diffusion-corrected (U-Th)/He ages (Danisik et al. 2013) indicate the following mineral formation ages in the Yandi paleochannel:

1. Formation of pisolith cores between 18.3 ± 3.5 and 14.3 ± 3.7 million years ago (Early to Middle Miocene)
2. Formation of goethite cortex at 11.6 at 11.6 at 11.6 ± 3.0 million years ago (late Middle to early Late Miocene)
3. Ferruginisation of wood fragments in the Channel Iron Deposits matrix 10–7 million years ago (Late Miocene).

At another Channel Iron Deposits site (Lynn Peak), ^{40}Ar/^{39}Ar dating of authigenic Mn oxides and (U-Th)/He dating of associated goethite cement (Vasconcelos et al. 2013) yield somewhat older ages than at Yandi, in the range 33–14 million years ago. Also, at Lynn Peak, dating of detrital MnO grains from the Channel Iron Deposits yields ages in the range 44–63 million years ago, indicating erosion from a pre-existing, intensely weathered landscape, and broadly similar to ages from a potential source weathering profile at Roy Hill (Vasconcelos et al. 2013). These combined results, from two Channel Iron Deposits, indicate a long and complex history of Channel Iron Deposit formation during the Oligocene and Miocene epochs.

Basal clays in the Yandi paleochannel have yielded an early Oligocene pollen flora (Macphail and Stone 2004) dominated by one or more of Casuarinaceae, Myrtaceae, Proteaceae, *Nothofagus* and *Podocarpus/Prumnopitys* and suggesting that the palaeovegetation included a mixture of dry forest and rainforest communities. Climate was significantly wetter than present but seasonally dry. The abundance of fossil wood in Channel Iron Deposits suggests wildfires in well-wooded catchments (Morris and Ramanaidou 2007). Hydrogen isotope analyses of goethite pisoliths, dated to 7 million years ago, imply that Late Miocene rainfall was derived mainly from summer season tropical cyclones (Yapp and Shuster 2017).

The Nullarbor Plain, on the southern margin of the Australian arid zone, became emergent from about 14 million years ago, partly in response to tectonic uplift and partly in response to a major sea-level fall associated with increased Antarctic ice (Miller et al. 2012). The middle Miocene Nullarbor Limestone forms the upper surface of the plain and records a long and complex history of subaerial weathering. Pollen assemblages extracted from dated speleothems (cave deposits such as stalagmites and flowstones) provide a vegetation and climate record for the latest Miocene to mid-Pliocene (5.6–3.5 million years ago). The data show that from 5.6 to 5 million years ago, the vegetation was a sparse shrubland or woodland; mean annual rainfall was around 480 mm, slightly higher than today (180–270 mm), indicating that a semiarid climate had already developed in the Nullarbor region by the latest Miocene. However, around 5 million years ago (earliest Pliocene), there was an abrupt change to forest vegetation (with *Eucalyptus*, *Corymbia*/*Angophora*, *Banksia* and *Doryanthes*), associated with an increase in rainfall to around 1200 mm, that persisted until 3.5 million years ago (Kale Sniderman et al. 2016). There is a gap in the speleothem pollen record after 3.5 million years, but by 400,000 years ago (mid-Pleistocene), rainfall had decreased to close to present levels, consistent with an arid-adapted fauna dated to between 200,000 and 400,000 years ago in Nullarbor caves (Prideaux et al. 2007). Similarly, evidence from the Adelaide region (Pillans and Bourman 2001) indicates a marked change from an oxide-dominated weathering regime to the modern carbonate-dominated weathering regime around 500–600,000 years ago, inferred to represent a major mid-Pleistocene arid shift in climate.

Geomorphic Evidence of Late Cenozoic Aridity in Central Australia

Direct evidence of aridity comes from four principal sources:

1. Stony deserts. A common arid landform in Central Australia is stony desert surfaces (Figs. 9 and 24) composed of a layer of stones, commonly known as gibber. Many of the clasts are composed of silcrete, with a surface coating of rock varnish. They can occur as a lag deposit on rocky pavements, or as surface floaters on alluvium or aeolian silt (Mabbutt 1977). Unlike sand dunes, stony desert surfaces are less susceptible to erosion and are therefore more likely to persist as landscape features. Fujioka et al. (2005) used cosmogenic ^{21}Ne-^{10}Be exposure dating to show that stony desert surfaces in northern South Australia have ages in the range 2–4 million years, broadly coinciding with global cooling that led to the Quaternary ice ages. Stony deserts are very similar in appearance to some stony surfaces on Mars (Thomas et al. 2005; West et al. 2010).

Fig. 24 Simpson stony desert landscape. (Photo courtesy Andreas Buisman)

Fig. 25 Longitudinal dunes in the Simpson Desert (25°12’S, 136°54′E), as viewed in satellite imagery. (From Google Earth)

2. Sand dunes. Aeolian dune building in Central Australia was presumably initiated in response to heightened aridity and devegetation of previously stable sand plains. The most widespread dunes are linear dunes, spectacularly visible on satellite imagery (Fig. 25). Cosmogenic nuclide burial dating indicates that the oldest dunes in the Simpson Desert began accumulating around 1 million years ago (Fujioka et al. 2009), significantly later than the development of stony deserts. Dunes in the Simpson Desert also contain palaeosols, indicating episodic dune building. Luminescence dating indicates that the two youngest major dune-building phases, broadly corresponded to the last two glacial periods.
3. Salt lakes. Lakes in the Australian arid zone are typically saltwater discharge playas that hold water only intermittently. Stratigraphic drilling reveals a

common pattern – that there was a major change from wetter to drier conditions in the early to mid-Pleistocene and that this change was time transgressive between about 1 million and 500,000 years ago. The critical chronologic marker is the last major reversal of the Earth's magnetic field, dated to 0.78 million years (the Matuyama-Brunhes reversal). The earliest dated change from lacustrine to saline sediments occurred prior to the Matuyama-Brunhes reversal, around 1 million years ago at Lake Amadeus (Chen and Barton 1991), whereas at nearby Lake Lewis the change occurred well after the Matuyama-Brunhes reversal, around 400,000 years ago (English et al. 2001). Similar changes are recorded at Lake Lefroy, in southern Western Australia (Zheng et al. 1998), and in palaeo-Lake Bungunnia in the western Murray Basin (An et al. 1986). The differing times of lake drying are largely explained by the differing hydrologic thresholds of each lake basin (Bowler 1981). For example, Lake Amadeus has a much smaller catchment/lake area ratio than Lake Lewis and would therefore be expected to dry out earlier in response to intensifying aridity.

4. Wind-blown dust (loess). Major dust storms can transport dust hundreds to thousands of kilometres downwind from source areas within the Australian arid zone (Hesse 2003). Aeolian dust has been identified in sediment cores from the Tasman Sea (Hesse 1994) and shows that significant dust transport began around 350,000 years ago, with highest dust fluxes during glacial periods. A similar pattern is evident in sediment cores off northwest Western Australia extending back to 550,000 years (Stuut et al. 2014), consistent with relatively arid glacials and relatively humid interglacials.

In summary, the geomorphic evidence reveals that aridity progressively intensified during the last 4 million years, beginning with the initiation of stony deserts, followed by the development of salt lakes and sand dunes from about 1 million year ago and increasing dust transport from around 350,000 years ago.

Red colours are pervasive in these arid landforms and associated regolith. Folk (1976) studied red sands in the Simpson Desert (Fig. 26) and demonstrated that the red colour comes from a hematitic clay coating on the dominantly quartz sand grains. He concluded that the coating was the product of intense Pleistocene weathering, enhanced by the passage of time as iron oxides dehydrate to form hematite. Wopfner and Twidale (1988) reached a similar conclusion, noting that dune redness tended to increase with distance from source. In contrast, Wasson (1983) concluded that reddening of dune sand in the Simpson and Strzelecki Deserts largely occurred prior to dune construction and that variation in dune sand colour was controlled by the colour of the sediment sources. Pell and Chivas (1995) found that most sand grains were poorly rounded and irregular in shape, with a predominance of chemically produced surface features, including grain coatings, leading them to conclude that the majority of dunes are currently stable, and that the sand has not been transported over long distances during its sedimentary history. Pell et al. (1999, 2000) also favoured derivation from local sources but showed, using zircon U/Pb ages, that the ultimate sources of local fluvial sediments were basement rocks hundreds of kilometres away. All researchers concur with Folk (1976) – the red colour was

Fig. 26 Red sand dunes in the Simpson Desert, partially stabilised by modern vegetation. (Photo courtesy Paul Hesse)

derived from hematitic clay coatings on otherwise pale-coloured sand grains, acquired through a combination of in situ weathering and inheritance from local source rocks.

Drivers of Australian Aridity

The progressive aridification of Central Australia over the last 4 million years is plausibly linked to the growth of the Antarctic ice sheet, coupled with northwards movement of the Australian continent. Bowler (1982) constructed an elegant model of Australian aridification which recognised the changing latitudinal position of the subtropical highs relative to the Australian continent (Fig. 27). At the present time, the hot subtropical deserts in both hemispheres are largely controlled by subtropical high pressure cells centred about 30°north and south of the equator. Flohn (1973) showed that the position of the subtropical highs was controlled by the equator-pole temperature gradient (ΔT) – when ΔT is low, the subtropical highs are located at higher latitude, and when ΔT is high, the subtropical highs move closer to the equator. Thus, Bowler argued, during the Miocene, when the Antarctic ice cap was much smaller and ΔT was much lower than present, the subtropical highs may have been anchored around 50°S. Even allowing for the northwards movement of Australia, this would place the subtropical highs belt to the south of Australia, and the continent

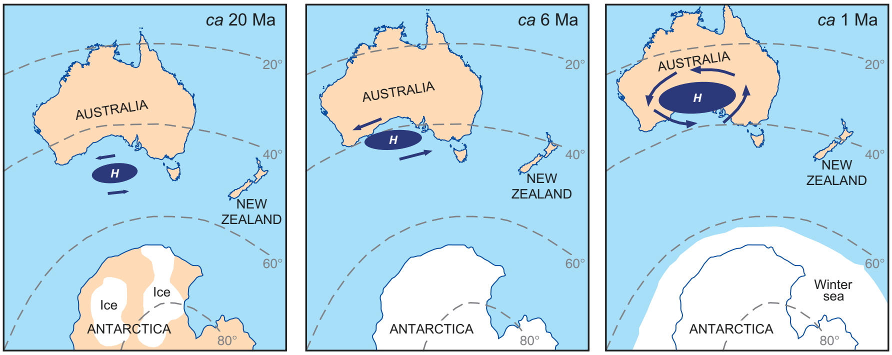


Fig. 27 Position of subtropical highs relative to Australia. (Blewett 2012, Fig. 5.5, p.233, after Bowler 1982 and Fujioka and Chappell 2010)

would have been under a summer rainfall regime. As the Antarctic ice sheet grew, ΔT increased and the subtropical highs moved north, overtaking the Australian continent from the south (at a faster rate than the continent was moving north). An alternative scenario, which assumes that the subtropical highs remained at 30°S and that the continent drifted north into the subtropical highs zone, would mean that northern Australia would have become arid first – for which there is no evidence.

A second major control on aridity may come from gradual tectonic uplift of the so-called Maritime Continent (the islands of Indonesia and surrounding area), over the last 5 million years, as a consequence of crustal shortening associated with the northwards movement of the Australian tectonic plate (Molnar and Cronin 2015). Uplift of the Maritime Continent caused progressive constriction of warm surface currents (Indonesian Throughflow) from the western Pacific to the Indian Ocean, resulting in cooler surface ocean temperatures in the eastern Indian Ocean, including a weakened Leeuwin Current from around 3.3 million years ago (Karas et al. 2011). Lower sea surface temperatures in turn lead to seasonally drier conditions in northwest Australia (Christensen et al. 2017).

A third major control on aridity is linked to global climate changes that are modulated by variations in Earth's orbital parameters – eccentricity, obliquity and precession – which play a major role in driving glacial-interglacial climate changes on 10^3–10^5 year timescales. In broad terms, in Australia, glacial periods are typically cold and arid, while interglacial periods are warm and wet. In northern Australia, the moisture balance is dominated by the Australian monsoon, which is a component of the Asian monsoon. Magee et al. (2004) reported a 150,000-year record of water level fluctuations in Lake Eyre, as a proxy for Australian monsoon intensity, and showed that, within the limits of dating uncertainties, wet phases correlated with Northern Hemisphere winter insolation minima. Furthermore, they showed that, despite similar, strong insolation forcing, lake levels in the Holocene were significantly lower than those during the Last Interglacial, implying a failure of the Australian monsoon in the Holocene. Miller et al. (2005, 2016) attributed this failure to a major change in vegetation and hydrological boundary conditions, as a consequence of regular Aboriginal burning and the extinction of the Australian megafauna from around 50,000 years ago (see also Johnson et al. 1999). Fu et al. (2017) extended the Lake Eyre record beyond 200,000 years and, with improved luminescence dating, concluded that insolation forcing was not the primary driver of long-term water levels in Lake Eyre and the strength of the Australian monsoon. Regardless of the underlying cause(s), the progressively decreasing water levels in Lake Eyre over the last 200,000 years are a clear indication of further, progressive aridification in Central Australia during that time.

Landscape Evolution

The survival of ancient landforms and regolith in Australia presents something of a paradox to geomorphologists. On the one hand, prolonged tectonic stability and slow rates of denudation in an arid environment are seen as promoting their preservation. On the other hand, while measured rates of long-term weathering and erosion in Australia are low by world standards (Bierman and Caffee 2002; Heimsath et al. 2010), they are not low enough to explain the survival of pre-Cenozoic landforms and regolith at or near the surface. Even at rates of 1 m per million years, at least 100 m would be stripped from surfaces formed more than 100 million years ago – sufficient to ensure their complete destruction.

A powerful technique for measuring long-term denudation on timescales of millions of years is apatite fission-track thermochronology. The technique utilises the linear damage zones (called fission tracks) caused by spontaneous fission of trace amounts of radioactive ^{238}U nuclei in the crystal lattice of apatite (chemical formula $Ca_5(PO_4)_3(F,Cl,OH)$). The number of fission tracks preserved in an apatite crystal depends on the U concentration, elapsed time and temperature and can be used to constrain the thermal (burial) history of a rock and hence its denudation history. Kohn et al. (2002) compiled apatite fission-track data to demonstrate that kilometre-scale denudation had occurred across much of Australia over the last 250 million years (Fig. 28), with an average continent-wide denudation rate of ~10 m per million years. At such average rates, preservation of ancient regolith and landforms would seem to be impossible and would certainly preclude the survival of Cambrian river terraces as persisting near-surface landforms, as claimed by Stewart et al. (1986).

A solution to the paradox of ancient landform survival, in the face of ongoing erosional destruction, is burial and exhumation (Kohn et al. 2002; Belton et al. 2004; Pillans 2007). Nowhere is this more clearly evidenced than with the Western Australian Shield, where remnants of late Carboniferous to early Permian regolith and landforms are widely preserved (Eyles and de Broekert 2001). Weber et al. (2005) derived a model, based on apatite fission-track and geological data, the key elements of which were surface exposure and weathering during the late Carboniferous, followed by rapid burial by up to ~3 km of Permian sediments and then slow exhumation until re-exposure in the late Cretaceous (Fig. 29).

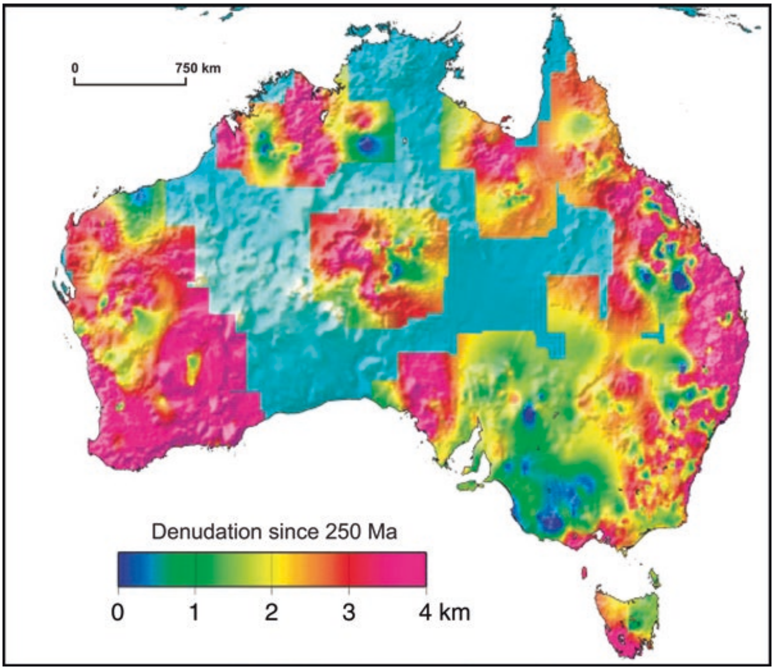


Fig. 28 Kilometre-scale denudation of Australia over the last 250 million years, based on apatite fission-track thermochronology. (Blewett 2012, Fig. 5.23, p. 261, after Kohn et al. 2002)

However, while burial and exhumation may be necessary to explain the survival of pre-Cenozoic landforms and regolith, it does not need to be invoked to explain the survival of Cenozoic features in the modern landscape. As discussed by Twidale (1976), factors that favour the survival of ancient features include resistant rocks (and regolith), low rainfall and tectonic stability. Furthermore, erosion can be quite localised, allowing the preservation of ancient features in certain parts of the landscape, for example, as relict upland surfaces remote from incising rivers. In the Australian arid zone, plateaus and mesas, capped by resistant silcrete or ferricrete, are typical end products of this process (Figs. 12 and 21). Clearly, the progressive aridification of Central Australia in the late Cenozoic has aided such preservation.

Aridity and Redness in Central Australia: Some Concluding Remarks

The progressive development of the Australian arid zone has its origins in the breakup and dispersal of the continental blocks that comprised the great southern continent of Gondwana – India, South America, Africa, Antarctica, Australia and Zealandia (Mortimer et al. 2017). Separation of Australia from Antarctica, to enable

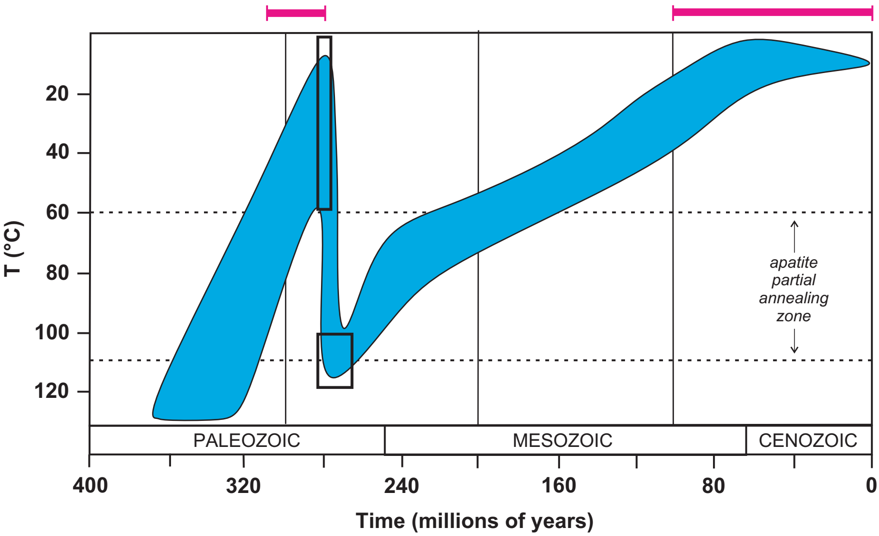


Fig. 29 Modelled thermal history of the central Western Australian shield, based on apatite fission-track thermochronology (Weber et al. 2005), showing excellent agreement with times of near-surface deep oxidisation of regolith (red bars), dated by palaeomagnetism (Pillans 2007, 2010). Black boxes are model constraints from geological evidence. Using a long-term geothermal gradient of 18 °C/km (Weber et al. 2005), the thermal history can be interpreted as a denudation history, incorporating kilometre-scale burial and exhumation episodes

establishment of the Antarctic Circumpolar Current in the late Oligocene, around 30 million years ago, reinforced the thermal isolation of Antarctica, promoting the growth of the Antarctic ice sheet, eventually leading to establishment of the modern ocean and atmosphere circulation patterns. The simultaneous northwards drift of the Australian continent and growth of the Antarctic ice sheet led to gradual juxtaposition of Central Australia with the belt of subtropical high pressure systems and intensifying aridity.

While palaeobotanical evidence suggests seasonal dryness from the Eocene onwards, the first truly arid landscapes, the stony deserts, did not develop until the Pliocene, some 3–4 million years ago (Fujioka et al. 2005), while sandy desert landforms came later, starting around 1 million years ago (Fujioka et al. 2009).

What then of Australia's Red Centre? Red regolith, both in situ and transported, is widely characteristic of the Australian arid zone, suggesting a strong link between aridity and redness. This is certainly true of the red sand dunes that occur throughout the Australian arid zone. However, the red pigment in regolith which comes from fine-grained hematite can be shown, in some cases, to predate aridity. Hematite acquires a stable magnetic remanence when it crystallises, and palaeomagnetic measurements indicate crystallisation ages that predate the formation of desert landforms by tens of millions, sometimes by hundreds of millions of years (e.g. Idnurm and Senior 1978; Smith et al. 2009; Abrajevitch et al. 2014; Schmidt and Williams 2017). A strong boundary condition on the formation of red pigmentation in rocks and regolith is atmospheric oxygen concentration, which has been at or above modern levels for the last ~600 million years. Even at very low atmospheric oxygen concentrations, the formation of hematite by oxidative weathering is feasible, and the Great Oxidation Event around 2.4–2.1 billion years ago, when atmospheric oxygen was only 1–3% of modern, is widely viewed as allowing red pigmentation to form. Whether there were "whiffs" of oxygen much earlier remains contentious, but the red hematite layers in the 3.5 billion-year-old Marble Bar Chert are one possible example.

Acknowledgements I gratefully acknowledge Geoscience Australia for permission to publish figures from "Shaping a Nation" (Blewett 2012) under the Creative Commons Attribution 4.0 International Licence. John Wilford, Richard Blewett and Penny Kilgour (Geoscience Austral) are thanked for providing valuable assistance with figures, and I also thank John for stimulating discussion on remote sensing of redness. Paul Hesse (Macquarie University), Brent Alloway (Auckland University) and Andreas Buisman are also thanked for providing images.

References

Abrajevitch A, Pillans BJ, Roberts AP (2014) Haematite pigmentation events and palaeomagnetic recording: implications from the Pilbara Print Stone, Western Australia. Geophys J Int 199:658–672

Alley NF, Frakes LA (2003) First known cretaceous glaciation: Livingston Tillite member of the Cadna-owie formation, South Australia. Aust J Earth Sci 50:139–144

Alley NF, Pledge NS (2000) The plants, animals and environments of the last 280 million years. In: Slaytor WJH (ed) The story behind the landscape, vol 5. Geographical Society of South Australia Monograph, pp 35–82

Alley NF, Krieg GW, Callen RA (1996) Early Tertiary Eyre Formation, lower Nellie Creek, southern Lake Eyre Basin, Australia: palynological dating of macrofloras and silcrete, and palaeoclimatic interpretations. Aust J Earth Sci 43:71–84

Allwood AC, Walter MR, Kamber BS, Marshall CP, Burch IW (2006) Stromatolite reef from the Early Archaean era of Australia. Nature 441:714–718

An ZS, Bowler JM, Opdyke ND, Macumber PG, Firman JB (1986) Palaeomagnetic stratigraphy of Lake Bungunnnia: Plio-Pleistocene precursor of aridity in the Murray Basin, Southeastern Australia. Palaeogeogr Palaeoclimatol Palaeoecol 54:219–239

Ashworth AC, Cantrill DJ (2004) Neogene vegetation of the Meyer Desert formation (Sirius Group) Transantarctic Mountains, Antarctica. Palaeogeogr Palaeoclimatol Palaeoecol 213:65–82

Bagas L (1988) Geology of Kings Canyon National Park, Northern Territory Geological Survey Report 4. Department of Mines & Energy, Daerwin, p 21

Barrows TT, Stone JO, Fifield LK, Cresswell RG (2001) Late Pleistocene glaciation of the Kosciuszko Massif, Snowy Mountains, Australia. Quat Res 55:179–189

Bell, J.G., Kilgour, P.L., English, P.M., Woodgate, M.F., Lewis, S.J., Wischusen, J.D.H., 2012. WASANT Palaeovalley map – distribution of Palaeovalleys in Arid and Semi-arid WA-SA-NT (First Edition), scale 1:4 500 000. Geoscience Australia, Canberra

Belton DX, Brown RW, Kohn BP, Fink D, Farley KA (2004) Quantitative resolution of the debate over antiquity of the central Australian landscape: implications for the tectonic and geomorphic stability of cratonic interiors. Earth Planet Sci Lett 219:21–34

Berner RA, Beerling DJ, Dudley R, Robinson JM, Wildman RA Jr (2003) Phanerozoic atmospheric oxygen. Annu Rev Earth Planet Sci 31:105–134

Bierman PR, Caffee M (2002) Cosmogenic exposure and erosion history of Australian bedrock landforms. Geol Soc Am Bull 114:787–803

Bird C, Hallam SJ (2006) Archaeology and rock art in the Dampier Archipelago. A report prepared for the National Trust of Australia (WA), p 32

Blewett RS (2012) Shaping a nation: a geology of Australia. Geoscience Australia/ANU E Press, Canberra, p 571

Blodgett RH (1988) Calcareous paleosols in the Triassic Dolores Formation, southwestern Colorado. Geol Soc Am Spec Pap 216:103–121

Bowler JM (1981) Australian salt lakes: a palaeohydrological approach. Hydrobiologia 82:431–444

Bowler JM (1982) Aridity in the late Tertiary and Quaternary of Australia. In: Barker WA, Greenslade PJM (eds) Evolution of the flora and fauna of arid Australia. Peacock Publications, Adelaide, pp 35–45

Brad P, Keith Fifield L (2013) Erosion rates and weathering history of rock surfaces associated with Aboriginal rock art engravings (petroglyphs) on Burrup Peninsula, Western Australia, from cosmogenic nuclide measurements. Quat Sci Rev 69:98–106

Brocks JJ, Jarrett AJM, Sirantoine E, Hallmann C, Hoshino Y, Liyanage T (2017) The rise of algae in Cryogenian oceans and the emergence of animals. Nature 548:578

Bullard JE, White K (2002) Quantifying iron oxide coatings on dune sands using spectrometric measurements: an example from the Simpson-Strzelecki Desert, Australia. J Geophys Res 107(B6)

Byrne M, Yeates DK, Joseph L, Kearney M, Bowler J, Williams MAJ, Cooper S, Donnellan SC, Keogh JS, Leys R, Melville J, Murphy DJ, Porch N, Wyrwoll K-H (2008) Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. Mol Ecol 17:4398–4417

Canfield DE, Poulton SW, Narbonne GM (2007) Late-Neoproterozoic deep-ocean oxygenation and the rise of animal life. Science 315:92–95

Carpenter RJ, Pole M (1995) Eocene plant fossils from the Lefroy and Cowan paleodrainages, Western Australia. Aust Syst Bot 8:1107–1154

Carpenter RJ, Goodwin MP, Hill RS, Kanold K (2011) Silcrete plant fossils from Lightning Ridge, New South Wales: new evidence for climate change and monsoon elements in the Australian Cenozoic. Aust J Bot 59:399–425

Carpenter RJ, Jordan GJ, Macphail MK, Hill RS (2012) Near-tropical Early Eocene terrestrial temperatures at the Australo-Antarctic margin, western Tasmania. Geology 40:267–270

Carpenter RJ, McLoughlan S, Hill RS, McNamara KJ, Jordan GJ (2014) Early evidence of xeromorphy in angiosperms: stomatal encryption in a new Eocene species of *Banksia* (Proteaceae) from Western Australia. Am J Bot 101:1486–1497

Catling DC, Claire MW (2005) How Earth's atmosphere evolved to an oxic state: a status report. Earth Planet Sci Lett 237:1–20

Chen XY, Barton CE (1991) Onset of aridity and dune-building in Central Australia: sedimentological and magnetostratigraphic evidence from Lake Amadeus. Palaeogeogr Palaeoclimatol Palaeoecol 84:55–71

Chen X, Ling H-F, Vance D, Shields-Zhou GA, Zhu M, Poulton SW, Och LM, Jiang S-Y, Li D, Cremonese L, Archer C (2015) Rise to modern levels of ocean oxygenation coincided with the Cambrian radiation of animals. Nat Commun 6:7142

Christensen BA, Renema W, Hendriks J, De Vleeschower D, Groeneveld J, Castenada IS, Reuning L, Bogus K, Auer G, Ishiwa T, McHugh CM, Gallagher SJ, Fulthorpe CS, IODP Expedition 356 Scientists (2017) Indonesian throughflow drove Australian climate from humid Pliocene to arid Pleistocene. Geophys Res Lett 44:6914

Crowell JC, Frakes LA (1971) Late Paleozoic glaciation of Australia. J Geol Soc Aust 17:115–155

Danisik M, Evans NJ, Ramanaidou ER, McDonald BJ, Mayers C, McInnes BIA (2013) (U-Th)/He chronology of the Robe River channel iron deposits, Hamersley Province, Western Australia. Chem Geol 354:150–162

English PM, Spooner NA, Chappell J, Questiaux DG, Hill NG (2001) Lake Lewis Basin, Central Australia: environmental evolution and OSL chronology. Quat Int 83-85:81–101

English PM, Lewis SJ, Bell JG, Wischusen JDH, Woodgate MF, Bastrakov EN, Macphail MK, Kilgour PL (2012) Water for Australia's arid zone – identifying and assessing Australia's palaeovalley groundwater resources: project summation, waterlines report series no 86, August 2012, Canberra, p 147

Eyles N, de Broekert P (2001) Glacial tunnel valleys in the Eastern Goldfields of Western Australia cut below the Late Paleozoic Pilbara ice sheet. Palaeogeogr Palaeoclimatol Palaeoecol 171:29–40

Flohn H (1973) Antarctica and the global Cenozoic evolution: a geophysical model. In: Van Zinderen Bakker EM (ed) Palaeoecology of Africa. Balkema, Netherlands, pp 37–53

Folk RL (1976) Reddening of desert sands: Simpson Desert, N.T., Australia. J Sediment Petrol 46:604–615

Frakes LA, Burger D, Apthorpe M, Wiseman J, Dettmann M, Alley N, Flint R, Gravestock D, Ludbrook N, Backhouse J, Skwarko S, Scheibnerova V, McMinn A, Moore PS, Bolton BR, Douglas JG, Christ R, Wade M, Molnar RE, McGowran B, Balme BE, Day RA (1987) Australian Cretaceous shorelines, stage by stage. Palaeogeogr Palaeoclimatol Palaeoecol 59:31–48

Fu X, Cohen TJ, Arnold LJ (2017) Extending the record of lacustrine phases beyond the last interglacial for Lake Eyre in Central Australia using luminescence dating. Quat Sci Rev 162:88–110

Fujioka T, Chappell J (2010) History of Australian aridity: chronology in the evolution of arid landscapes. Geol Soc Lond Spec Publ 346(1):121–139

Fujioka T, Chappell J, Honda M, Yatsevich I, Fifield K, Fabel D (2005) Global cooling initiated stony deserts in Central Australia 2-4 Ma, dated by cosmogenic ^{21}Ne-^{10}Be. Geology 33:993–996

Fujioka T, Chappell J, Fifield LK, Rhodes EJ (2009) Australian desert dunes initiated with Pliocene-Pleistocene global climatic shift. Geology 37:51–54

Glasspool IJ, Scott AC (2010) Phanerozoic concentrations of atmospheric oxygen reconstructed from sedimentary charcoal. Nat Geosci 3(9):627–630

Gradstein FM, Ogg JG, Schmitz M, Ogg G (2012) The geological time scale. Elsevier, Oxford, p 1142

Greenwood DR (1996) Eocene monsoon forests in Central Australia? Aust Syst Bot 9:95–112

Greenwood DR, Haines PW, Steart DC (2001) New species of *Banksieaeformis* and a *Banksia* 'Cone' (Proteaceae) from the tertiary of Central Australia. Aust Syst Bot 14:871–890

Harris WK, Twidale CR (1991) Revised age for Ayers rock and the Olgas. Trans R Soc S Aust 115:109

Heimsath AM, Chappell J, Fifield K (2010) Eroding Australia: rates and processes from Bega Valley to Arnhem Land. In: Bishop P, Pillans B (eds) Australian landscapes. The Geological Society of London, London, pp 225–241

Hesse PP (1994) The record of continental dust from Australia in Tasman Sea sediments. Quat Sci Rev 13:257–272

Hesse P (2003) Australian dust deposits: modern processes and the Quaternary record. Quat Sci Rev 22(18–19):2007–2035

Hoashi M, Bevacqua DC, Otake T, Watanabe Y, Hickman AH, Utsonomiya S, Ohmoto H (2009) Primary haematite formation in an oxygenated sea 3.46 billion years ago. Nat Geosci 2:301–306

Hofmann HJ, Grey K, Hickman AH, Thorpe RI (1999) Origin of 3.45 Ga coniform stromatolites in Warrawoona Group, Western Australia. Geol Soc Am Bull 111:1256–1262

Hou B, Frakes LA, Sandiford M, Worrall L, Keeling J, Alley NF (2008) Cenozoic Eucla Basin and associated palaeovalleys, southern Australia – climatic and tectonic influences on landscape evolution, sedimentation and heavy mineral accumulation. Sediment Geol 203:112–130

Idnurm M, Senior BR (1978) Palaeomagnetic ages of late cretaceous and tertiary weathered profiles in the Eromanga Basin, Queensland. Palaeogeogr Palaeoclimatol Palaeoecol 24:263–277

Jennings JN, Mabbutt JA (1967) Landform studies from Australia and New Guinea. ANU Press, Canberra, 434 pp

Johnson BJ, Miller GH, Fogel ML, Magee J, Gagan MK, Chivas AR (1999) 65,000 years of vegetation change in Central Australia and the Australian summer monsoon. Science 284:1150–1152

Jutson JT (1914) Physiographical geology (physiography) of Western Australia. Government Printer, Perth

Kale Sniderman JM, Woodhead JD, Hellstrom J, Jordan GJ, Drysdale RN, Tyler JJ, Porch N (2016) Pliocene reversal of late Neogene aridification. Proc Natl Acad Sci 113(8):1999–2004

Karas C, Nurnberg D, Tiedemann R, Garbe-Schonberg D (2011) Pliocene Indonesian Throughflow and Leeuwin current dynamics: implications for Indian Ocean polar heat flux. Paleoceanography 26:PA2217

Kohn BP, Gleadow AJW, Brown RW, Gallagher K, O'Sullivan PB, Foster DA (2002) Shaping the Australian crust over the last 300 million years: insights from fission track thermotectonic imaging and denudation studies of key terranes. Aust J Earth Sci 49:697–717

Lagabrielle Y, Godderis Y, Donnadieu Y, Malavieille J, Suarez M (2009) The tectonic history of drake passage and its possible impacts on global climate. Earth Planet Sci Lett 279:197–211

Lawver LA, Gahagan LM (2003) Evolution of Cenozoic seaways in the circum-Antarctic region. Palaeogeogr Palaeoclimatol Palaeoecol 198:11–37

Lyons TW, Reinhard CT, Planavsky NJ (2014) The rise of oxygen in Earth's early ocean and atmosphere. Nature 506:307–315

Mabbutt JA (1977) Desert landforms. ANU Press, Canberra

Mack CL, Milne LA (2015) Eocene palynology of the Mulga Rocks deposits, Southern Gunbarrel Basin, Western Australia. Alcheringa 39:444–458

Macphail MK, Stone MS (2004) Age and palaeoenvironmental constraints on the genesis of the Yandi channel iron deposits, Marillana formation, Pilbara, Northwestern Australia. Aust J Earth Sci 51:497–520

Magee JW, Miller GH, Spooner NA, Questiaux D (2004) Continuous 150 k.y. monsoon record from Lake Eyre, Australia: insolation-forcing implications and unexpected Holocene failure. Geology 32:885–888

Martin HA (2006) Cenozoic climatic change and the development of arid vegetation in Australia. J Arid Environ 66:533–563

McBride EF (1974) Significance of color in red, green, purple, olive, brown, and gray beds of Difunta Group, Northeastern Mexico. J Sediment Petrol 44:760–773

McKenzie N, Jacquier D, Isbell R, Brown K (2004) Australian soils and landscapes. An illustrated compendium. CSIRO Publishing, Melbourne

Miller G, Mangan J, Pollard D, Thompson S, Felzer B, Magee J (2005) Sensitivity of the Australian monsoon to insolation and vegetation: implications for human impact on continental moisture balance. Geology 33:65–68

Miller CR, James NP, Bone Y (2012) Prolonged carbonate diagenesis under an evolving late cenozoic climate: Nullarbor Plain, Southern Australia. Sediment Geol 261-262:33–49

Miller GH, Fogel ML, Magee JW, Gagan MK (2016) Disentangling the impacts of climate and human colonization on the flora and fauna of the Australian arid zone over the past 100 ka using stable isotopes in avian eggshell. Quat Sci Rev 151:27–57

Molnar P, Cronin TW (2015) Growth of the maritime continent and its possible contribution to recurring ice ages. Paleoceanography 30:196–225

Morris RC, Ramanaidou ER (2007) Genesis of the channel iron deposits (CID) of the Pilbara region, Western Australia. Aust J Earth Sci 54:733–756

Morris RV, Lauer HV Jr, Lawson CA, Gibson EK Jr, Nace GA, Stewart C (1985) Spectral and other physicochemical properties of submicron powders of hematite (α-Fe_2O_3), maghemite (γ-Fe_2O_3), magnetite (Fe_3O_4), goethite (α-FeOOH) and lepidocrocite (γ-FeOOH). J Geophys Res 90:3126–3144

Mortimer N, Campbell HJ, Tulloch A, King PR, Stagpoole VM, Wood RA, Rattenbury MS, Sutherland R, Adams CJ, Collot J, Seton M (2017) Zealandia: earth's hidden continent. GSA Today 27:27–35

Munsell Color Company (1975) Munsell soil colour charts. Macbeth Division of Kollmorgen, Baltimore

Nutman AP, Bennett VC, Friend CRL, Van Kranendonk MJ, Chivas AR (2016) Rapid emergence of life shown by discovery of 3,700-million-year-old microbial structures. Nature 537:535

Pain CF, Ollier CD (1995) Inversion of relief – a component of landscape evolution. Geomorphology 12:151–165

Pain CF, Pillans BJ, Roach IC, Worrall L, Wilford JR (2012) Old, flat and red – Australia's distinctive landscape. In: Blewett RS (ed) Shaping a nation: a geology of Australia. Geoscience Australia and ANU E Press, Canberra, pp 226–275

Pell SD, Chivas AR (1995) Surface features of sand grains from the Australian Continental Dunefield. Palaeogeogr Palaeoclimatol Palaeoecol 113:119–132

Pell SD, Chivas AR, Williams IS (1999) Great Victoria Desert: development and sand provenance. Aust J Earth Sci 46:289–299

Pell SD, Chivas AR, Williams IS (2000) The Simpson, Strzelecki and Tirari Deserts: development and sand provenance. Sediment Geol 130:107–130

Pillans B (2007) Pre-Quaternary landscape inheritance in Australia. J Quat Sci 22:439–447

Pillans B (2010) Late Carboniferous-Early Permian paleomagnetic poles from regolith in cratonic Australia. J Geol Soc Aust Abstr 98:74–75

Pillans B, Bourman R (2001) Mid Pleistocene arid shift in Southern Australia, dated by magnetostratigraphy. Aust J Soil Res 39:89–98

Playford PE, Cockbain AE, Berry PF, Roberts AP, Haines PW, Brooke BP (2013) The geology of Shark Bay, geological survey of Western Australia Bulletin 146. Geological Survey of Western Australia, Perth, p 281

Pole MS, Macphail MK (1996) Eocene Nypa from Regatta Point, Tasmania. Rev Palaeobot Palynol 92(1–2):55–67

Prideaux GJ, Long JA, Ayliffe LK, Hellstrom JC, Pillans B, Boles WE, Hutchinson MN, Roberts RG, Cupper ML, Arnold LJ, Devine PD, Warburton NM (2007) An arid-adapted middle Pleistocene vertebrate fauna from south-central Australia. Nature 445(7126):422–425

Ramanaidou ER, Morris RC, Horwitz RC (2003) Channel iron deposits of the Hamersley Province, Western Australia. Aust J Earth Sci 50:669–690

Rasmussen B, Buick R (1999) Redox state of the Archean atmosphere: evidence from detrital heavy minerals in ca. 3250-2750 a sandstones from the Pilbara Craton, Australia. Geology 27:115–118

Rasmussen B, Fletcher IR, Muhling JR, Thorne WS, Broadbent GC (2007) Prolonged history of episodic fluid flow in giant hematite ore bodies: evidence from U-Pb geochronology of hydrothermal xenotime. Earth Planet Sci Lett 258:249–259

Rasmussen B, Fletcher IR, Bekker A, Muhling JR, Gregory CJ, Thorne AM (2012) Deposition of 1.88-billion-year-old iron formations as a consequence of rapid crustal growth. Nature 484:498–501

Rasmussen B, Krapež B, Meier DB (2014a) Replacement origin for hematite in 2.5 Ga banded iron formation: evidence for postdepositional oxidation of iron-bearing minerals. Geol Soc Am Bull 136:438–446

Rasmussen B, Krapež B, Muhling JR (2014b) Hematite replacement of iron-bearing precursor sediments in the 3.46-b.y.-old Marble Bar Chert, Pilbara craton, Australia. Geol Soc Am Bull 126:1245–1258

Rey PF (2013) Opalisation of the Great Artesian Basin (Central Australia): an Australian story with a Martian twist. Aust J Earth Sci 60:291–314

Rossman GR (1996) Why hematite is red: correlation of optical absorption intensities and magnetic moments of Fe^{3+} minerals. In: Dyar MD, McGammon C, Schaefer MW (eds) Mineral spectroscopy: a tribute to Roger G. Burns. The Geochemical Society, special publication no 5, pp 23–27

Sandiford M (2007) The tilting continent: a new constraint on the dynamic topographic field from Australia. Earth Planet Sci Lett 261:152–163

Scher HD, Whittaker JM, Williams SE, Latimer JC, Kordesch WEC, Delaney ML (2015) Onset of Antarctic Circumpolar Current 30 million years ago as Tasmanian Gateway aligned with westerlies. Nature 523:580–583

Schmidt PW, Clark DA (1994) Palaeomagnetism and magnetic anisotropy of Proterozoic banded-iron formations and iron ores of the Hamersley Basin, Western Australia. Precambrian Res 69:133–155

Schmidt PW, Williams GE (2017) Paleomagnetic age of ferruginous weathering beneath the Hamersley surface, Pilbara, Western Australia, and the Cenozoic apparent polar wander path. Aust J Earth Sci 64:239–249

Sheppard S, Krapez B, Zi J-W, Rasmussen B, Fletcher IR (2017) Young ores in old rocks: Proterozoic iron mineralisation in Mesoarchean banded iron formation, northern Pilbara Craton, Australia. Ore Geol Rev 89:40–67

Smith ML, Pillans BJ, McQueen KG (2009) Paleomagnetic evidence for periods of intense oxidative weathering, McKinnons mine, Cobar, New South Wales. Aust J Earth Sci 56:201–212

Stewart AJ, Blake DH, Ollier CD (1986) Cambrian river terraces and ridgetops in Central Australia: oldest persisting landforms? Science 233:758–761

Stuut J-BW, Temmesfeld F, De Deckker P (2014) A 550 ka record of aeolian activity near North West Cape, Australia: inferences from grain-size distributions and bulk chemistry of SE Indian Ocean deep-sea sediments. Quat Sci Rev 83:83–94

Sweet IP, Stewart AJ, Crick IH (2012) Uluru and Kata Tjuta: a geological guide. Geoscience Australia, Canberra, 63 pp

Thomas M, Clarke JDA, Pain CF (2005) Weathering, erosion and landscape processes on Mars identified from recent rover imagery, and possible earth analogues. Aust J Earth Sci 52:365–378

Thornbury WD (1954) Principles of geomorphology. Wiley, New York

Travouillon KJ, Legendre S, Archer M, Hand SJ (2009) Palaeoecological analyses of Riversleigh's Oligo-Miocene sites: Implications for Oligo-Miocene climate change in Australia. Palaeogeogr Palaeoclimatol Palaeoecol 276(1–4):24–37

Twidale CR (1976) On the survival of paleoforms. Am J Sci 276:77–95

Valley JW, Cavosie AJ, Ushikubo T, Reinhard DA, Lawrence DF, Larson DJ, Clifton PH, Kelly TF, Wilde SA, Moser DE, Spicuzza MJ (2014) Hadean age for a post-magma-ocean zircon confirmed by atom-probe tomography. Nat Geosci 7:219–223

Vasconcelos PM, Heim JA, Farley KA, Monteiro H, Waltenberg K (2013) ^{40}Ar/^{39}Ar and (U-Th)/He – ^{4}He/^{3}He geochronology of landscape evolution and channel iron deposit genesis at Lynn Peak, Western Australia. Geochim Cosmochim Acta 117:283–312

Viscarra Rossel RA, Minasny B, Roudier P, McBratney AB (2006) Colour space models in soil science. Geoderma 133:320–337

Viscarra Rossel RA, Bui EN, de Caritat P, McKenzie NJ (2010) Mapping iron oxides and the color of Australian soil using visible-near-infrared reflectance spectra. J Geophys Res 115:F04031

Walker TR (1979) Red color in dune sand. In: McKee ED (ed) A study of global sand seas. US Government Printer, Washington, DC, pp 61–81

Wasson RJ (1983) Dune sediment types, sand colour, sediment provenance and hydrology in the Strzelecki-Simpson dunefield, Australia. In: Brookfield ME, Ahlbrandt TS (eds) Eolian sediments and processes. Elsevier, Amsterdam, pp 165–195

Weber UD, Kohn BP, Gleadow AJW, Nelson DR (2005) Low temperature Phanerozoic history of the Northern Yilgarn Craton, Western Australia. Tectonophysics 400:127–151

West MD, Clarke JDA, Thomas M, Pain CF, Walter MR (2010) The geology of Australian Mars analogue sites. Planet Space Sci 58:447–458

Wilford J (2012) A weathering index for the Australian continent using airborne gamma-ray spectrometry and digital terrain analysis. Geoderma 183–184:124–142

Woodburne MO, MacFadden BJ, Case JA, Springer MS, Pledge NS, Power JD, Woodburne JM, Springer KB (1994) Land mammal biostratigraphy and magnetostratigraphy of the Etadunna formation (late Oligocene) of South Australia. J Vertebr Paleontol 13:483–515

Woodhead J, Hand SJ, Archer M, Graham I, Sniderman K, Arena DA, Black KH, Godthelp H, Creaser P, Price E (2016) Developing a radiometrically-dated chronologic sequence for Neogene biotic change in Australia, from the Riversleigh World Heritage Area of Queensland. Gondwana Res 29(1):153–167

Wopfner H, Twidale CR (1988) Formation and age of desert dunes in the Lake Eyre depocentres in Central Australia. Geol Rundsch 77:815–834

Yapp CJ, Shuster DL (2017) D/H of late Miocene meteoric waters in Western Australia: Paleoenvironmental conditions inferred from the δD of (U-Th)/He-dated CID goethite. Geochim Cosmochim Acta 213:110–136

Zachos J, Pagani M, Sloan L, Thomas E, Billups K (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292:686–693

Zachos JC, Dickens GR, Zeebe RE (2008) An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. Nature 451:279–283

Zheng H, Wyrwoll K-H, Li Z, Powell CM (1998) Onset of aridity in Southern Western Australia – a preliminary palaeomagnetic appraisal. Glob Planet Chang 18:175–187

Evolutionary History

Margaret Byrne, Leo Joseph, David K. Yeates, J. Dale Roberts, and Danielle Edwards

Introduction

Australia is a vast continent with a range of environments broadly differentiated into three major biomes. The best studied of these, the mesic biome, is confined to the eastern coast and the southeast and southwest corners and has pockets of ever-wet rainforest along the east coast. The monsoon tropics biome occurs in the northern part of the continent including Cape York Peninsula in the east, and the arid-zone biome covers the vast central and western parts of the continent, generally west of the Great Dividing Range. The arid zone is Australia's largest biome, occupying approximately 70% of the entire continent (Fig. 1a) and broadly corresponding to the Eremaean and northern desert regions of the Australian Bioregionalisation Atlas (Ebach et al. 2015) (Fig. 1b). It covers a range of environments such as sandy

M. Byrne (✉)
Biodiversity and Conservation Science, Department of Biodiversity, Conservation and Attractions, Kensington, WA, Australia

School of Biological Sciences, The University of Western Australia, Perth, WA, Australia
e-mail: margaret.byrne@dbca.wa.gov.au

L. Joseph
Australian National Wildlife Collection, CSIRO National Facilities and Collections, Canberra, Australian Capital Territory, Australia

D. K. Yeates
Australian National Insect Collection, CSIRO National Research Collections Australia, Canberra, ACT, Australia

J. D. Roberts
Centre for Excellence in Natural Resource Management, The University of Western Australia, Albany, Western Australia, Australia

D. Edwards
Life and Environmental Sciences, University of California, Merced, CA, USA

H. Lambers (ed.), *On the Ecology of Australia's Arid Zone*,
https://doi.org/10.1007/978-3-319-93943-8_3

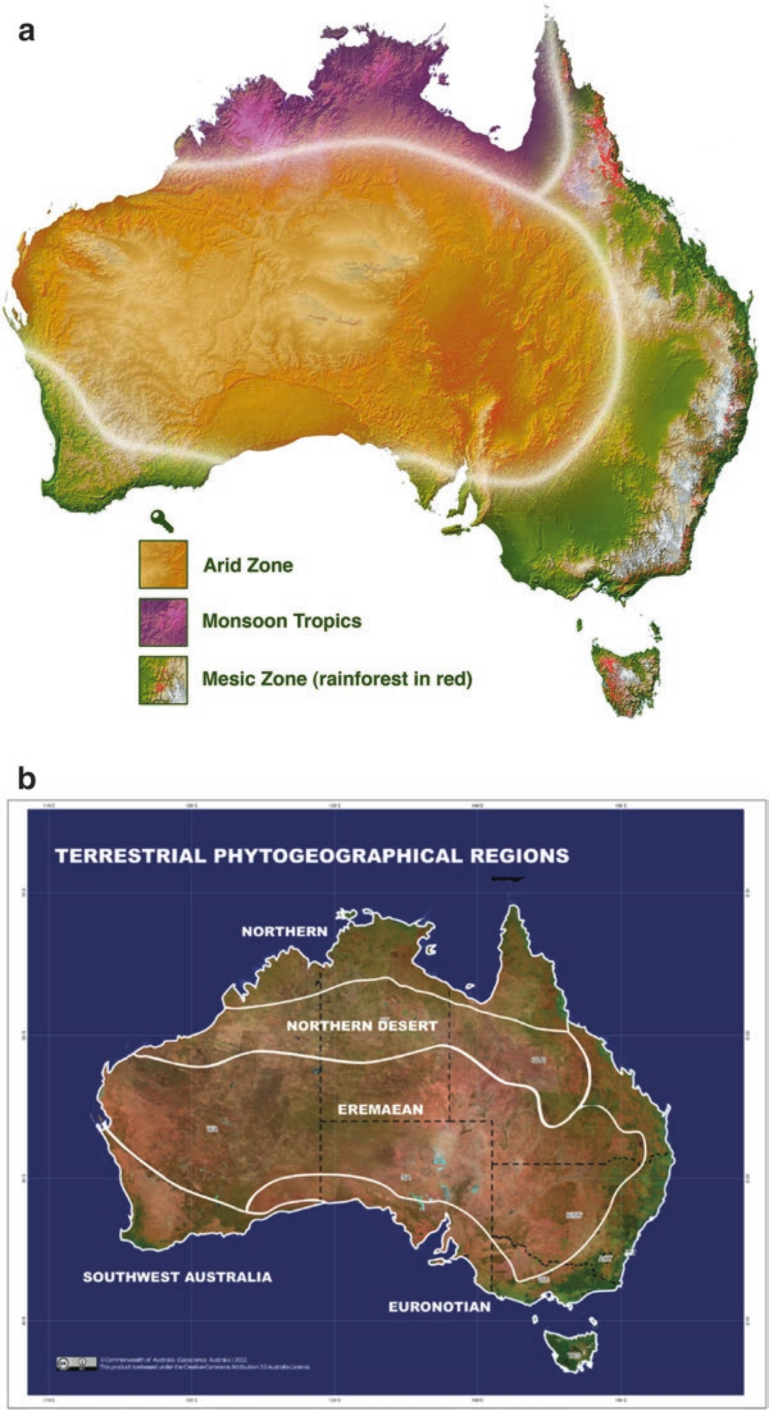


Fig. 1 (**a**) Geomorphological map of Australia showing the three major biomes of Australia with the arid zone encompassing the central and western parts of the continent (Anne Hastings, CSIRO). (**b**) The arid zone broadly corresponds to the Eremaean and northern desert phytogeographical regions of Australia. (From Ebach et al. 2015)

deserts, gibber deserts and steppes, ranges and coastal plains and hosts a variety of vegetation types, shrub woodlands, acacia and mallee eucalypt shrublands, spinifex grasslands, tussock and hummock grasslands and chenopod shrublands. On average, the arid zone is only 300 m above sea level with low relief and a broad flat plain covering most of the central western area (Williams 1984; Pain et al. 2012; Pillans 2018).

Although the arid zone covers a vast area of often inhospitable environments, the diversity of plants, animals, birds, reptiles and invertebrates that make up the biota of this biome is reasonably well understood (Barker and Greenslade 1982; Cogger and Cameron 1984; Cracraft 1986, 1991; Dawson and Dawson 2006; Schodde 1982; Stafford Smith and Morton 1990). Assessments of species diversity have revealed greatest diversity in the reptiles and invertebrates; 43% of the continent's reptiles and a similar proportion of termites and ants inhabit arid environments (Byrne et al. 2008), the majority of Australia's 7500 ant species occurring in the arid zone (Andersen 2016). The diversity of other groups is less; only 15% of birds and 10% of plant species are endemic to the arid zone (Barker and Greenslade 1982; Schodde 1982, 2006). Analysis of turnover of species from six groups of vascular plants and three groups of non-vascular plants identified major change in vegetation communities within the arid zone and specified nine phytogeographical subregions, the western, central and eastern deserts, the Pilbara and Great Sandy Desert interzone, the Central Queensland area and the Nullarbor, Eyre Peninsula and Adelaide areas (Ebach et al. 2015).

The current arid zone is defined here as having a moisture index (mean annual rainfall divided by evaporation) of 0.4, annual rainfall that is generally below 250 mm and unpredictable, and little seasonality (Stafford Smith and Morton 1990). Byrne et al. (2008) provided a detailed summary of the environmental history of arid Australia, based on a review of evidence from plant macro- and microfossils, sedimentology, fossil faunal assemblages, palaeodrainage, geomorphology and isotope analyses. We provide a short contextual summary here and in Fig. 2.

The arid zone is considered to be younger than the mesic zone. This is because the rainforest vegetation of the Australian continent in the Eocene (55–35 million years ago) reflects far more mesic conditions historically than currently (Hill 1994; Schodde 2006). Geomorphological evidence indicates that the whole of Australia was warm and wet in the Early to Mid-Miocene (23–20 million years ago) (Alley and Lindsay 1995; Martin 2006). Progressive aridification of the Australian environment occurred from the Mid-Miocene (~20 million years ago), the first signs of aridity evident in cessation of regular flows in western palaeodrainage channels (Bowler et al. 2006). Pockets of arid environments may have been present in the current arid zone in the Mid-Miocene, but the stony and sandy desert environments did not fully develop until the Pliocene (6–2.8 million years ago) and Mid-Pleistocene (~1 million years ago) respectively (Fujioka et al. 2009, 2005). The Nullarbor Plain, a large limestone plateau in the central southern region of Australia, was subject to marine inundation in the Mid-Miocene (~15 million years ago) (McGowran et al. 2004), effectively separating the mesic environments of the southwest and southeast

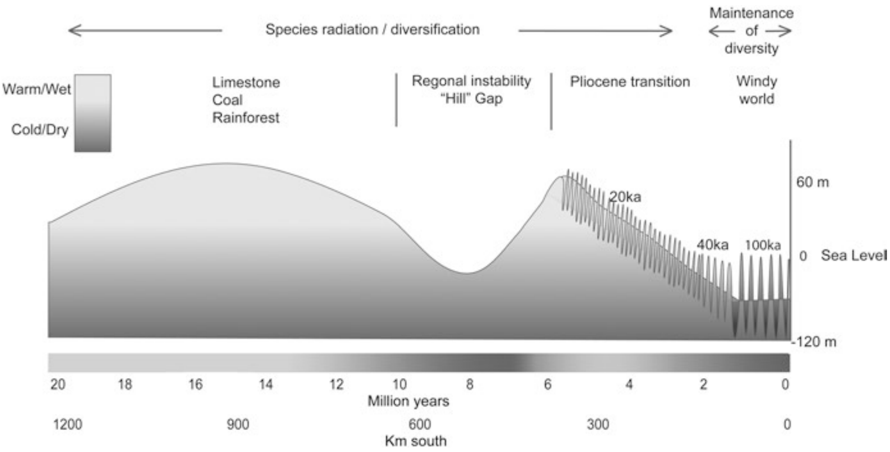


Fig. 2 Diagrammatic representation of the palaeoclimatic conditions of Australia during the evolution of the arid zone over the last 20 million years. Horizontal axes represent (i) time in the past and (ii) distance that the Australian continent was further south than present during the past. Vertical axis representing sea level is not to scale. Development of cycling of climatic conditions and sea level changes are evident through the Pliocene and Pleistocene. Shading indicates warm/wet vs. cold/dry climatic conditions. (From Byrne et al. 2008)

(Crisp and Cook 2007). At this time, the sea level fell around Southern Australia, and the ocean's incursions into the south-eastern marine basins retreated (Murray, Otway and Gippsland), leaving repeated shoreline ridges evident in the Murray Basin (Bowler et al. 2006).

As highlighted in an earlier review (Byrne et al. 2008), the environmental changes of the Late Miocene (10–6 million years ago) remain poorly understood. A major termination of the previous warm, wet environments and very high levels of erosion indicate destabilisation of vegetation cover. Fossil evidence shows that rainforest contracted, and sclerophyllous taxa like *Eucalyptus* and *Casuarina* expanded, as did dry, open woodlands and chenopod shrublands (Martin 2006). Conditions in the Pliocene (6–2.6 million years ago) showed a temporary return of warmer, wetter conditions than those of the Late Miocene, but not to the extent of the Early Miocene (Sniderman et al. 2016). Depositional activity in the Pliocene is indicative of drier conditions (Bowler et al. 2006), and the vegetation comprised sclerophyllous forest and woodlands and development of shrublands and grasslands (Martin 2006; Sniderman et al. 2007). Development of the first stony desert pavements in Central Australia occurred 3–2 million years ago at the end of the Pliocene (Fujioka et al. 2005).

The onset of the Pleistocene heralded the development of glacial and interglacial cycles of 20,000–40,000 years duration in the northern hemisphere (Williams et al. 1998). In Australia, these were manifest as arid-mesic cycles. These climatic oscillations became more intense, having major increases in amplitude and periodicity of 100,000 years from the Mid-Pleistocene, concomitant with the development of the sandy deserts (Fujioka et al. 2009). The last 400,000 years saw major change in hydrological conditions, such as drying of inland lakes and widespread erosion and wind-blown dust (Bowler et al. 1998; Revel-Rolland et al. 2006). Conditions at the Last Glacial Maximum (~25–15,000 years ago) were extremely arid. Sea level was ~120 m lower than present, freshwater lakes dried out or became saline, streams showed large sand and gravel flows, mobile dune systems were activated, and large areas were treeless or devoid of vegetation (Williams 2000, 2001). Analysis of isotopes in emu eggshells shows evidence for a peak in aridity between 30,000 and 15,000 years ago (Miller et al. 2016).

The environmental changes throughout the Miocene, Pliocene and Pleistocene led to development of the current arid zone and contraction of mesic environments to the southwest and southeast, eastern seaboard and northern areas of Australia (Byrne et al. 2011). These environmental changes must have had significant impact on the plants and animals inhabiting these areas, and they led to the evolution of the current arid-zone biota. Modern approaches to understanding the evolutionary history of these plants and animals complement a rich, earlier literature built on morphological data. They are based on molecular genetic data and analysis of phylogenies and phylogeographic studies of the biota. Further, they are conducted in the context of historical climatic and geological events and so can reveal significant, novel insights into the response of the biota to changing environmental conditions. Byrne et al. (2008) reviewed the phylogenetic and phylogeographic evidence for the development of the arid-zone biota and found two broad phases of development. First, there is evidence for diversification and radiation of lineages through the Miocene and Pliocene when arid environments were forming throughout Central Australia. Second, there was a phase of maintenance of species diversity through the Pleistocene, when extreme aridity occurred through cyclic climatic conditions. Here, we assess molecular analyses published since 2008 to test and explore the generality of these conclusions.

Origins and Diversification of the Arid-Zone Biota

In their review of the origins of the arid-zone biota, Byrne et al. (2008) found evidence of both adaptive diversification in situ from ancestral forms present in Central Australia prior to the Miocene and for multiple independent divergences from mesic ancestors over time. Assessment of molecular phylogenies showed origin of arid lineages from mesic ancestors in plants and in animals (Fig. 3). A pattern of sister arid-mesic lineages showing divergence of arid lineages was present in plant phylogenies of *Tetratheca* (Crayn et al. 2006), *Calotis* (Watanabe et al. 2006), *Lepidium* (Mummenhoff et al. 2001) and *Halosarcia* (Shepherd et al. 2004) and in the agamid lizards (Hugall et al. 2008), the *Egernia whitii* complex of skinks (Chapple and Keogh 2004), diving beetles, amphipods (Cooper et al. 2007; Leys et al. 2003; Rix and Harvey 2012; Schmidt and Walter 2014) and *Artamus* woodswallows (Joseph et al. 2006). More recent studies have found further evidence for this, as phylogenetic analysis of the large plant family Goodeniaceae suggests a most likely south-western Australian origin, with the *Goodenia* clade diversifying

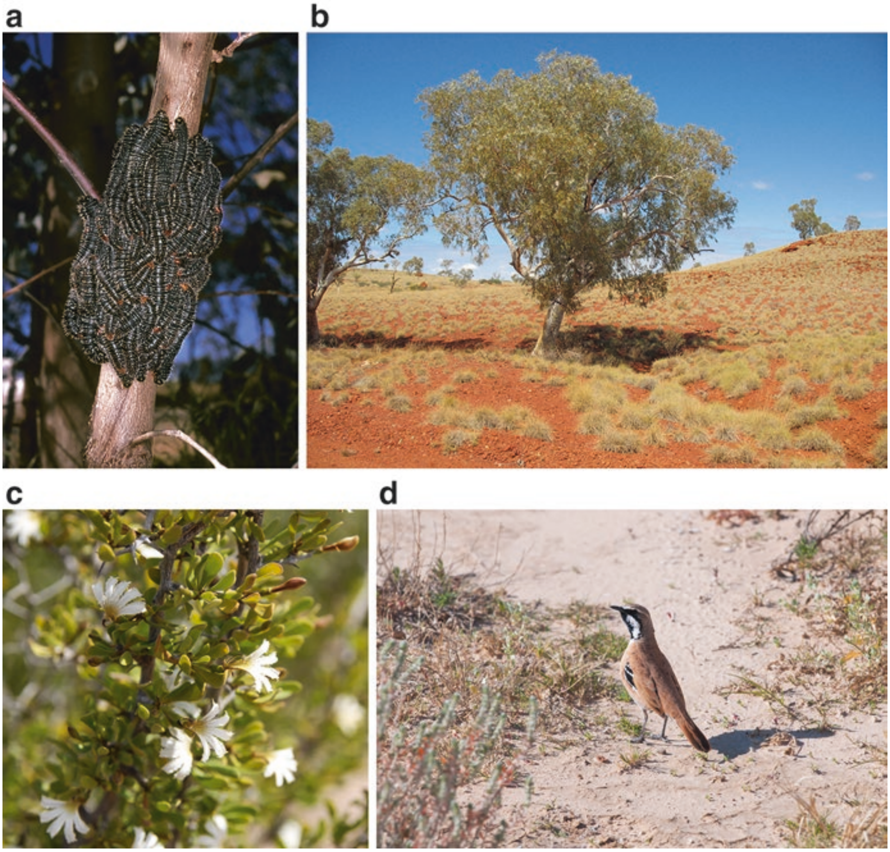


Fig. 3 Many arid-zone groups have diversified from mesic ancestors such as (**a**) sawflies. (Photo David Yeates), (**b**) eucalypts. (Photo Margaret Byrne), (**c**) *Scaevola.* (Photo Kelly Shepherd) and (**d**) quail-thrush. (Photo Chris Sanderson)

within the arid zone as it developed and the *Dampiera*/*Lechenaultia* clade diversifying mainly in the southwest (Jabaily et al. 2014). Eucalypts diversified from the Early Miocene with south-western Australia resolving as the most ancestral area (Ladiges et al. 2011a). Area phylogenetic analysis in the plant genus *Nicotiana* shows older taxa in peripheral mesic areas and derived taxa in arid inland areas (Ladiges et al. 2011b). Biogeographic and phylogenetic analysis of the *Hakea* shows multiple biome shifts, but the majority of arid diversification arises from mesic biomes, particularly south-western Australia (Cardillo et al. 2017), and arid-adapted species of *Callitris* have diversified from mesic ancestors (Larter et al. 2017). Similar patterns have been observed in sawflies (Schmidt and Walter 2014), flightless weevils (Toussaint et al. 2015b), *Delma* geckoes (Brennan et al. 2016) and several birds such as the nectarivorous lorikeets and budgerigar (Schweizer et al. 2015; Wright et al. 2008), platycercine parrots (Schweizer et al. 2012), honeyeaters (Joseph et al. 2014), *Cinclosoma* quail-thrush (Toon et al. 2012), whipbirds and wedgebills (Toon et al. 2013) and malurid fairy wrens (Driskell et al. 2011; Lee et al. 2012). Among marsupials, Mitchell et al. (2014) found a pattern of mesic-adapted lineages evolving to use more arid and open habitats that is broadly consistent with regional climate and environmental change. Additionally, several mammal groups, including Dasyuromorphia, Vombatiformes, Trichosurini and Peramelemorphia, appear to have made the transition to open environments prior to the onset of widespread Miocene aridification, possibly reflecting lineages that survived from drier periods in the Oligocene (34–23 million years ago) when limited open forest habitats may have been available (Kear et al. 2016; Travouillon et al. 2009). Phylogenies show multiple radiations into the arid zone during the Miocene in the *Pauropsalta* complex of cicadas (Owen et al. 2017), the spiny trapdoor spiders (Rix et al. 2017) and the *Melophorus* ants (Heterick et al. 2017). Phylogeny of the truffle-like fungi also shows radiation of arid-zone species from mesic ancestors (Sheedy et al. 2016). Evidence from multiple stygobiont invertebrates suggests that microallopatric speciation within individual calcretes is significant and that the fauna may total to almost 3,000 species (Guzik et al. 2009, 2011a, b). In contrast, some amphipods, isopods and copepods appear to have entered the underground environments through separate colonisation events (Bradford et al. 2010; Finston et al. 2009; Javidkar et al. 2016; Karanovic and Cooper 2012; King et al. 2012).

While many arid lineages are derived from mesic ancestors (e.g. Pepper and Keogh 2014), there is also evidence of divergence from tropical ancestors in the plant genera *Gossypium* (Liu et al. 2001; Seelanan et al. 1999) and *Flindersia* (Scott et al. 2000). More recent studies have identified similar divergence from tropical ancestors in the plant genus *Atriplex* (Kadereit et al. 2010); in the frog genera *Uperoleia* (Catullo et al. 2011, 2014; Catullo and Keogh 2014), *Platyplectrum* and *Litoria* (Pyron and Wiens 2011) (Fig. 4); and in the *Heteronotia*, *Diplodactylus*, *Oedura* and *Strophurus* geckoes (Fujita et al. 2010; Oliver et al. 2016; Oliver and McDonald 2016; Laver et al. 2017).

Broad estimates of the relative timing of divergence events can be determined through molecular dating of phylogenies. In their review Byrne et al. (2008) found that in general, lineages that diversified in situ tended to occur at the genus and subgenus level and showed older diversification times during the Mid- to Late Miocene, e.g. *Gossypium* (Liu et al. 2001; Seelanan et al. 1999), *Ctenophorus* lizards (Melville et al. 2001) and elapid snakes (Sanders et al. 2008). Similar patterns have been found more recently in the plant genera *Triodia* (Toon et al. 2015), *Atriplex* (Kadereit et al. 2010), and *Eucalyptus* (Ladiges et al. 2011a) and the chenopods (Kadereit and Freitag 2011), in *Uperoleia* frogs (Catullo et al. 2011, 2014; Catullo and Keogh 2014) and in *Diporiphora* agamids (Edwards and Melville 2011; Smith et al. 2011) and *Oedura* geckoes (Oliver et al. 2014). While most arid species of *Oedura* geckoes diverged in the last 5 million years, an early diverging lineage over 10 million years was also recently identified (Oliver and McDonald 2016). The vacronini Tenebrionidae beetles of arid Australia have closest relatives in North America, originated in the Early Cretaceous (~145 million years ago), and may have inhabited coastal dune systems before the Australian arid biome developed (Kergoat et al. 2014; Matthews 2000). *Warramaba* grasshoppers diverged in the

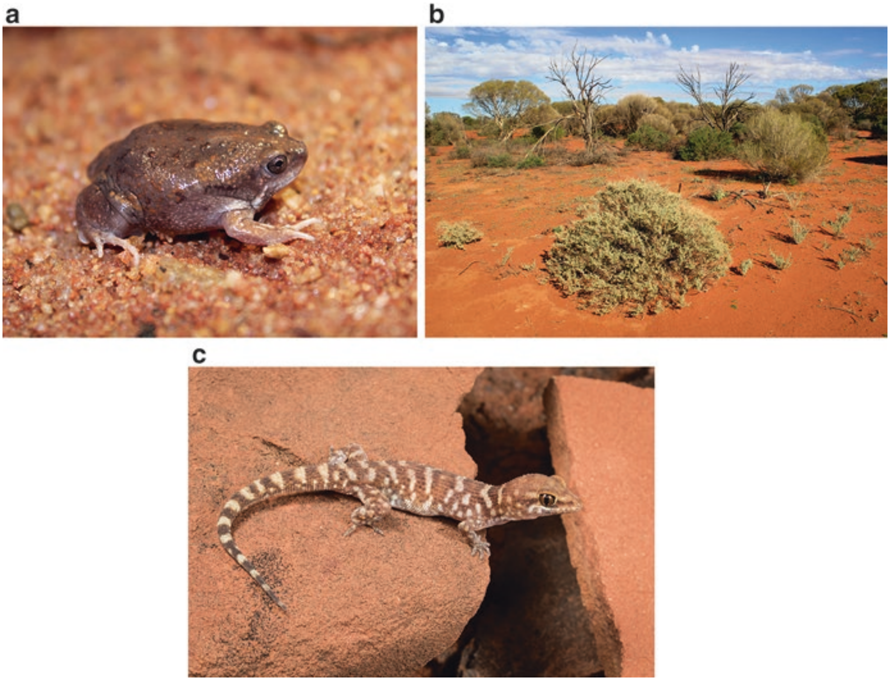


Fig. 4 Some arid-zone groups have diversified from tropical ancestors such as (**a**) *Uperoleia* toadlets. (Photo Renee Catullo), (**b**) *Atriplex.* (Photo Kelly Shepherd), (**c**) *Heteronotia* gecko. (Photo Stephen Zozaya)

Pliocene; northern sexual lineages persisted in local refugia in the Pleistocene, but parthenogenetic lineages expanded in the Pleistocene, suggesting that habitats became unsuitable in the north (Kearney and Blacket 2008).

While many phylogenies show patterns of divergence of major lineages as discussed above, Byrne et al. (2008) also found a second pattern of individual arid species or lineages present throughout phylogenies indicating multiple origins of arid species in the large plant genus *Acacia* (Ariati et al. 2006; Murphy et al. 2003), dasyurid marsupials (Crowther and Blacket 2003; Krajewski et al. 2000), the sphenomorphine skinks (Rabosky et al. 2007) and *Neobatrachus* frogs (Mable and Roberts 1997). This pattern has also been found more recently in the plant genera *Dampiera* and *Lechenaultia* (Jabaily et al. 2014), and *Hakea* and *Grevillea* (Mast et al. 2015; Cardillo et al. 2017), as well as in pseudoscorpions (Harrison et al. 2014) and the *Pauropsalta* complex of cicadas (Owen et al. 2017). Among birds, the radiation of the iconic Australo-Pacific family of honeyeaters, Meliphagidae, neatly illustrates the independent evolution of several arid-zone genera in the Mid- to Late Miocene (20–6 million years ago). These include a number of monotypic genera of the arid and semiarid zones (*Sugomel*, *Purnella*, *Certhionyx*, *Acanthagenys*, *Epthianura*, *Ashbyia*, *Grantiella*, *Plectorhyncha*) (Joseph et al. 2014). In general, most groups show diversification of species or lineages in the Late Miocene to

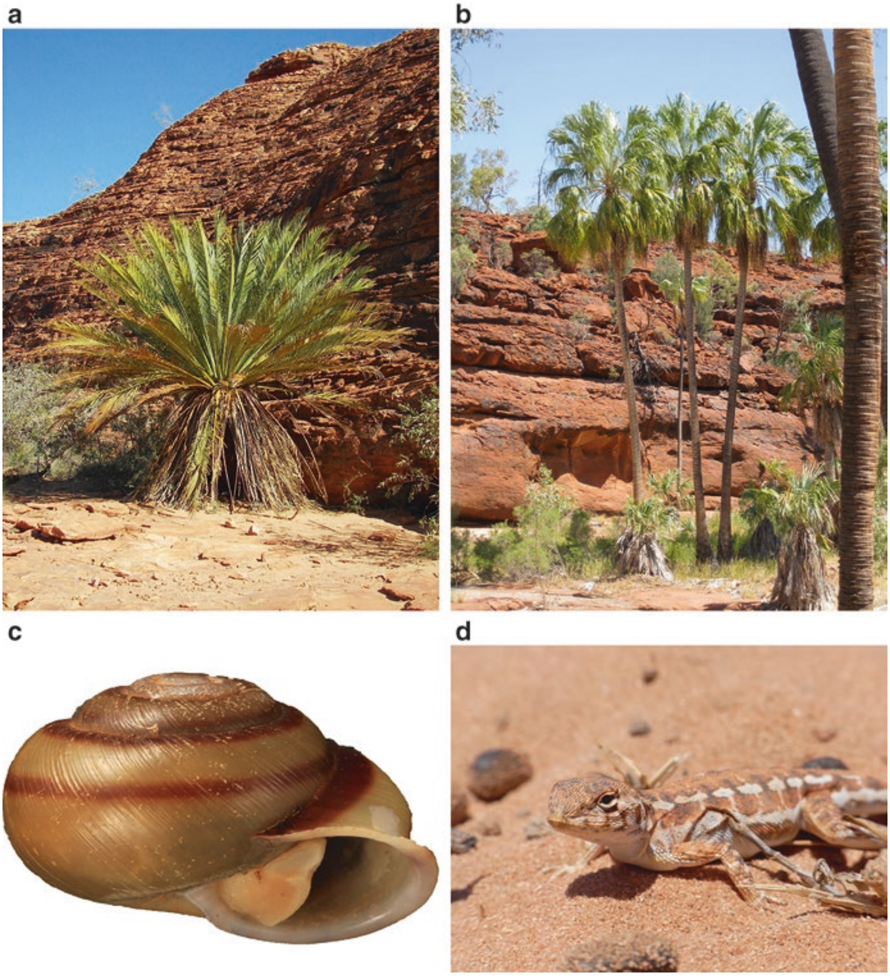


Fig. 5 While most diversification of arid-zone biota occurred in the Miocene and Pliocene, some groups diversified in the Pleistocene: (**a**) *Macrozamia macdonnellii.* (Image James Ingham), (**b**) *Livistona.* (Photo Mike Crisp), (**c**) *Granulomelon* land snails. (Photo Francesco Criscione), (**d**) *Ctenophorus maculatus.* (Photo Dan Edwards)

Pliocene, e.g. *Acacia* (Ariati et al. 2006; Murphy et al. 2003), *Hakea* (Cardillo et al. 2017) and the dasyurid marsupials (Krajewski et al. 2000), and there is less evidence for species divergence in the Pleistocene. Byrne et al. (2008) only found three cases of Pleistocene speciation that had been documented, Australian species of *Lepidium* (Mummenhoff et al. 2004); the geographically restricted shrub, *Acacia sciophanes* (Byrne et al. 2001); and a number of gall-forming *Kladothrips* species associated with *Acacia* (McLeish et al. 2007). More recent studies have revealed more cases of Pleistocene speciation (Fig. 5). Ingham et al. (2013) found that *Macrozamia macdonnellii*, the only species in the arid zone among 41 *Macrozamia* species, diverged approximately 1.08 million years ago, much later than the divergence of the south-western and south-eastern mesic species of the genus; and divergence of two arid-zone species of *Livistona* from monsoon tropical congeners occurred in the Late Pleistocene (Crisp et al. 2010). Divergence among species in *Nicotiana* section *Suaveolentes* began 6 million years ago but accelerated in the Pleistocene from 2.6 million years ago (Clarkson et al. 2017). Two species of *Granulomen* land snails are widespread in the arid zone and diverged in the Mid-Pleistocene (Criscione and Köhler 2016), and there is evidence of in situ speciation between river systems in the Pilbara Craton and the Gascoyne drainages in *Uperoleia* frogs (Catullo and Keogh 2014). Species within the *Ctenophorus maculatus* species complex further show rapid divergence throughout the Pleistocene, coincident with the diversification of sand plain and dune habitats (Edwards et al. 2015); similar sand habitat diversification has likely been involved in the diversification of other species-rich arid clades (e.g. *Lerista* (Lee et al. 2013)). Diversification of lineages of golden perch in upland basins from coastal areas is believed to represent speciation during the Upper to Middle Pleistocene (Beheregaray et al. 2017).

The above examples illustrate diversification of arid lineages and species from mesic and tropical ancestors. So it is interesting to see that more recent work has revealed the converse of diversification of some species or lineages into mesic and tropical biomes from ancestral arid groups. Phylogenetic analysis of *Triodia* indicates that the arid zone is ancestral in this group, with multiple shifts and range expansion of species into the tropical savannah and into the southern mesic biomes during the Mid–Late Miocene and Pliocene (Toon et al. 2015). Similarly, diversification of mesic species is evident within the mainly arid plant genera *Scaevola* and *Goodenia* (Jabaily et al. 2014) and in the paper daisies *Leucochrysum* (Schmidt-Lebuhn and Smith 2016). Derived mesic species from arid ancestors are evident within *Ctenophorus* lizards (McLean et al. 2013, 2014) and *Strophurus* geckoes (Nielsen et al. 2016). Analysis of pygopodoid geckoes shows diversification of arid species along with some transition of species back to mesic biomes (Brennan and Oliver 2017). Area phylogenetic analysis led Ladiges et al. (2011b) to propose that *Nicotiana* section *Suaveolentes* had a widespread ancestral distribution with diversification in the arid zone as aridification progressed from the Mid-Miocene, along with persistence in peripheral mesic areas. Nyari and Joseph (2012) identified instances in the acanthizid bird genus *Gerygone*, where ancestry of tropical mangrove endemics may have involved arid-zone ancestors. In marsupials, some instances of lineages reverting from drier to more mesic habitats are apparent in several clades and individual species of Macropodidae and Dasyuridae (Mitchell et al. 2014). Several reptile groups confirm complex dynamic patterns between mesic, tropical and arid biomes, whereby all groups likely had a tropical or mesic ancestor, followed by derived arid lineages and then repeated recolonisation of mesic and tropical environments, including the lygosomine (Skinner et al. 2011) and *Lerista* (Lee et al. 2013; Skinner and Lee 2009) skinks; carphodactyline (Oliver and Bauer 2011), diplodactine (Oliver et al. 2009, 2010) and gekkotan (Sistrom et al. 2009, 2014) geckoes; and *Tympanocryptis* (Shoo et al. 2008), *Ctenophorus* (Edwards et al. 2015; Melville et al. 2016) and *Lophognathus/Amphibolurus* (Melville et al. 2011) agamids. Mesic species of *Pseudophryne* frogs appear to have been derived from an arid lineage (Donnellan et al. 2012).

Analysis in the plant *Nicotiana* section *Suaveolentes* shows marked radiation into arid environments (Clarkson et al. 2017), and species differentiated into the northern desert before they did in the central desert, suggesting that aridification occurred earlier in the northern desert than in the central western and eastern deserts (Ladiges et al. 2011b). Biogeographical analysis of *Acacia* also indicates a break in species turnover between the northern and southern regions of the arid zone, corresponding with the summer-winter rainfall divide (Gonzalez-Orozco et al. 2013; Foster 2017).

Although rigorous analysis of diversification rate is not possible for most studies, evaluation of phylogenies shows diversification rates can be relatively constant such as in the salt lake-adapted tiger beetles over the past 4 Ma (Pons et al. 2006), or rates can differ by mediation through different ecological contexts. Comparison of diversification rates between arid lineages and their mesic sister lineages shows some cases of similar diversification rates, such as in the *Egernia whitii* group (Chapple and Keogh 2004), in the *Pauropsalta* complex of cicadas (Owen et al. 2017) and in gall thrips (*Kladothrips*) that specialise on arid species of *Acacia* section *Juliflorae* (McLeish et al. 2007), but increased diversification in arid lineages compared with mesic lineages in the plant genus *Tetratheca* (Crayn et al. 2006) and *Nicotiana* section *Suaveolentes* (Clarkson et al. 2017) and in the sphenomorphine skinks (Rabosky et al. 2007) and the pygopodoid geckoes (Brennan et al. 2016; Brennan and Oliver 2017). In contrast, a slower rate of diversification is evident in the arid lineage of *Gossypium* compared with its tropical sister lineage (Liu et al. 2001; Seelanan et al. 1999). More recent analysis has found similar variation in rates and diversification in arid lineages having increased compared with mesic lineages in the plant genus *Ptilotus* (Hammer et al. 2015) and in the arid lineages of *Strophurus* geckoes compared to tropical sister lineages (Laver et al. 2017), but a slower rate in arid lineages of *Scaevola* compared with mesic lineages (Jabaily et al. 2014). Onstein et al. (2017) found a higher rate of diversification in open vegetation compared to the ancestral state of closed vegetation in Proteaceae, and Goldie et al. (2010) tested mutation rate in the internal transcribed spacer in mesic-arid pairs of woody species and found higher substitution rates in the majority (76%) of mesic species. Lineage through time plots of the arid genus *Triodia* shows progressive increase in diversification rate from the Mid-Miocene, consistent with rapidly intensifying aridification, and then decreasing diversification in the Pliocene (Toon et al. 2015). Surface and subsurface sister lineages of diving beetles show declining and variable diversification rates, respectively, related to the availability and distribution of their epigean and hypogean habitats (Toussaint et al. 2015a). Mesic lineages of allodapine bees experienced acceleration radiation during the Hill Gap (10–6 mya), but xeric groups did not (Chenoweth and Schwarz 2011). The genus *Pseudotetracha* of nocturnal tiger beetles also appears from molecular data to have undergone speciation and divergence among individual lakes or palaeodrainage basins in response to their isolation in turn produced by aridification of Australia (López-López et al. 2016), consistent with the findings of Pons et al. (2006) on *Rivacindela* tiger beetles.

Adaptation to Aridity

The question of whether adaptation occurred in conjunction with aridification or whether lineages were preadapted to arid conditions is difficult to answer. The divergence of lineage radiations during the Mid- to Late Miocene when the arid zone was emerging suggests preadaptation may have enabled rapid colonisation of arid environments by some plant and animal groups. Early dispersal into Australia from arid and semiarid areas facilitated large radiation of the *Maireana*/*Sclerolaena* tribe during the Pliocene (Cabrera et al. 2011) (Fig. 6). The development of aridification was not constant and was punctuated by development of more arid conditions during the "Hill Gap" (10–6 million years ago), followed by more mesic conditions before a return to arid conditions in the Pliocene and Pleistocene. So, this early development of aridity may have enabled evolution of adaptive traits that facilitated life under the arid conditions of the Pliocene and Pleistocene (Fig. 7). Phylogenetic clustering seen as lower levels of phylogenetic diversity in Australian angiosperms in arid regions compared to mesic and tropical biomes has been interpreted as indications of fewer clades having adaptation to arid conditions (Thornhill et al. 2016). In a study of community structure across six arid lineages of squamates and marsupials, Lanier et al. (2013) showed that each group displayed distinct patterns of phylogenetic structure suggesting that neither current climate nor historical habitat stability resulted in a uniform response by arid assemblages, and that taxon-specific history is important in determining patterns of phylogenetic community relatedness.

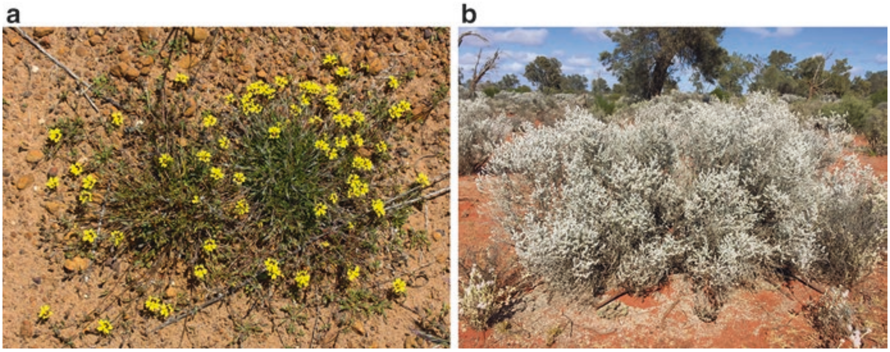


Fig. 6 Early dispersal into Australia of arid-zone adapted groups facilitated diversification within the arid zone as it developed. (**a**) *Goodenia*/*Scaevola* lineages diversified during the Miocene. (Photo Kelly Shepherd). (**b**) *Maireana*/*Sclerolaena* lineages diversified during the Pliocene. (Photo Margaret Byrne)

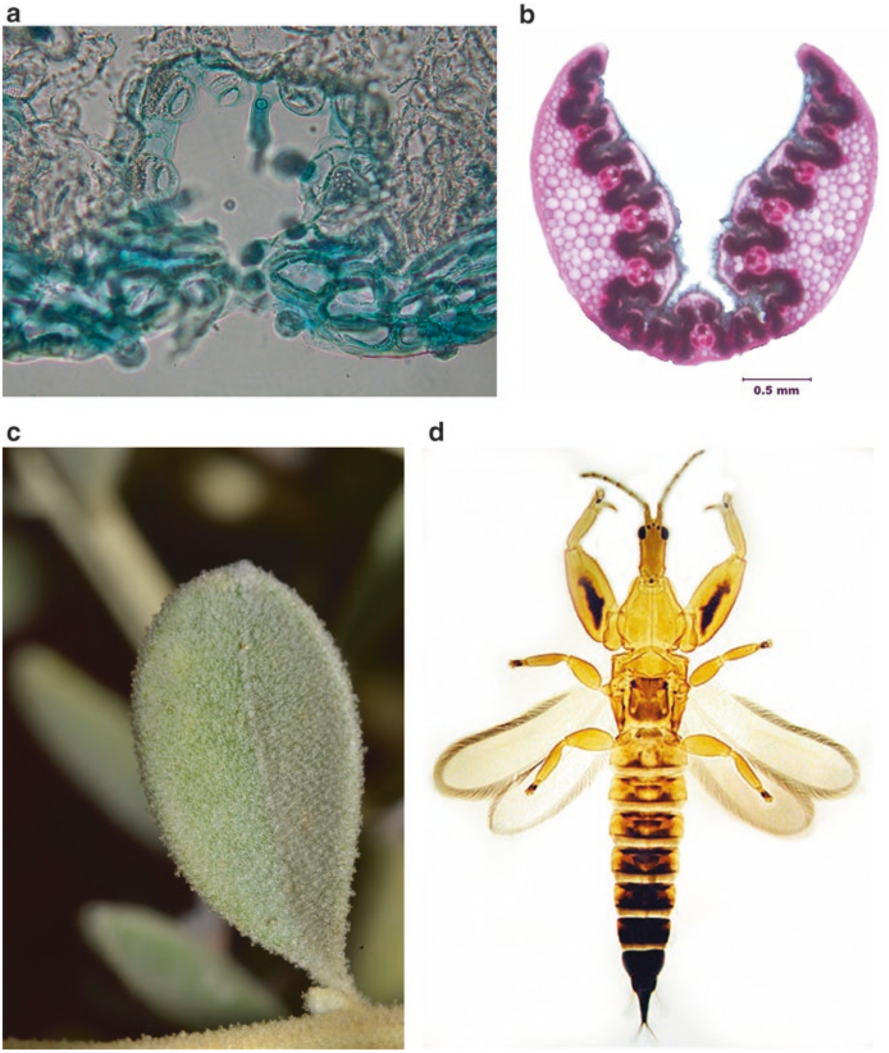


Fig. 7 Many arid-zone groups possess adaptations to aridity, such as (**a**) encrypted stomata in Proteaceae. (Photo Greg Jordan), (**b**) loss of abaxial stomata in *Triodia.* (Photo Harshi Gamage), (**c**) dense indumentum in *Ptilotus.* (Photo Tim Hammer), (**d**) a gall thrip, *Lichanothrips pastinus*, which produces domiciles by glueing phyllodes of *Acacia harpophylla.* (Photo Laurence Mound)

Evidence of adaptations to aridity in plants is considered to have occurred in the evolution of deeply encrypted stomata that has occurred 11 times in species of Proteaceae in arid environments compared to other stomatal features that have evolved in species present in both arid and wet environments (Jordan et al. 2008) but may contribute to effective gas exchange rather than reducing transpiration (Hassiotou et al. 2009; Roth-Nebelsick et al. 2009). Adaptations to low-nutrient environments are found in many sclerophyllous plant groups (Hill 1994), dense indumentum on stems and leaves in *Ptilotus* (Hammer et al. 2015) are thought to increase reflectance and reduces heat load, and the salinity tolerance of chenopods enabled them to colonise saline habitats (Cabrera et al. 2011). Evolution of embolism resistance in xylem hydraulic function facilitated the diversification of the *Callitris* into arid environments (Larter et al. 2017), and increased leaf thickness and leaf venation in eucalypts are considered to be an adaptation in arid environments (de Boer et al. 2017). Similarly, the low metabolic requirements and tolerance to heat and desiccation of many reptiles can be considered preadaptations to aridity. The presence of specialised groups in specific environments within the arid zone suggests specific adaptations to changing conditions, for example, the diversification of halophytic chenopods appears related to the emergence of saline water bodies through arid regions during the Late Pliocene (Shepherd et al. 2004), and the divergence of hydrobiid snails is related to development of freshwater springs in the Great Artesian Basin (Perez et al. 2005). Similarly, the transition from primarily surface-dwelling organisms to groundwater dwelling in diving beetles, amphipods and isopods between 11 and 3 Ma appears to be correlated with a reduction in permanent surface water (Cooper et al. 2007, 2008; Leys et al. 2003; Toussaint et al. 2015a). In contrast, more recently, Toon et al. (2015) considered the loss of abaxial stomata in the largely arid zone genus *Triodia* to represent an adaptation that developed after radiation into the arid zone rather than a trait conferring preadaptation to arid conditions. The domiciles of arid-zone gall thrips protect against desiccation (Gilbert 2014), and these gall thrips diversify through drift in allopatry due to the paucity of host species, in contrast to mesic-zone species that diversify ecologically in sympatry through host shifting (McLeish 2011; McLeish et al. 2011). The heleine Tenebrionidae lack the physiological adaptations to reduce water loss that characterise day-active desert tenebrionid beetle species, so they have become nocturnal (Duncan and Dickman 2009), and adaptations to phragmotic burrow-plugging have evolved multiple times in arid taxa of spiny trapdoor spiders (Rix et al. 2017). Physiological adaptation to heat stress and evaporative water loss along with transition to nocturnality are considered to be preadaptations to aridity facilitating diversification (Brennan and Oliver 2017). In birds, the ancestor of the familiar budgerigar may well have been preadapted morphologically and in social structure to life in the arid zone. The budgerigar is the sister group to lorikeets (Joseph et al. 2011), which have a streamlined morphology for rapid and sustained flight required to search for food resources that are patchily distributed in space and time. Genomic approaches to understanding adaptation to aridity in birds are exemplified by two recent studies in birds. McElroy et al. (2018) found strong evidence for purifying selection across all codons in the mitogenome of the mulga parrot *Psephotellus varius*, a species widespread across the arid zone. Lamb et al. (2018) studied mitochondrial DNA variation in 17 oscine passerines (songbirds) and found that climate was a significant predictor of mitochondrial variation in 8 species.

Ancestral polyploidy and hybridisation in *Nicotiana* section *Suaveolentes* may have facilitated adaptation to arid environments, because polyploids are considered to be well adapted to aridity (Winterfeld et al. 2009), and other Australian plant genera that are common in the arid zone are polyploid (e.g. *Cassia*, *Eremophila*, *Senna*) (Barlow 1981). Two tetraploid frogs are common in the arid zone (Anstis 2013; Mahony and Robinson 1980), but many other arid-zone frogs are diploid, and polyploid species also occur widely in mesic areas (Roberts and Edwards 2018), suggesting ploidy levels have not provided additional advantage in arid environments. Within the *Ctenophorus maculatus* species complex, rapid (0.3–1.5 million years) adaptive diversification in both ecomorphological and social signalling traits suggests complex interactions between adaptation and species interactions may have driven speciation in response to dynamic shifts in arid habitats (Edwards et al. 2015). Traits that reduce water loss in frogs, such as waterproof cocoons and burrowing, may enable persistence of frogs in the arid zone, but these traits are not exclusive to arid-zone frogs (Roberts and Edwards 2018).

Species Persistence and Intraspecific Divergence

The previous review of the arid-zone biota (Byrne et al. 2008) found two key points concerning intraspecific divergences. First, most arid-zone lineages and species had radiated within the biome by the end of the Pliocene, and, second, the Pleistocene was a time of maintenance of lineages and phylogeographic structuring in response to environmental changes. The dramatic climatic oscillations of the Pleistocene have led to major redistribution of species throughout the world (Hewitt 2001, 2004), particularly leading to major contraction and expansion of species in temperate biomes. Byrne et al. (2008) found evidence of intraspecific diversification in many arid lineages with three main patterns of genetic structure, reflecting multiple localised refugia, broad expansion and hybridisation or contraction and persistence of mesic relicts.

Many phylogeographic studies of arid-zone species have shown a common pattern of high diversity, but deep divergences among geographically structured intraspecific lineages (Byrne et al. 2008), and the divergence most commonly traced to the Mid-Pleistocene, which correlates with increased aridity and development of sandy deserts (Fujioka et al. 2009). The high diversity, but divergent lineages, suggests persistence of species during the climatic changes of the Pleistocene through localised contraction and expansion and presence of multiple localised refugia throughout the distribution of species (Fig. 8). Retention of localised refugia throughout species distributions would facilitate rapid colonisation of habitat under suitable climatic conditions. Application of Approximate Bayesian Computation methods to bird populations from a range of species supported a model of most of the populations showing a signal of a single co-expansion in the period just prior to the LGM when aridity was at a peak (Chan et al. 2014) indicating similar responses to environmental conditions. In further work, Dolman and Joseph (2012, 2015, 2016) explored the number of divergence events that have shaped present-day phylogeographic structure in Australian birds, especially those of the arid zone, and linked phylogeographic patterns to the birds' natural history and ecological diversity. The

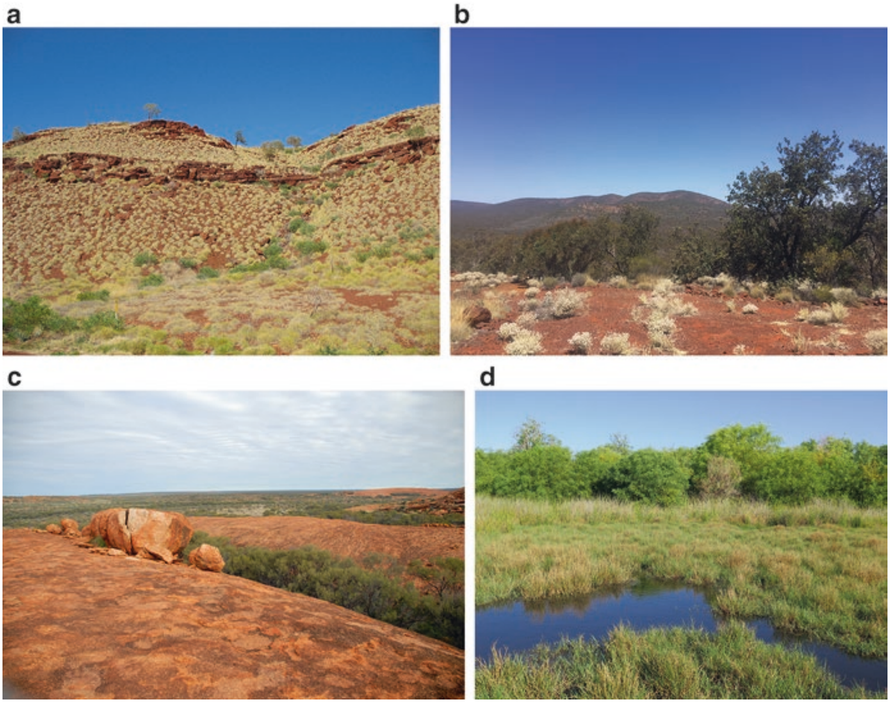


Fig. 8 Features of the arid zone providing heterogeneous environments that act as refugia (**a**) Hamersley Range. (Photo Margaret Byrne), (**b**) banded ironstone ranges. (Photo Margaret Byrne), (**c**) granite outcrops, (**d**) mound springs. (Photo Val English)

earliest event identified by Dolman and Joseph (2012), from the Middle to the Early Pleistocene explains the divergence of mesic populations of two species groups in south-eastern and south-western Australia, consistent with the increased aridification identified by McLaren and Wallace (2010). Conversely, the most recent divergence of semiarid south-eastern and south-western population pairs had its upper limit at the Mid-Pleistocene, but including the Last Glacial Maximum, and may be related to changes in plants with palatable leaves and fleshy fruits that were present in the Nullarbor Region between 180,000 and 400,000 years ago but now are found in remnant stands on the fringes of the Nullarbor Plain (Prideaux et al. 2007). Similarly, Hocknull et al. (2007) noted extinction of mesic fauna in central eastern Australia within this timeframe. Phylogeographic analysis of southern hairy-nosed wombat identified six lineages across the southern arid region (Alpers et al. 2016).

In contrast to the majority pattern of diverse but divergent lineages, there is evidence for a second pattern of widespread, low-diversity lineages in more vagile species (e.g. birds, snakes, lizards, freshwater fish, crayfish) (Bostock et al. 2006; Byrne et al. 2003; Joseph and Wilke 2006, 2007; Joseph et al. 2002, 2006; Kearns et al. 2008; Kuch et al. 2005; Nguyen et al. 2004; Strasburg and Kearney 2005; Toon et al. 2007), and this was also found more recently in pied butcherbirds (Kearns et al. 2010), variegated fairy-wren (McLean et al. 2017) and clam shrimps (Schwentner et al. 2012). This pattern is indicative of widespread recent expansions across all or part of the arid zone, a characteristic being little phylogenetic structuring and little evidence of specific refugia. Several lineages were identified in blacksnakes using multilocus nuclear genes (Maddock et al. 2017) where no mitochondrial diversity was previously identified (Kuch et al. 2005), indicating several expansion events. Evidence for refugia was noted for some birds in inland southeastern Australia (Joseph and Wilke 2006; Kearns et al. 2008) and in northern and western regions (e.g. the galah, *Eolophus roseicapilla*) (Engelhard et al. 2015). Phylogeographic data from the galah (Engelhard et al. 2015) may well be consistent with the idea advanced in Byrne et al. (2008) that refugia for some species may have been linear, that is, in riparian woodland. In some species, rapid expansion of lineages has occurred following hybridisation, parthenogenesis and polyploidisation, as these processes produce instant reproductive isolation (Coyne and Orr 2004). This has resulted in diverse and widespread lineages of *Neobatrachus* frogs (Mahony et al. 1996), *Heteronotia* and *Menetia* lizards (Adams et al. 2003; Fujita et al. 2010; Moritz 1993), insects (*Sipyloidea*, *Warramaba*) and plants (*Acacia aneura*, *Senna artemisiodes*, *Cassia* sp.) (Andrew et al. 2003; Holman and Playford 2000; Randell 1970). Subspecies in the polyploid *Atriplex nummularia* are proposed to have multiple origins through hybridisation (Sampson and Byrne 2012). The expansion of the lineages in all these species is a result of evolutionary processes, rather than the contraction and expansion of species due to glacial cycles in temperate regions of the northern hemisphere.

An interesting pattern to have emerged in one species group of birds runs counter to the general pattern of reduction to refugia during the Pleistocene and particularly in response to the Last Glacial Maximum (LGM). Kearns et al. (2014) integrated palaeomodelling of the Last Glacial Maximum (~25–15,000 years ago) distributions and multilocus phylogenetic and phylogeographic analyses to argue that the grey butcherbird, *Cracticus torquatus*, expanded its range in arid, inland Australia at the Last Glacial Maximum. This led to introgressive hybridisation with a northern, tropical non-sister species, the silver-backed butcherbird, *C. argenteus*, and so explains an otherwise anomalous pattern of mtDNA diversity in these birds. Similarly, the use of past species distribution models shows vast increases in coastal sand plain habitats in reptile-plant arid hotspot on the mid-western Australian coast in a range of endemic reptile species (Edwards et al. 2012). Using explicit habitat-demographic models shows that shifts in suitable habitat explain intraspecific divergence (He et al. 2013).

While the majority of species show high diversity of divergent lineages, and some show widespread distribution of low-diversity lineages, there are some species that appear to represent species restricted to mesic habitat within the arid zone. More mesic environments, such as the springs of the Great Artesian Basin and granite outcrops, are areas where mesic relicts occur. An early study showed high genetic divergence in species of hydrobiid snails (*Jardinella* sp.) that are restricted to different groups of springs (Perez et al. 2005). More recent studies have revealed a suite of invertebrate species, including Crustaceae, molluscs and insects, which are restricted to these desert springs and diverged well before the deserts developed, indicating they diverged in these tiny mesic refugia in isolation (Guzik et al. 2012; Murphy et al. 2012, 2015). In contrast, the frog *Limnodynastes tasmaniensis*, which also occurs in these spring systems, is broadly distributed through the Flinders Ranges and across most of eastern Australia in both mesic and arid systems. The arid-adapted fish species, *Chlamydogobius*, shows little differentiation among Lake Eyre waters, indicating periodic connectivity (Mossop et al. 2015). Many species of the arid plant genus *Goodenia* are annuals and are confined to mesic environments in the arid zone (Jabaily et al. 2014). Granite outcrops often harbour more mesic habitats within the arid zone and have been hypothesised to have acted as mesic refugia during extreme aridity (Byrne 2008; Byrne and Hopper 2008). The relictual species, *Acacia lobulata*, has no close relatives and is now restricted to mesic south-facing slopes on two granite outcrops (Byrne et al. 2001). In contrast, *Eucalyptus caesia*, which is also restricted to granite outcrops, shows high divergence but appears to be adapted to the specific granite rock habitat and does not show evidence of repeated cycles of population expansion and contraction (Byrne and Hopper 2008). More recent analysis of two very widespread plant species restricted to granite outcrops in both arid and mesic environments showed similar levels of high haplotype diversity with divergence among populations, with less diversity in more arid populations than in mesic populations (Tapper et al. 2014a, b).

Recent work has also focused on the Banded Ironstone Formation ranges of the Yilgarn and Pilbara cratons that are also areas that harbour more mesic environments. Analysis of species diversity in the western area of the arid zone shows the ranges to have higher species diversity than the surrounding lowland areas, and those on the arid-zone boundary have higher beta diversity and greater endemism and diversity than those further inland (Gibson et al. 2012). Recent studies have shown mixed patterns of phylogeographic diversity and structure. Some more restricted species, a *Grevillea* and a millipede, show patterns of persistence and divergence between isolated formations (Nistelberger et al. 2014, 2015a), while in other plant species, a combination of moderate diversity with persistence of ancestral haplotypes suggests maintenance of larger populations with some isolation (Binks et al. 2015; Millar et al. 2017; Nistelberger et al. 2015b). In contrast, a rare species of *Acacia* restricted to a localised group of formations shows evidence of local connectivity (Millar et al. 2013), as do two other regionally distributed plant species, having common haplotypes shared among populations (Millar et al. 2016). The arid lineages of the conifer *Callitris columellaris*, which are restricted to ranges, granite rocks and inselbergs, show evidence of strong bottlenecks and range contraction over multiple Pleistocene climatic cycles, indicating contraction to mesic refugia, in contrast to signals of population expansion in the mesic lineages in southern temperate areas (Sakaguchi et al. 2013). The arid-zone outliers of the mesic species of the *Egernia whitii* complex of skinks have been interpreted as relicts of a broader range now contracted to southern mesic areas (Chapple and Keogh 2004).

Ranges in the arid zone were predicted by Byrne et al. (2008) to be refugia for species. In a series of studies on reptiles, Pepper et al. (2008, 2011a, b, 2013a, b) explored the lineage divergence and the evolutionary consequences of relatively recent development of widespread sand deserts between these arid-zone ranges. Pepper et al. (2011a) used multilocus phylogenetic analyses to show that among rock-dwelling *Heteronotia* geckoes, each range harbours a divergent lineage; substantial intraspecific diversity is likely due to topographic complexity in these areas. Old divergences (~4 Ma) among lineages predate the formation of the geologically young sand deserts (<1 Ma), suggesting that Pliocene climate shifts fractured the distributions of biota long before the spread of the deserts. In further analyses of multiple mitochondrial DNA datasets from four species complexes of Australian geckoes from three genera (*Heteronotia*, *Lucasium*, *Rhynchoedura*), Pepper et al. (2011b) found that topographically complex mountain regions harbour high nucleotide diversity, up to 18 times greater than that of the surrounding desert lowlands. Taxa in topographically complex areas have older coalescent histories than those in the geologically younger deserts and that both ancient and more recent aridification events have contributed to these patterns. In a later analysis, Pepper et al. (2013a) reviewed patterns of diversity in one region of inland ranges, the Pilbara, more extensively. While noting some repeated phylogeographic patterns, they also highlighted the importance of species-specific ecological differences in shaping idiosyncratic elements of these patterns of diversification. Similar high divergence between lineages in ranges and presence of two highly divergent lineages in the Central Ranges was observed in *Oedura* geckoes (Oliver and McDonald 2016). The plant *Triodia basedowii* complex occurs across the Pilbara and central arid zone, and diversification has been identified within the Pilbara compared with that in the deserts (Anderson et al. 2016). In addition, similar to reptiles, substrate was hypothesised to be important in diversification within the plant *Triodia basedowii* complex (Anderson et al. 2016). Substrate was also identified as an important feature explaining the genetic diversity of reptile communities along the Western Australian coast (Edwards et al. 2012). In *Uperoleia* froglets, species boundaries appear correlated with geological and substrate boundaries as well as major drainages between the Pilbara and Gascoyne (Catullo et al. 2011)

Phylogeographic analysis of plant species revealed high diversity in Pilbara ranges and lower diversity in the surrounding areas for *Eucalyptus leucophloia*, consistent with the ranges being refugia (Byrne et al. 2017). Although this pattern was not evident in either a widespread *Acacia* or its restricted congener that showed differing patterns, with high diversity throughout the distribution in the widespread species, and low diversity in the species restricted to the ranges, and there was evidence for greater genetic connectivity in populations of the widespread species in the ranges, suggesting maintenance of larger effective populations size (Levy et al. 2016).

New Insights

Our evaluation of molecular phylogenetic and phylogeographic studies conducted since the review of Byrne et al. (2008) has revealed further support for the main hypotheses identified there, particularly divergence and diversification of arid-zone species and lineages derived from both mesic and tropical ancestors, and variation in diversification rates. Interestingly, more recent studies have also found evidence of mesic and tropical species being derived from ancestral arid groups and also some transition back to arid lineages. In addition, while few cases of speciation in the Pleistocene were previously noted, more recent studies have identified more cases in plants, land snails, frogs and fish. Distinct patterns of phylogenetic structure in mammals and squamates also suggest that neither current climate nor historical habitat stability resulted in a uniform response by arid assemblages highlighting that idiosyncratic historical and biogeographical aspects of community composition are important and that studies of individual taxa are necessary to fully understand the responses of species to aridity. Further evidence of adaptation to aridity was found in plants and reptiles.

More recent phylogeographic studies have found similar evidence of the two broad patterns of diverse but highly differentiated lineages, and widespread low-diversity lineages. Further investigations support the hypothesis that mesic habitats, such as salt lakes, desert springs, granite outcrops, banded ironstone ranges and Pilbara ranges, provide refugia enabling species to persist within the arid zone with high diversity and differentiation in these mesic arid-zone habitats. Evidence of range expansion after the LGM remains limited but has been identified in a study on butcherbirds.

Opportunities and Challenges

The ready availability of molecular tools has seen a huge growth in the number and scale of studies investigating evolutionary history in arid-zone species, with over three times as many studies available now compared to 2008. These studies highlight the complexity in patterns and processes of the evolutionary history of the arid-zone biota and demonstrate the diversity of responses to aridification across the vast Australian environment.

While the large number of studies on arid-zone species has shown commonality in a range of patterns, there is much still to learn about specific responses of the biota to arid environments. Patterns of refugia within arid environments remain enigmatic, beyond the obvious mesic habitats of ranges, inselbergs and mound springs, although the concept of linear corridors of habitats being refugia for birds appears validated in the galah. Despite sandy habitats dominating arid environments, there is a great deal we don’t know about the evolution of species specific to sand habitats, particularly in reptiles, where there are many species with unique adaptations to sandy habitats and evidence that substrate has a role in generating intra- and interspecific divergences.

The revolution in molecular technology has facilitated major advances in our knowledge of evolutionary history, yet there is now much opportunity to integrate molecular techniques with advances in other fields. We are only just beginning to see the incorporation of other powerful tools like ecological modelling, hypothesis testing frameworks, biogeographic model testing and morphological and behavioural analyses, with molecular studies in an integrative approach. We envisage that such integrative studies will have much more to reveal about the intricacies of the evolutionary history of the arid-zone biota in the years to come.

References

Adams M, Foster R, Hutchinson MN, Hutchinson RG, Donnellan SC (2003) The Australian scincid lizard *Mentia greyii*: a new instance of widespread vertebrate parthenogenesis. Evolution 57:2619–2627

Alley NF, Lindsay JM (1995) Tertiary. In: Drexel JF, Preiss WV (eds) The geology of South Australia. Vol. 2 The phanerozoic. South Australia Geological Survey, Bulletin 54, pp 151–217

Alpers DL, Walker FM, Taylor AC, Sunnucks P, Bellman S, Hansen BD, Sherwin WB (2016) Evidence of subdivisions on evolutionary timescales in a large, declining marsupial distributed across a phylogeographic barrier. PLoS ONE 11(10):e0162789

Andersen AN (2016) Ant megadiversity and its origins in arid Australia. Aust Entomol 55:132–137

Anderson BM, Barrett MD, Krauss SL, Thiele K (2016) Untangling a species complex of arid zone grasses (*Triodia*) reveals patterns congruent with co-occurring animals. Mol Phylogenet Evol 101:142–152

Andrew R, Miller JT, Peakall R, Crisp MD (2003) Genetic, cytogenetic and morphological patterns in a mixed mulga population: evidence for apomixis. Aust Syst Bot 16:69–80

Anstis M (2013) Tadpoles and frogs of Australia. New Holland, London

Ariati SR, Murphy DJ, Udovicic F, Ladiges PY (2006) Molecular phylogeny of three groups of acacias (*Acacia* subgenus *Phyllodineae*) in arid Australia based on the internal and external transcribed spacer regions of nrDNA. Syst Biodivers 4:417–426

Barker WR, Greenslade PJM (1982) Evolution of the flora and fauna of arid Australia. Peacock Publications, Adelaide

Barlow BA (1981) The Australian flora: its origin and evolution. Flora Aust 1:25–75

Beheregaray LB, Pfeiffer LV, Attard CRM, Sandoval-Castillo J, Domingos FMCB, Faulks LK, Gilligan DM, Unmack PJ (2017) Genome-wide data delimits multiple climate-determined species ranges in a widespread Australian fish, the golden perch (*Macquaria ambigua*). Mol Phylogenet Evol 111:65–75

Binks RM, Millar MA, Byrne M (2015) Not all rare species are the same contrasting patterns of genetic diversity and population structure in two narrow endemic sedges. Biol J Linn Soc 114:873–886

Bostock BM, Adams M, Laurenson LJB, Austin CM (2006) The molecular systematics of *Leiopotherapon unicolor* (Gunther, 1859): testing for cryptic speciation in Australia's most widespread freshwater fish. Biol J Linn Soc 87:537–552

Bowler JM, Duller GAT, Perret N, Prescott JR, Wyrwoll K-H (1998) Hydrological changes in monsoonal climates of the last glacial cycle: stratigraphy and luminescence dating of Lake Woods, N.T., Australia. Palaeoclimates 3:179–207

Bowler JM, Kotsonis A, Lawrence CR (2006) Environmental evolution of the Mallee region, Western Murray Basin. Proc Roy Soc Victoria 118:161–210

Bradford T, Adams M, Humphreys WF, Austin AD, Cooper SJB (2010) DNA barcoding of stygofauna uncovers cryptic amphipod diversity in a calcrete aquifer in Western Australia's arid zone. Mol Ecol Resour 10:41–50

Brennan IG, Oliver PM (2017) Mass turnover and recovery dynamics of a diverse Australian continental radiation. Evolution 71:1352–1365

Brennan IG, Bauer AM, Jackman TR (2016) Mitochondrial introgression via ancient hybridization, and systematics of the Australian endemic pygopodid gecko genus *Delma*. Mol Phylogenet Evol 94:577–590

Byrne M (2008) Evidence for multiple refugia at different time scales during Pleistocene climatic oscillations in southern Australia inferred from phylogeography. Quat Sci Rev 27:2576–2585

Byrne M, Hopper SD (2008) Granite outcrops as ancient islands in old landscapes: evidence from the phylogeography and population genetics of *Eucalyptus caesia* in Western Australia. Biol J Linn Soc 93:177–188

Byrne M, Tischler G, Macdonald B, Coates DJ, McComb J (2001) Phylogenetic relationships between two rare acacias and their common, widespread relatives in south-western Australia. Conserv Genet 2:157–166

Byrne M, Macdonald B, Brand J (2003) Phylogeography and divergence in the chloroplast genome of Western Australian Sandalwood (*Santalum spicatum*). Heredity 91:389–395

Byrne M, Yeates DK et al (2008) Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. Mol Ecol 17:4398–4417

Byrne M, Steane DA, Joseph L, Yeates DK, Jordan GJ, Crayn D, Aplin K, Cantrill DJ, Cook LG, Crisp MD, Keogh JS, Melville J, Moritz C, Porch N, Sniderman JMK, Sunnucks P, Weston P (2011) Decline of a biome: contraction, fragmentation, extinction and invasion of the Australian mesic zone biota. J Biogeogr 38:1635–1656

Byrne M, Millar MA, Coates DJ, Macdonald BM, McArthur S, Zhou M, van Leeuwen S (2017) Refining expectations for environmental characteristics of refugia: two ranges of differing elevation and topographical complexity are mesic refugia in an arid landscape. J Biogeogr 44:2539–2550

Cabrera J, Jacobs SWL, Kadereit G (2011) Biogeography of Camphorosmeae (Chenopodiaceae): tracking the Tertiary history of Australian aridification. Telopea 13:313–326

Cardillo M, Weston PH, Reynolds ZKM, Olde PM, Mast AR, Lemmon EM, Lemmon AR, Bromham L (2017) The phylogeny and biogeography of *Hakea* (Proteaceae) reveals the role of biome shifts in a continental plant radiation. Evolution 71:1928–1943

Catullo RA, Keogh JS (2014) Aridification drove repeated episodes of diversification between Australian biomes: Evidence from a multi-locus phylogeny of Australian toadlets (*Uperoleia*: Myobatrachidae). Mol Phylogenet Evol 79:104–116

Catullo RA, Doughty P, Roberts JD, Keogh JS (2011) Multi-locus phylogeny and taxonomic revision of *Uperoleia* toadlets (Anura: Myobatrachidae) from the western arid zone of Australia, with a description of a new species. Zootaxa 2902:1–43

Catullo RA, Lanfear R, Doughty P, Keogh JS (2014) The biogeographical boundaries of northern Australia: evidence from ecological niche models and a multi-locus phylogeny of *Urperoleia* toadlets (Anura: Myobatrachidae). J Biogeogr 41:659–672

Chan YL, Schanzenbach D, Hickerson MJ (2014) Detecting concerted demographic response across community assemblages using hierarchical Approximate Bayesian Computation. Mol Biol Evol 31:2501–2515

Chapple DG, Keogh JS (2004) Parallel adaptive radiations in arid and temperate Australia: molecular phylogeography and systematics of the *Egernia whitii* (Lacertilia: Scincidae) species group. Biol J Linn Soc 83:157–173

Chenoweth LB, Schwarz MP (2011) Biogeographical origins and diversification of the exoneurine allodapine bees of Australia (Hymenoptera, Apidae). J Biogeogr 38:1471–1483

Clarkson JJ, Dodsworth SD, Chase MW (2017) Time-calibrated phylogenetic trees establish a lag between polyploidisation and diversification in *Nicotiana* (Solanaceae). Plant Syst Evol 303:1001–1012

Cogger HG, Cameron EE (1984) Arid Australia. Australian Museum, Sydney

Cooper SJB, Bradbury JH, Saint KM, Leys R, Austin AD, Humphreys WF (2007) Subterranean archipelago in the Australian arid zone: mitochondrial DNA phylogeography of amphipods from central Western Australia. Mol Ecol 16:1533–1544

Cooper SJB, Saint KM, Taiti S, Austin AD, Humphreys WF (2008) Subterranean archipelago: mitochondrial DNA phylogeography of stygobitic isopods (Oniscidea: Haloniscus) from the Yilgarn region of Western Australia. Invertebr Syst 22:195–203

Coyne JA, Orr HA (2004) Speciation. Sinauer Associates, Sunderland

Cracraft J (1986) Origin and evolution of continental biotas: speciation and historical congruence within the Australian avifauna. Evolution 40:977–996

Cracraft J (1991) Patterns of diversification within continental biotas: heirarchical congruence among the areas of endemism of Australian vertebrates. Aust Syst Bot 4:211–227

Crayn DM, Rossetto M, Maynard DJ (2006) Molecular phylogeny and dating reveals an Oligo-Miocene radiation of dry-adapted shrubs (former Tremandraceae) from rainforest tree progenitors (Elaeocarpaceae) in Australia. Am J Bot 93:1328–1342

Criscione F, Köhler F (2016) Snails in the desert: Assessing the mitochondrial and morphological diversity and the influence of aestivation behavior on lineage differentiation in the Australian endemic *Granulomelon* Iredale, 1933 (Stylommatophora: Camaenidae). Mol Phylogenet Evol 94:101–112

Crisp MD, Cook LG (2007) A congruent molecular signature of vicariance across multiple plant lineages. Mol Phylogenet Evol 43:1106–1117

Crisp MD, Isagi Y, Kato Y, Cook LG, Bowman DMS (2010) *Livistona* palms in Australia: ancient relics or opportunistic immigrants? Mol Phylogenet Evol 54:512–523

Crowther MS, Blacket MJ (2003) Biogeography and speciation in the Dasyuridae: why are there so many Dasyurids? In: Jones ME, Dickman C, Archer M (eds) Predators with pouches: the biology of carnivorous marsupials. CSIRO Publishing, Melbourne, pp 124–130

Dawson TJ, Dawson L (2006) Evolution of arid Australia and consequences for vertebrates. In: Merrick JR, Archer M, Hickey GM, Lee MSY (eds) Evolution and biogeography of Australasian vertebrates. Australian Scientific Publishing, Oatlands, pp 51–71

de Boer HJ, Drake PL, Wendt E, Price CA, Schulze E, Turner NC, Nicolle D, Veneklaas EJ (2017) Apparent over-investment in leaf venation relaxes leaf morphological constraints on photosynthesis in arid habitats. Plant Physiol 172:2286–2299

Dolman G, Joseph L (2012) A species assemblage approach to comparative phylogeography of birds in southern Australia. Ecol Evol 2:354–369

Dolman G, Joseph L (2015) Evolutionary history of birds across southern Australia: structure, history and taxonomic implications of mitochondrial DNA diversity in an ecologically diverse suite of species. Emu 115:35–48

Dolman G, Joseph L (2016) Multi-locus sequence data reveal Pleistocene speciation in semi-arid southern Australian birds (*Cinclosoma* spp.) was associated with increased genetic drift. BMC Evol Biol 16:226

Donnellan SC, Mahony MJ, Bertozzi T (2012) A new species of *Pseudophryne* (Anura: Myobatrachidae) from the central Australian ranges. Zootaxa 3476:69–85

Driskell AC, Norman JA, Pruett-Jones S, Mangall E, Sonsthagen S, Christidis L (2011) A multigene phylogeny examining evolutionary and ecological relationships in the Australo-papuan wrens of the subfamily Malurinae (Aves). Mol Phylogenet Evol 60:480–485

Duncan FD, Dickman CR (2009) Respiratory strategies of tenebrionid beetles in arid Australia: does physiology beget nocturnality? Physiol Entomol 34:52–60

Ebach MC, Murphy DJ, Gonzalez-Orozco CE, Miller JT (2015) A revised area taxonomy of phytogeographical regions within the Australian Bioregionalisation Atlas. Phytotaxa 208:261–277

Edwards DL, Melville J (2011) Extensive phylogeographic and morphological diversity in *Diporiphora nobbi* (Agamidae) leads to taxonomic review and a new species description. J Herpetol 45:530–546

Edwards DL, Keogh JS, Knowles LL (2012) Effects of vicariant barriers, habitat stability, population isolation and environmental features on species divergence in the south-western Australian coastal reptile community. Mol Ecol 21:3809–3822

Edwards DL, Melville J, Joseph L, Keogh JS (2015) Ecological divergence, adaptive diversification, and the evolution of social signaling traits: An empirical study in arid Australian lizards. Am Nat 186:E144–E161

Engelhard D, Joseph L, Toon A, Pedler L, Wilke T (2015) Rise (and demise?) of subspecies in the Galah (*Eolophus roseicapilla*), a widespread and abundant Australian cockatoo. Emu 115:289–301

Finston TL, Francis CJ, Johnson MS (2009) Biogeography of the stygobitic isopod *Pygolabis* (Malacostraca: Tainisopidae) in the Pilbara, Western Australia: Evidence for multiple colonisations of the groundwater. Mol Phylogenet Evol 52:448–460

Foster I (2018) Climate change. In: Lambers H (ed) On the ecology of Australia's arid zone. Springer Nature, Dordrecht pp 375–388

Fujioka T, Chappell J, Honda M, Yatsevich I, Fifield K, Fabel D (2005) Global cooling initiated stony deserts in central Australia 2-4 Ma, dated by cosmogenic ^{21}Ne-^{10}Be. Geology 33:993–996

Fujioka T, Chappell J, Fifield LK, Rhodes EJ (2009) Australian desert dune fields initiated with Pliocene-Pleistocene global climatic shift. Geology 37:51–54

Fujita MK, McGuire JA, Donnellan SC, Moritz C (2010) Diversification and persistence at the arid-monsoonal interface: Australia-wide biogeography of the Bynoe's gecko (*Heteronotia binoei*; Gekkonidae). Evolution 64:2293–2314

Gibson N, Meissner R, Markey AS, Thompson WA (2012) Patterns of plant diversity in ironstone ranges in arid south western Australia. J Environ 77:25–31

Gilbert JDJ (2014) Thrips domiciles protect larvae from desiccation in an arid environment. Behav Ecol 25:1338–1346

Goldie X, Gillman L, Crisp M, Wright S (2010) Evolutionary speed limited by water in Australia. Proce R Soc B Biol Sci 277:2645–2653

Gonzalez-Orozco CE, Laffan S, Knerr N, Miller JT (2013) A biogeographical regionalization of Australian *Acacia* species. J Biogeogr 40:2156–2166

Guzik MT, Cooper SJB, Humphreys WF, Austin AD (2009) Fine-scale comparative phylogeography of a sympatric sister species triplet of subterranean diving beetles from a single calcrete aquifer in Western Australia. Mol Ecol 18:3683–3698

Guzik MT, Austin AD et al (2011a) Is the Australian subterranean fauna uniquely diverse? Invertebr Syst 24:407–418

Guzik MT, Cooper SJB, Humphreys WF, Ong S, Kawakami T, Austin AD (2011b) Evidence for population fragmentation within a subterranean aquatic habitat in the Western Australian desert. Heredity 107:215–230

Guzik MT, Adams MA, Murphy NP, Cooper SJB, Austin AD (2012) Desert springs: deep phylogeographic structure in an ancient endemic crustacean (*Phreatomerus latipes*). PLoS ONE 7:e37642

Hammer T, Davis R, Thiele K (2015) A molecular framework phylogeny for *Ptilotus* (Amaranthaceae): Evidence for the rapid diversification of an arid Australian genus. Taxon 64:272–285

Harrison SE, Guzik MT, Harvey MS, Austin AD (2014) Molecular phylogenetic analysis of Western Australian troglobitic chthoniid pseudoscorpions (Pseudoscorpiones: Chthoniidae) points to multiple independent subterranean clades. Invertebr Syst 28:386–400

Hassiotou F, Evans JR, Ludwig M, Veneklaas EJ (2009) Stomatal crypts may facilitate diffusion of CO_2 to adaxial mesophyll cells in thick sclerophylls. Plant Cell Environ 32:1596–1611

He Q, Edwards DL, Knowles LL (2013) Integrative testing of how environments from the past to the present shape genetic structure across landscapes. Evolution 67:3386–3402

Heterick BE, Castalanelli M, Shattuck SO (2017) Revision of the ant genus *Melophorus* (Hymenoptera, Formicidae). ZooKeys 700:1–420

Hewitt G (2001) Speciation, hybrid zones and phylogeography- or seeing genes in space and time. Mol Ecol 10:537–549

Hewitt GM (2004) Genetic consequences of climatic oscillations in the Quarternary. Philos Trans R Soc Lond Ser B 359:183–195

Hill RS (1994) The history of selected Australian taxa. In: Hill RS (ed) History of the Australian vegetation: cretaceous to recent. Cambridge Unversity Press, Cambridge, pp 390–419

Hocknull SA, Zhao J, Feng Y, Webb GE (2007) Responses of Quaternary rainforest vertebrates to climate change in Australia. Earth Planet Sci Lett 264:317–331

Holman JE, Playford J (2000) Molecular and morphological variation in the *Senna artemisoides* complex. Aust J Bot 48:569–579

Hugall AF, Foster R, Hutchinson M, Lee MSY (2008) Phylogeny of Australian agamid lizards based on nuclear and mitochondrial genes: implications for morphological evolution and biogeography. Biol J Linn Soc 93:343–358

Ingham JA, Forster PI, Crisp MD, Cook LG (2013) Ancient relicts or recent dispersal: how long have cycads been in central Australia? Divers Distrib 19:307–316

Jabaily RS, Shepherd KA, Gardner AG, Gustafsson MHG, Howarth DG, Motley TJ (2014) Historical biogeography of the predominantly Australian plant family Goodeniaceae. J Biogeogr 41:2057–2067

Javidkar M, Cooper SJB, King RA, Humphreys WF, Bertozzi T, Stevens MI, Austin AD (2016) Molecular systematics and biodiversity of oniscidean isopods in the groundwater calcretes of central Western Australia. Mol Phylogenet Evol 104:93–98

Jordan GJ, Weston PH, Carpenter RJ, Dillon RA, Brodribb TJ (2008) The evolutionary relations of sunken, covered and encrypted stomata to dry habitats in Proteaceae. Am J Bot 95:521–530

Joseph L, Wilke T (2006) Molecular resolution of population history, systematics and historical biogeography of the Australian ringneck parrots *Barnardius*: are we there yet? Emu 106:49–62

Joseph L, Wilke T (2007) Lack of phylogeographic structure in three widespread Australian birds reinforces emerging challenges in Australian historical biogeography. J Biogeogr 34:612–624

Joseph L, Wilke T, Alpers D (2002) Reconciling genetic expectations from host specificity with historical population dynamics in an avian brood parasite, Horsfield's Bronze-Cuckoo *Chalcites basalis* of Australia. Mol Ecol 11:829–837

Joseph L, Wilke T, Have JT, Chesser RT (2006) Implications of mitochondrial DNA polyphyly in two ecologically undifferentiated but morphologically distinct migratory birds, the masked and white-browed woodswallows *Artamus* spp. of inland Australia. J Avian Biol 37:625–636

Joseph L, Toon A, Schirtzinge EE, Wright TF (2011) Molecular systematics of two enigmatic genera *Psittacella* and *Pezoporus* illuminate the ecological radiation of Australo-Papuan parrots (Aves: Psittaciformes). Mol Phylogenet Evol 59:675–684

Joseph L, Toon A, Nyári ÁS, Trueman J, Gardner J (2014) A new synthesis of the molecular systematics and biogeography of honeyeaters (Passeriformes: Meliphagidae) highlights biogeographical complexity of a spectacular avian radiation. Zool Scr 43:235–248

Kadereit G, Freitag H (2011) Molecular phylogeny of Camphorosmeae (Camphorosmoideae, Chenopodiaceae): implications for biogeography, evolution of C-4-photosynthesis and taxonomy. Taxon 60:51–78

Kadereit G, Mavrodiev EV, Zacharias EH, Sukhorukov AP (2010) Molecular phylogeny of Atripliceae (Chenopodioideae, Chenoopodiaceae): Implications for systematics, biogeogrpahy, flower and fruit evolution, an dthe origion of C_4 photosymthesis. Am J Bot 97:1664–1687

Karanovic T, Cooper SJB (2012) Explosive radiation of the genus *Schizopera* on a small subterranean island in Western Australia (Copepoda: Harpacticoida): unravelling the cases of cryptic speciation, size differentiation and multiple invasions. Invertebr Syst 26:115–192

Kear BP, Aplin KP, Westerman M (2016) Bandicoot fossils and DNA elucidate lineage antiquity amongst xeric-adapted Australasian marsupials. Sci Rep 6:37537

Kearney M, Blacket MJ (2008) The evolution of sexual and parthenogenetic *Warramaba*: a window onto Plio–Pleistocene diversification processes in an arid biome. Mol Ecol 17:5257–5275

Kearns A, Joseph L, Double M, Edwards S (2008) Inferring the phylogeography and evolutionary history of the Splendid Fairy-wren (*Malurus splendens)* from mitochondrial DNA and spectrophotometry. J Avian Biol 40:7–17

Kearns A, Joseph L, Cook L (2010) The impact of Pleistocene climatic and landscape changes on Australian birds: a test using the pied butcherbird (*Cracticus nigrogularis*). Emu-Aust Ornithol 110:285–295

Kearns A, Joseph L, Toon A, Cook L (2014) Australia's arid-adapted butcherbirds experienced range expansions during Pleistocene glacial maxima. Nat Commun 5:3994

Kergoat GJ, Bouchard P, Clamens A-L, Abbate JL, Jourdan H, Jabbour-Zahab R, Genson G, Soldati L, Condamine FL (2014) Cretaceous environmental changes led to high extinction rates in a hyperdiverse beetle family. BMC Evol Biol 14(220):1–13

King RA, Bradford T, Austin AD, Humphreys WF, Cooper SJB (2012) Divergent molecular lineages and not-so-cryptic species: the first descriptions of stygobitic chiltoniid amphipods (Talitroidea: Chiltoniidae) from Western Australia. J Crustac Biol 32:465–488

Krajewski C, Wroe S, Westerman M (2000) Molecular evidence for the pattern and timing of cladogenesis in dasyurid marsupials. Zool J Linn Soc 130:375–404

Kuch U, Keogh JS, Weigel J, Smith LA, Mebs D (2005) Phylogeography of Australia's king brown snake (*Pseudechis australis*) reveals Pliocene divergence and Pleistocene dispersal of a top predator. Naturwissenschaften 92:121–127

Ladiges P, Parra-O C, Gibbs A, Udovicic F, Nelson G, Bayly M (2011a) Historical biogeographical patterns in continental Australia: congruence among areas of endemism of two major clades of eucalypts. Cladistics 27:29–41

Ladiges PY, Marks CE, Nelson G (2011b) Biogeography of *Nicotiana* section Suaveolentes (Solanaceae) reveals geographical tracks in arid Australia. J Biogeogr 38:2066–2077

Lamb AM, Gan HM, Greening C, Joseph L, Lee YP, Morán-Ordóñez A, Sunnucks P, Pavlova A (2018) Climate-driven mitochondrial selection: a test in Australian birds. Mol Ecol 27:898–918

Lanier HC, Edwards DL, Knowles LL (2013) Phylogenetic structure of vertebrate communities across the Australian arid zone. J Biogeogr 40:1059–1070

Larter M, Pfautsch S, Domec J-C, Trueba S, Nagalingum N, Delzon S (2017) Aridity drove the evolution of extreme embolism resistance and the radiation of conifer genus *Callitris*. New Phytol 215:97–112

Laver RJ, Nielsen SV, Rosauer DF, Oliver PM (2017) Trans-biome diversity in Australian grass-specialist lizards (Diplodactylidae: *Strophurus*). Mol Phylogenet Evol 115:62–70

Lee J-Y, Joseph L, Edwards S (2012) A species tree for the Australo-Papuan fairy-wrens and their allies (Aves: Maluridae). Syst Biol 61:253–271

Lee MSY, Skinner A, Camacho A (2013) The relationship between limb reduction, body elongation and geographical range in lizards (*Lerista*, Scincidae). J Biogeogr 40:1290–1297

Levy E, Byrne M, Coates DJ, Macdonald BM, McArthur S, van Leeuwen S (2016) Contrasting influences of geographic range and ditsribution of populations on patterns of genetic diversity in two sympatric Pilbara acacias. PLoS One 11(10):e0163995

Leys R, Watts CHS, Cooper SJB, Humphreys WF (2003) Evolution of subterranean diving beetles (Coleoptera: Dytiscidae: Hydroporini, Bidessini) in the arid zone of Australia. Evolution 57:2819–2834

Liu Q, Brubaker CL, Green AG, Marshall DR, Sharp PJ, Singh SP (2001) Evolution of the *FAD2-1* fatty acid desaturase 5' UTR intron and the molecular systematics of *Gossypium* (Malvaceae). Am J Bot 88:92–102

López-López A, Hudson P, Galián J (2016) Islands in the desert: species delimitation and evolutionary history of *Pseudotetracha* tiger beetles (Coleoptera: Cicindelidae: Megacephalini) from Australian salt lakes. Mol Phylogenet Evol 101:279–285

Mable BK, Roberts JD (1997) Mitochondrial DNA evolution of tetraploids in the genus *Neobatrachus* (Anura: Myobatrachidae). Copeia 1997:680–689

Maddock ST, Childerstone A, Fry BG, Williams DJ, Barlow A, Wüster W (2017) Multi-locus phylogeny and species delimitation of Australo-Papuan blacksnakes (*Pseudechis* Wagler, 1830: Elapidae: Serpentes). Mol Phylogenet Evol 107:48–55

Mahony MJ, Robinson ES (1980) Polyploidy in the Australian Leptodactylid frog genus *Neobatrachus*. Chromosoma 81:199–212

Mahony MJ, Donnellan SC, Roberts JD (1996) An electrophoretic investigation of relationships of diploid and tetraploid species of Australian desert frogs *Neobatrachus* (Anuira: Mypbatrachidae). Aust J Zool 4:639–650

Martin HA (2006) Cenozoic climatic changes and the development of the arid vegetation of Australia. J Arid Environ 66:533–563

Mast AR, Olde PM, Makinson RO, Jones R, Kubes A, Miller ET, Weston PH (2015) Paraphyly changes understanding of timing and tempo of diversification in subtribe Hakeinae (Proteaceae), a giant Australian plant radiation. Am J Bot 102:1634–1646

Matthews EG (2000) Origins of Australian arid-zone tenebrionid beetles. Invertebr Taxon 14:941–951

McElroy K, Beattie K, Symonds M, Joseph L (2018) Mitogenomic diversity in the Mulga Parrot of the Australian arid-zone: cryptic subspecies and tests for selection. Aust Ornithol 118:22

McGowran B, Holdgate GR, Li Q, Gallagher SJ (2004) Cenozoic stratigraphic succession in southeastern Australia. Aust J Earth Sci 51:459–496

McLaren S, Wallace MW (2010) Plio-Pleistocene climate change and the onset of aridity in southeastern Australia. Glob Planet Chang 71:55–72

McLean CA, Mousalli A, Sass S, Stuart-Fox D (2013) Taxonomic assessment of the *Ctenophorus decresii* complex (Reptilia: Agamidae) reveals a new species of dragon lizard from western New South Wales. Rec Aust Mus 65:51–63

McLean CA, Stuart-Fox D, Mousalli A (2014) Phylogeographic structure, demographic history and morph composition in a colour polymorphic lizard. J Evol Biol 27:2123–2137

McLean A, Toon A, Schmidt D, Hughes J, Joseph L (2017) Phylogeography and geno-phenotypic discordance in a widespread Australian bird, the variegated fairy-wren, *Malurus lamberti* (Aves: Maluridae). Biol J Linn Soc 121:655–669

McLeish MJ (2011) Speciation in gall-inducing thrips on *Acacia* in arid and non-arid areas of Australia. J Arid Environ 75:793–801

McLeish MJ, Chapman TW, Schwarz MP (2007) Host driven diversification of gall inducing *Acacia* thrips and the aridification of Australia. BMC Biol 5:1–13

McLeish MJ, Schwarz MP, Chapman TW (2011) Gall inducers take a leap: host-range differences explain speciation opportunity (Thysanoptera: Phlaeothripidae). Aust J Entomol 50:405–417

Melville J, Schulte JA, Larson A (2001) A molecular phylogenetic study of ecological diversification in the Australian lizard genus *Ctenophorus*. J Exp Zool 291:339–353

Melville J, Ritchie EG, Chapple SNJ, Glor RE, Schulte JAI (2011) Evolutionary origins and diversification of dragon lizards in Australia's tropical savannas. Mol Phylogenet Evol 58:257–270

Melville J, Hines ML, Hale J, Chapple S, Ritchie EG (2016) Concordance in phylogeography and ecological niche modelling identify dispersal corridors for reptiles in arid Australia. J Biogeogr 43:1844–1855

Millar MA, Coates DJ, Byrne M (2013) Genetic connectivity and diversity in inselberg populations of *Acacia woodmaniorum*, a rare endemic plant of the Yilgarn Craton Banded Iron Formations. Heredity 111:437–444

Millar MA, Byrne M, Coates DJ, Roberts JD (2016) Contrasting diversity and demographic signals in sympatric narrow-range endemic shrubs of the south-west Western Australian semi-arid zone. Biol J Linn Soc 118:315–329

Millar MA, Byrne M, Coates DJ, Roberts JD (2017) Comparative analysis indicates historical persistence and contrasting contemporary structure in sympatric woody perennials of semi-arid southwest Western Australia. Biol J Linn Soc 120:771–787

Miller GH, Fogel ML, Magee JW, Gagan MK (2016) Disentangling the impacts of climate and human colonization on the flora and fauna of the Australian arid zone over the past 100 ka using stable isotopes in avian eggshell. Quat Sci Rev 151:27–57

Mitchell KJ, Pratt RC et al (2014) Molecular phylogeny, biogeography, and habitat preference evolution of marsupials. Mol Biol Evol 31:2322–2330

Moritz C (1993) The origin and evolution of parthenogenesis in *Heteronotia binoei* (Gekkonidae): Synthesis. Genetica 90:269–280

Mossop KD, Adams M, Unmack PJ, Smith Date KL, Wong BBM, Chapple DG (2015) Dispersal in the desert: ephemeral water drives connectivity and phylogeography of an arid-adapted fish. J Biogeogr 12:2374–2388

Mummenhoff K, Bruggemann H, Bowman JL (2001) Chloroplast DNA phylogeny and biogeography of *Lepidium* (Brassicaceae). Am J Bot 88:2051–2063

Mummenhoff K, Linder P, Friesen N, Bowman JL, Lee JY, Franzke A (2004) Molecular evidence for bicontinental hybridogenous genomic constitution in *Lepidium* senu stricto (Brassicaceae) species from Australia and New Zealand. Am J Bot 91:254–261

Murphy DJ, Miller JT, Bayer RJ, Ladiges PY (2003) Molecular phylogeny of *Acacia* subgenus *Phyllodineae* (Mimosoideae: Leguminosae) based on DNA sequences of the internal transcribed spacer region. Aust Syst Bot 16:19–26

Murphy NP, Breed MF, Guzik MT, Cooper SJB, Austin AD (2012) Trapped in desert springs: phylogeography of Australian desert spring snails. J Biogeogr 39:1573–1582

Murphy NP, Guzik MT, Cooper SJB, Austin AD (2015) Desert spring refugia: museums of diversity or evolutionary cradles? Zool Scr 44:693–701

Nguyen TTT, Austin CM, Meewan MM, Schultz MB, Jerry DR (2004) Phylogeography of the freshwater crayfish *Cherax destructor* Clark (Parastacidae) in inland Australia: historical fragmentation and recent range expansion. Biol J Linn Soc 83:539–550

Nielsen SV, Oliver PM, Laver R, Bauer AM, Noonan BP (2016) Stripes, jewels and spines: further investigations into the evolution of defensive strategies in a chemically defended gecko radiation (*Strophurus*, Diplodactylidae). Zool Scr 45:481–493

Nistelberger H, Byrne M, Coates DJ, Roberts JD (2014) Strong phylogeographic structure in a millipede indicates Pleistocene vicariance between populations on banded iron formations in semi-arid Australia. PLOS One 9:e93038

Nistelberger HM, Byrne M, Coates DJ, Roberts JD (2015a) Genetic drift drives evolution in the bird pollinated terrestrial island endemic *Grevillea georgeana* (Proteaceae). Bot J Linn Soc 178:155–168

Nistelberger HM, Byrne M, Coates DJ, Roberts JD (2015b) Phylogeography and population differentiation in terrestrial island populations of *Banksia arborea* (Proteaceae). Biol J Linn Soc 114:860–872

Nyari A, Joseph L (2012) Evolution in Australasian mangrove forests: multilocus phylogenetic analysis of the *Gerygone* warblers (Aves: Acanthizidae). PLoS ONE 7:e31840

Oliver P, Bauer A (2011) Systematics and evolution of the Australian knob-tail geckos (*Nephrurus*, Carphodactylidae, Gekkota): pleisomorphic grades and biome shifts through the Miocene. Mol Phylogenet Evol 59:664–674

Oliver PM, McDonald PJ (2016) Young relicts and old relicts: a novel palaeoendemic vertebrate from the Australian Central Uplands. R Soc Open Sci 3:160018

Oliver PM, Adams M, Lee MSY, Hutchinson MN, Doughty P (2009) Cryptic diversity in vertebrates: molecular data double estimates of species diversity in a radiation of Australian lizards (Diplodactylus, Gekkota). Proc R Soc B 276:2001–2007

Oliver PM, Adams M, Doughty P (2010) Molecular evidence for ten species and Oligo-Miocene vicariance within a nominal Australian gecko species (*Crenadactylus ocellatus*, Diplodactylidae). BMC Evol Biol 10:386

Oliver PM, Smith KL, Laver RJ, Doughty P, Adams M (2014) Contrasting patterns of persistence and diversification in vicars of a widespread Australian lizard lineage (the *Oedura marmorata* complex). J Biogeogr 41:2068–2079

Oliver PM, Couper PJ, Pepper M (2016) Independant transitions between monsoonal and arid biomes revealed by systematic revision of a complex of Australian geckos (*Diplodactylus*; Diplodactylidae). PLoS ONE 9(12):e11895

Onstein RE, Jordan GJ, Sauquet H, Weston PH, Bouchenak-Khelladi Y, Carpenter RJ, Linder HP (2017) Evolutionary radiations of Proteaceae are triggered by the interaction between traits and climates in open habitats. Glob Ecol Biogeogr 25:1239–1251

Owen CL, Marshall DC, Hill KBR, Simon C (2017) How the aridification of Australia structured the biogeography and influenced the diversification of a large lineage of Australian cicadas. Syst Biol 66:569–589

Pain CF, Pillans BJ, Roach IC, Worrall L, Wilford JR (2012) Old, flat and red – Australia's distinctive landscape. In: Blewett RS (ed) Shaping a nation: a geology of Australia. Geoscience Australia and ANU E Press, Canberra, pp 227–275

Pepper M, Keogh JS (2014) Biogeography of the Kimberley, Western Australia: a review of landscape evolution and biotic response in an ancient refugium. J Biogeogr 41:1443–1455

Pepper M, Doughty P, Arculus R, Keogh JS (2008) Landforms predict phylogenetic structure on one of the world's most ancient surfaces. BMC Evol Biol 8:152

Pepper M, Fujita MK, Moritz C, Keogh JS (2011a) Palaeoclimate change drove diversification among isolated mountain refugia in the Australian arid zone. Mol Ecol 20:1529–1545

Pepper M, Ho S, Fujita MK, Keogh JS (2011b) The genetic legacy of aridification: Miocene refugia fostered diversification while Pleistocene climatic cycles erased diversity in desert lizards. Mol Phylogenet Evol 61:750–759

Pepper M, Doughty P, Fujita MK, Moritz C, Keogh JS (2013a) Speciation on the rocks: integrated systematics of the *Heteronotia spelea* species complex (Gekkota; Reptilia) from Western and central Australia. PLoS ONE 11:e78110

Pepper M, Doughty P, Keogh JS (2013b) Geodiversity and endemism in the iconic Australian Pilbara region: a review of landscape evolution and biotic response in an ancient refugium. J Biogeogr 40:1225–1239

Perez KE, Ponder WF, Colgan DJ, Clark SA, Lydeard C (2005) Molecular phylogeny and biogeography of spring-associated hydrobiid snails of the Great Artesian Basin, Australia. Mol Phylogenet Evol 34:545–556

Pillans B (2018) Seeing red: some aspects of the geological and climatic history of the Australian arid zone. In: Lambers H (ed) On the ecology of Australia's arid zone. Springer Nature, Dordrecht pp 5–43

Pons J, Barraclough TG, Gomez-Zurita J, Cardoso A, Duran DP, Hazell S, Kamoun S, Sumlin WD, Vogler AP (2006) Sequence-based species delimitation for the DNA Taxonomy of undescribed insects. Syst Biol 55:595–609

Prideaux G, Long J et al (2007) An arid-adapted middle Pleistocene vertebrate fauna from south-central Australia. Nature 445:422–425

Pyron RA, Wiens JJ (2011) A large scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders and caecilians. Mol Phylogenet Evol 61:543–583

Rabosky DL, Donnellan SC, Talaba AL, Lovette IJ (2007) Exceptional among-lineage variation in diversification rates during the radiation of Australia's most diverse vertebrate clade. Proc R Soc Lond Ser B 274:2915–2923

Randell BR (1970) Adaptations in the genetic system of Australian arid zone Cassia species (Leguminosae, Caesalpinioideae). Aust J Bot 18:77–97

Revel-Rolland M, De Deckker P, Delmonte B, Hesse PP, Magee JM, Basile-Doelsch I, Grousset F, Bosch D (2006) Eastern Australia: A possible source of dust in East Antarctica interglacial ice. Earth Planet Sci Lett 249:1–13

Rix MG, Harvey MS (2012) Phylogeny and historical biogeography of ancient assassin spiders (Araneae: Archaeidae) in the Australian mesic zone: Evidence for Miocene speciation within Tertiary refugia. Mol Phylogenet Evol 62:375–396

Rix MG, Cooper SJB, Meusemann K, Klopfstein S, Harrison SE, Harvey MS, Austin AD (2017) Post-Eocene climate change across continental Australia and the diversification of Australasian spiny trapdoor spiders (Idiopidae: Arbanitinae). Mol Phylogenet Evol 109:302–320

Roberts JD, Edwards DL (2018) The evolution, physiology and ecology of the Australian arid zone frog fauna. In: Lambers H (ed) On the ecology of Australia's arid zone. Springer Nature, Dordrecht pp 149–180

Roth-Nebelsick A, Hassiotou F, Veneklaas EJ (2009) Stomatal crypts have small effects on transpiration: a numerical model analysis. Plant Physiol 151:2018–2027

Sakaguchi S, Bowman DMJS, Prior LD, Crisp MD, Linde CC, Tsumura Y, Isagi Y (2013) Climate, not Aboriginal landscape burning, controlled the historical demography and distribution of fire-sensitive conifer populations across Australia. Proc R Soc B Biol Sci 280:2013182

Sampson JF, Byrne M (2012) Genetic diversity and multiple origins of polyploid *Atriplex nummularia* Lindl. (Chenopodiaceae). Biol J Linn Soc 105:218–230

Sanders KL, Lee MSY, Leijs R, Foster R, Keogh JS (2008) Molecular phylogeny and divergence dates for Australasian elapids and sea snakes (Hydrophiinae): Evidence from seven genes for rapid evolutionary radiations. J Evol Biol 21:882–895

Schmidt S, Walter GH (2014) Young clades in an old family: Major evolutionary transitions and diversification of the eucalypt-feeding pergid sawflies in Australia (Insecta, Hymenoptera, Pergidae). Mol Phylogenet Evol 74:111–121

Schmidt-Lebuhn AN, Smith KJ (2016) From the desert it came: evolution of the Australian paper daisy genus *Leucochrysum* (Asteracaea; Gnaphalieae). Aust Syst Bot 29:176–184

Schodde R (1982) Origin, adaptation and evolution of birds in arid Australia. In: Barker WR, Greenslade PJM (eds) Evolution of the flora and fauna of arid Australia. Peacock Publications, Adelaide, pp 191–224

Schodde R (2006) Australasia's bird fauna today-origins, and evolutionary development. In: Merrick JR, Archer M, Hickey GM, Lee MSY (eds) Evolution and biogeography of Australasian vertebrates. Auscipub, Sydney, pp 413–458

Schweizer M, Güntert M, Hertwig S (2012) Phylogeny and biogeography of the parrot genus *Prioniturus* (Aves: Psittaciformes). J Zool Syst Evol Res 50:145–156

Schweizer M, Wright TF, Penalba J, Schirtzinger EE, Joseph L (2015) Molecular phylogenetics suggests a New Guinean origin and frequent episodes of founder-event speciation in the nectarivorous lories and lorikeets (Aves: Psittaciformes). Mol Phylogenet Evol 90:34–48

Schwentner M, Timms BV, Richter S (2012) Flying with the birds? Recent large-area dispersal of four Australian *Limnadopsis* species (Crustacea: Branchiopoda: Spinicaudata). Ecol Evol 2:1605–1626

Scott KD, McIntyre CL, Playford J (2000) Molecular analyses suggest a need for a significant rearrangement of Rutaceae subfamilies and a major reassessment of species relationships within *Flindersia*. Plant Syst Evol 223:15–27

Seelanan T, Brubaker CL, Stewart JM, Craven LA, Wendel JE (1999) Molecular systematics of Australian *Gossypium* section *Grandicalyx* (Malvaceae). Syst Bot 24:183–208

Sheedy EM, Ryberg M, Lebel T, May TW, Bougher NL, Matheny B (2016) Dating the emergence of truffle-like fungi in Australia, by using an augmented meta-analysis. Aust Syst Bot 29:284–302

Shepherd KA, Waycott M, Calladine A (2004) Radiation of the Australian Salicornioideae (Chenopodiaceae) – based on evidence from nuclear and chloroplast DNA sequences. Am J Bot 91:1387–1397

Shoo LP, Rose R, Doughty P, Austin JJ, Melville J (2008) Diversification patterns of pebble-mimic dragons are consistent with historical disruption of important habitat corridors in arid Australia. Mol Phylogenet Evol 48:528–542

Sistrom MJ, Hutchinson MN, Hutchinson RG, Donnellan SC (2009) Molecular phylogeny of Australian *Gehyra* (Squamata:Gekkonidae) and taxonomic revision of *Gehyra variegata* in south-eastern Australia. Zootaxa 2277:14–32

Sistrom M, Hutchinson M, Bertozzi T, Donnellan S (2014) Evaluating evolutionary history in the face of high gene tree discordance in Australian *Gehyra* (Reptilia: Gekkonidae). Heredity 113:52–63

Skinner A, Lee MSY (2009) Body-form evolution in the Scincid lizard clade *Lerista* and the mode of macroevolutionary transitions. Evol Biol 36:292–300

Skinner A, Hugal lAF, Hutchinson MN (2011) Lygosomine phylogeny and the origins of Australian scincid lizards. J Biogeogr 38:1044–1058

Smith KL, Harmon LJ, Shoo LP, Melville J (2011) Evidence of constrained phenotypic evolution in a cryptic species complex of agamid lizards. Evolution 65:976–992

Sniderman JMK, Pillans B, O'Sullivan PB, Kershaw AP (2007) Climate and vegetation in southeastern Australia respond to Southern Hemisphere insolation forcing in the late Pliocene-early Pleistocene. *Geology* 35:41–44

Sniderman JMK, Woodhead JD, Hellstrom J, Jordan GJ, Drysdale RN, Tyler JJ, Porch N (2016) Pliocene reversal of late Neogene aridification. Proc Natl Acad Sci USA 113:1999–2004

Stafford Smith DM, Morton SR (1990) A framework for the ecology of arid Australia. J Arid Environ 18:255–278

Strasburg JL, Kearney M (2005) Phylogeography of sexual *Heteronotia binoei* (Gekkonidae) in the Australian arid zone: climatic cycling and repetitive hybridisation. Mol Ecol 14:2755–2772

Tapper S-L, Byrne M, Yates CJ, Keppel G, Hopper SD, Van Niel K, Schut AGT, Mucina L, Wardell-Johnson GW (2014a) Isolated with persistence or dynamically connected? Genetic patterns in a common granite outcrop endemic. Divers Distrib 20:987–1001

Tapper S-L, Byrne M, Yates CJ, Keppel G, Hopper SD, Van Niel K, Schut AGT, Mucina L, Wardell-Johnson GW (2014b) Prolonged isolation and persistence of a common endemic on granite outcrops in both mesic and semi-arid environments in southwestern Australia. J Biogeogr 41:2032–2044

Thornhill AH, Mishler BD, Knerr NJ, Gonz_alez-Orozco CE, Costion CM, Crayn DM, Laffan SW, Miller JT (2016) Continental-scale spatial phylogenetics of Australian angiosperms provides insights into ecology, evolution and conservation. J Biogeogr 43:2085–2309

Toon A, Mather P, Baker A, Durrant K, Hughes J (2007) Pleistocene refugia in an arid landscape: analysis of a widely distributed Australian passerine. Mol Ecol 16:2525–2541

Toon A, Austin J, Dolman G, Pedler L, Joseph L (2012) Evolution of arid zone birds in Australia: leapfrog distribution patterns and mesic-arid connections in quail-thrush. Mol Phylogenet Evol 62:286–295

Toon A, Joseph L, Burbidge A (2013) Genetic analysis of the Australian whipbirds and wedgebills illuminates the evolution of their plumage and vocal diversity. Emu 113:359–366

Toon A, Crisp MD, Gamage H, Mant J, Morris DC, Schmidt S, Cook LG (2015) Key innovation or adaptive change? A test of leaf traits in Triodiinae in Australia. Sci Rep 5:12398

Toussaint EFA, Condamine FL, Hawlitschek O, Watts CH, Porch N, Hendrich L, Balke M (2015a) Unveiling the diversification dynamics of Australasian predaceous diving beetles in the Cenozoic. Syst Biol 64:3–24

Toussaint EFA, Tänzler R, Rahmadi C, Balke M, Riedel A (2015b) Biogeography of Australasian flightless weevils (Curculionidae, Celeuthetini) suggests permeability of Lydekker's and Wallace's Lines. Zool Scr 44:632–644

Travouillon KJ, Legendre S, Archer M, Hand SJ (2009) Palaeoecological analyses of Riversleigh's Oligo-Miocene sites: implications for Oligo-Miocene climate change in Australia. Palaeogeogr Palaeoclimatol Palaeoecol 276:24–37

Watanabe K, Kosuge K, Shimamura R, Konishi N, Taniguchi K (2006) Molecular systematics of Australian Calotis (Asteraceae: Astereae). Aust Syst Bot 19:155–168

Williams MAJ (1984) Cenozoic evolution of arid Australia. In: Cogger HG, Cameron EE (eds) Arid Australia. Australian Museum, Sydney, pp 59–78

Williams MAJ (2000) Quaternary Australia: extremes in the last glacial-interglacial cycle. In: Veevers JJ (ed) Billion-year earth history of Australia and neighbours in Gondwanaland. GEMOC Press, Sydney, pp 55–59

Williams MAJ (2001) Morphoclimatic maps at 18 ka, 9 ka, & 0 ka. In: Veevers JJ (ed) Atlas of billion-year earth history of Australia and neighbours in Gondwanaland. GEMOC Press, Sydney, pp 45–48

Williams M, Diunkerley D, De Dekker P, Kershaw P, Chappell J (1998) Quaternary Environments, 2nd edn. Arnold, London

Winterfeld G, Schneider J, Röser M (2009) Allopolyploid origin of Mediterranean species in *Helictotrichon* (Poaceae) and its consequences for karyotype repatterning and homogenisation of rDNA repeat units. Syst Biodivers 7:277–295

Wright T, Schirtzinger E et al (2008) A multi-locus molecular phylogeny of the parrots (Psittaciformes): Support for a Gondwanan origin during the Cretaceous. Mol Biol Evol 25:2141–2156

Mineral Nutrition of Plants in Australia's Arid Zone

Honghua He, David J. Eldridge, and Hans Lambers

Introduction

Australia's arid-zone soils are highly leached and resorted (Winkworth 1967; Pillans 2018) and characterised by low levels of available water and nutrients (Orians and Milewski 2007). These soils are particularly low in total phosphorus (P) and nitrogen (N) (Islam et al. 2000; Bennett and Adams 2001; Grigg et al. 2008a). The distribution of these and other nutrients is typically heterogeneous, due to the development of 'islands of fertility' and tight nutrient cycling beneath the canopies of long-lived perennial plants (Tongway and Ludwig 1994; He et al. 2011). Nutrient cycling and decomposition of leaf litter are largely restricted to periods after rain, when bacteria (Skopp et al. 1990; Ford et al. 2007) and cyanobacteria, either free-living or as components of biological soil crusts (biocrusts), are active (Austin et al. 2004). Termites also play an important role in litter decomposition and nutrient cycling and contribute to the patchy distribution of nutrients (Tongway et al. 1989; Park et al. 1994).

H. He (✉)
State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau,
Northwest A&F University, Yangling, Shaanxi, China
e-mail: honghuahe@ms.iswc.ac.cn

D. J. Eldridge
Schoolof Biological, Earth and Environmental Sciences, University of New South Wales,
Sydney, NSW 2052, Australia

H. Lambers
School of Biological Sciences, The University of Western Australia,
Crawley (Perth), WA 6009, Australia

H. Lambers (ed.), *On the Ecology of Australia's Arid Zone*,
https://doi.org/10.1007/978-3-319-93943-8_4

Unlike many ecosystems in which herbivores and detritivores are the primary consumers of foliage, fire is the primary consumer of the nutrient-poor and woody plant tissues in the arid zone and is a significant recycler of nutrients (Orians and Milewski 2007; van Etten and Burrows 2018). Getzin et al. (2016) developed a 'Nutrient-Poverty/Intense-Fire Theory' and postulated that the most unusual characteristics of Australian ecosystems and their organisms are the evolutionary consequences of adaptations to nutrient poverty and the presence of intense fires, which tend to exacerbate nutrient impoverishment. Intense fire reinforces nutrient poverty by volatilising nutrients such as N and sulfur (S). This produces a temporal pattern of either feast or famine in nutrients contained in ash, depleting the soluble fractions of nutrients through flooding and leaching. There are also brief nutrient pulses following fires (Orians and Milewski 2007; Getzin et al. 2016).

Nitrogen is continuously lost from the system, predominantly as a result of fire, when most N is volatilised (Orians and Milewski 2007). Nitrogen fixation is therefore critically important to compensate for these losses. Many plants such as acacias can fix N_2 through symbiotic associations with rhizobia and are able to replenish N depleted by volatilisation (Schortemeyer et al. 2002; Orians and Milewski 2007). Some termite species, cyanobacteria and cyanolichens (those containing cyanobacteria as one of their partners) can also fix N_2. Termites and biocrust organisms such as cyanobacteria are likely major contributors of N to this system (Tongway et al. 1989; Pate et al. 1998).

Most soils in Australia's arid zone have a low-P availability, due to long-term weathering and sorption of P by iron (Fe) and aluminium (Al) oxides and hydroxides (Morton et al. 2011). For example, plant-available P concentrations in some soils in the Great Sandy Desert are less than 2 $\mu g\ g^{-1}$; foliage P concentrations of most woody plants grown in these soils are less than 1 $mg\ g^{-1}$, and those of some *Triodia* (spinifex) species are even lower than 0.2 $mg\ g^{-1}$ (Grigg et al. 2008a, b; He et al. 2011). In addition to P, concentrations of micronutrient such as zinc (Zn) are likely to be low in soils in Australia's arid zone (Orians and Milewski 2007). Some plants, however, are able to accumulate high levels of elements such as manganese (Mn) in their foliage, even when the availability of these elements in the soil is relatively low (Fernando et al. 2009). Furthermore, the availability of some micronutrients such as nickel (Ni) in some soils is very high, and certain plants growing on such soils become Ni-hyperaccumulators (Severne and Brooks 1972).

Dinitrogen-fixing acacias (Fabaceae) are major components of most vegetation types in Australia's arid zone (Orians and Milewski 2007; Gonzalez-Orozco et al. 2011). Other major plant species include *Grevillea* and *Hakea* (Proteaceae), *Eucalyptus* and *Corymbia* (Myrtaceae) and *Triodia* (Poaceae) (Grigg et al. 2008b; Goldie et al. 2010). In this chapter, we focus on the mineral nutrition of some major plant families in Australia's arid zone, including the mineral nutrition of *Acacia* species and non-mycotrophic plants (mainly Proteaceae). The role of desert biocrusts, and termites and their symbionts, in nutrient cycling, is also discussed, and species with high levels of metals such as Mn, Ni and gold (Au) are presented.

Mineral Nutrition of *Acacia* Species

Acacias are often associated with rhizobia and are therefore capable of N_2 fixation (Marsudi et al. 1999; Schortemeyer et al. 2002). Acacias play a prominent role in the long-term maintenance, or increase, in N stocks across many ecosystems in Australia's arid zone, particularly following fire, when most N is lost (Hingston et al. 1982; Orians and Milewski 2007). Mean N concentration in mature phyllodes (i.e. modified petioles that function as leaves) of four *Acacia* species in the Telfer region of the Great Sandy Desert is 14.8 mg N g^{-1} (He et al. 2011) and that of four *Acacia* species in an area near the Nifty Copper Operation in the Great Sandy Desert is 16.7 mg g^{-1} (Grigg et al. 2008a; A.M. Grigg *pers. comm.*) (Fig. 1). These values are equivalent to or exceed the concentration of N in plant shoot dry matter (15 mg g^{-1}), which is sufficient to sustain crop growth (Kirkby 2012). The $\delta^{15}N$ values of phyllodes of the four species in the Telfer region were between −0.8‰ and 1.4‰, and the values of their associated *Triodia* species ranged from 0.5‰ to 1.7‰, with three out of the four *Acacia* species having significantly lower $\delta^{15}N$ values than their associated *Triodia* species. This suggests that all but one of the four *Acacia* species fixed N_2. The estimated proportion of phyllode N derived from symbiotic N_2 fixation (%Ndfa) for *Acacia ancistrocarpa*, *Acacia stellaticeps* and *Acacia robeorum* was 25%, 40% and 75%, respectively (He et al. 2011). Some *Acacia* species in an area near the Nifty Copper Operation of the Great Sandy Desert display $\delta^{15}N$ values that are less than half those of their non-fixing neighbours, and their phyllode $\delta^{15}N$ values are very close to zero, indicating that these *Acacia* species fix N_2 symbiotically (Grigg et al. 2008a). However, the $\delta^{15}N$ data for Australian mulga ecosystems strongly indicate that symbiotic N_2 fixation by *Acacia* species is virtually non-existent in these mulga species, as the $\delta^{15}N$ values for both putative N_2-fixing species (9·1 ± 0·6‰; mean ± SE) and

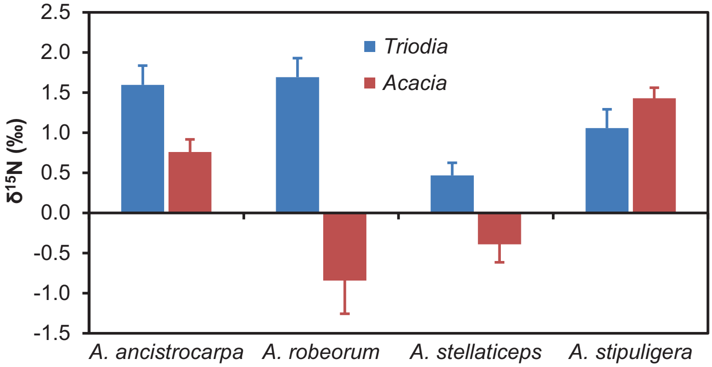


Fig. 1 Foliar $\delta^{15}N$ values of four *Acacia* species and their associated *Triodia* species growing in the Telfer region of the Great Sandy Desert. All values are presented as means ± SE ($n = 6$). (Based on He et al. 2011)

associated nonleguminous species (9·1 ± 0·5‰) are identical, and there is no evidence of nodulation in these *Acacia* roots (Pate et al. 1998). Nitrate-nitrogen (NO_3^--N) is present in high concentrations and is the predominant form of available N in mulga soils. It is likely, therefore, that nodulation and associated symbiotic N_2 fixation are inhibited by high soil N availability (Erskine et al. 1996; Pate et al. 1998).

As acacias are capable of symbiotic N_2 fixation, they may have an unlimited N supply from the air, thus freeing them from N limitation in N-poor soils. However, the energy and P costs of N_2 fixation are relatively high. Nitrogen-fixing legumes commonly require more inorganic P than nonlegume species reliant on mineral N assimilation (Kouas et al. 2009). Phosphorus deficiency has negative effects on the growth of the host plant and/or on the growth and functioning of the nodules, thus impairing symbiotic N_2 fixation (Almeida et al. 2000). Phosphorus concentrations in mature phyllodes of four *Acacia* species growing in P-impoverished soils in the Telfer region ranged between 0.31 and 0.44 mg g^{-1} (He et al. 2011). Those of four *Acacia* species growing in an area near the Nifty Copper Operation varied between 0.28 and 0.73 mg g^{-1} (Grigg 2009) (Table 1), being much lower than the average P concentration considered sufficient for crop plants (2 mg g^{-1}) (Kirkby 2012).

The high N:P ratios in *Acacia* phyllodes indicate that P is more limiting than N for acacias in Australia's arid zone. For four *Acacia* species growing in P-impoverished soils in the Telfer region, N:P ratios in mature phyllodes are between 27 and 55, with a mean value of 44 (He et al. 2011), and those in phyllodes of four *Acacia* species growing in an area near the Nifty Copper Operation are between 23 and 47, with a mean value of 34 (Grigg 2009) (Table 1). This indicates that these species are more severely limited by P than by N (Koerselman and Meuleman 1996; Güsewell 2004; Greenwood et al. 2008), consistent with results for species capable of symbiotic N_2 fixation. These species often resorb P more efficiently than they resorb N, with some species resorbing up to 80% P from senescing phyllodes (He et al. 2011). Some species can access P from poorly available forms of P such as iron phosphate through carboxylate exudation (He et al. 2012a).

A few *Acacia* species, for example, *Acacia robeorum*, *Acacia bivenosa*, *Acacia ligulata*, *Acacia didyma* and *Acacia startii*, growing in Australia's desert environments accumulate S in their phyllodes at values exceeding 25 mg g^{-1} dry matter (He et al. 2012b; Reid et al. 2016) (Table 2). These species are classified as thiophores, i.e. plants with a S concentration in their foliage ranging from 25 to 82 mg S g^{-1} dry matter (Ernst 1998). These species also have higher calcium (Ca) and magnesium (Mg) concentrations than other non-thiophore *Acacia* species growing in nearby habitats, and S actually co-precipitates with Ca and Mg and forms biominerals in phyllodes, very likely in the form of oxalates and sulfates (He et al. 2012b; Reid et al. 2016). The function of these S-rich biominerals is unclear. These gypsum-forming thiophores may be adapted to S-rich substrates concomitantly enriched in Ca; they do not remobilise S when phyllodes senesce but return S to the soil as tissue-encapsulated and sparingly soluble minerals (Fig. 2). This suggests that they do not tightly regulate S uptake or use biomineralisation to immobilise or detoxify S (Robson et al. 2017a, b). However, some *Acacia* species growing in the soils

Table 1 Concentrations of nitrogen (N), phosphorus (P) and N:P ratios in foliage of several *Acacia* species growing in the Telfer region and in an area near the Nifty Copper Operation in the Great Sandy Desert

Location	Telfer				Nifty			
Species	*A. ancistrocarpa*	*A. robeorum*	*A. stellaticeps*	*A. stipuligera*	*A. ancistrocarpa*	*A. hilliana*	*A. jensenii*	*A. transluscence*
N (mg g^{-1})	16.9 (14.3–20.1)	11.7 (10.7–12.7)	13.9 (13.0–15.0)	16.9 (15.5–18.6)	16.7 (11.4–19.2)	12.3 (10.8–14.1)	20.7 (17.9–24.3)	19.3 (17.4–21.6)
P (mg g^{-1})	0.31 (0.24–0.35)	0.44 (0.37–0.52)	0.32 (0.26–0.38)	0.36 (0.32–0.38)	0.41 (0.27–0.60)	0.42 (0.24–0.66)	0.73 (0.60–0.80)	0.61 (0.40–0.70)
N:P	55 (48–64)	27 (23–32)	44 (36–54)	48 (41–52)	43 (30–61)	33 (20–45)	29 (22–35)	33 (27–45)

Note: Data are mean values of at least six individuals per species. Numbers in brackets are ranges of the data. Data based on He et al. (2011) and A.M. Grigg (unpublished data)

Table 2 Concentrations of sulfur (S), calcium (Ca) and magnesium (Mg) in foliage of several *Acacia* species growing in the Great Sandy Desert (GSD), Tanami Desert (TD) and Stuart Shelf (SS) and of specimens from a few Australian herbaria (AH)

Species	Sample location	S (mg g^{-1})	Ca (mg g^{-1})	Mg (mg g^{-1})	References
Acacia ancistrocarpa	GSD (Telfer)	0.6	8.8	2.6	H. He unpublished data
*A. robeorum**	GSD (Telfer)	42.2	72.0	10.3	He et al. (2012b)
A. stellaticeps	GSD (Telfer)	3.0	13.0	3.8	H. He unpublished data
A. stipuligera	GSD (Telfer)	1.3	9.4	3.4	H. He unpublished data
A. ancistrocarpa	GSD (Nifty)	1.6	6.4	2.3	A.M. Grigg unpublished data
A. hilliana	GSD (Nifty)	1.2	8.5	2.4	A.M. Grigg unpublished data
A. jensenii	GSD (Nifty)	1.4	7.3	2.0	A.M. Grigg unpublished data
A. translucens	GSD (Nifty)	3.2	10.7	2.9	A.M. Grigg unpublished data
A. ancistrocarpa	GSD	1.3	8.0	1.6	Reid et al. (2016)
A. bivenosa x *sclerosperma* subsp. *sclerosperma*	GSD	11.7	38.7	3.4	Reid et al. (2016)
*A. bivenosa**	TD	25.7	51.4	5.1	Reid et al. (2016)
A. coriacea	TD	1.6	25.7	3.9	Reid et al. (2016)
A. aneura	SS	1.4	16.6	1.6	Reid et al. (2016)
*A. ligulata**	SS	26.9	52.8	11.1	Reid et al. (2016)
*A. ampliceps**	AH	21.5	44.7	7.4	Reid et al. (2016)
A. blakelyi	AH	3.2	13.0	2.6	Reid et al. (2016)
*A. didyma**	AH	40.4	54.9	5.3	Reid et al. (2016)
*A. cupularis**	AH	22.1	34.3	2.0	Reid et al. (2016)
A. myrtifolia	AH	1.5	10.2	0.7	Reid et al. (2016)
*A. robeorum**	AH	56.9	89.1	7.1	Reid et al. (2016)
A. rostellifera	AH	2.9	40.5	4.1	Reid et al. (2016)
*A. salicina**	AH	18.4	41.2	2.6	Reid et al. (2016)
A. saligna	AH	4.8	17.0	6.2	Reid et al. (2016)
*A. slcerosperma**	AH	17.5	46.8	4.0	Reid et al. (2016)
*A. startii**	AH	36.0	53.3	4.4	Reid et al. (2016)
A. telmica	AH	7.8	32.7	2.4	Reid et al. (2016)
*A. tysonii**	AH	19.5	20.5	6.1	Reid et al. (2016)
A. xanthina	AH	9.4	45.1	3.1	Reid et al. (2016)

Note: Species with an asterisk indicate potential thiophores. For non-herbarium samples, data are means of at least six individuals per species per location

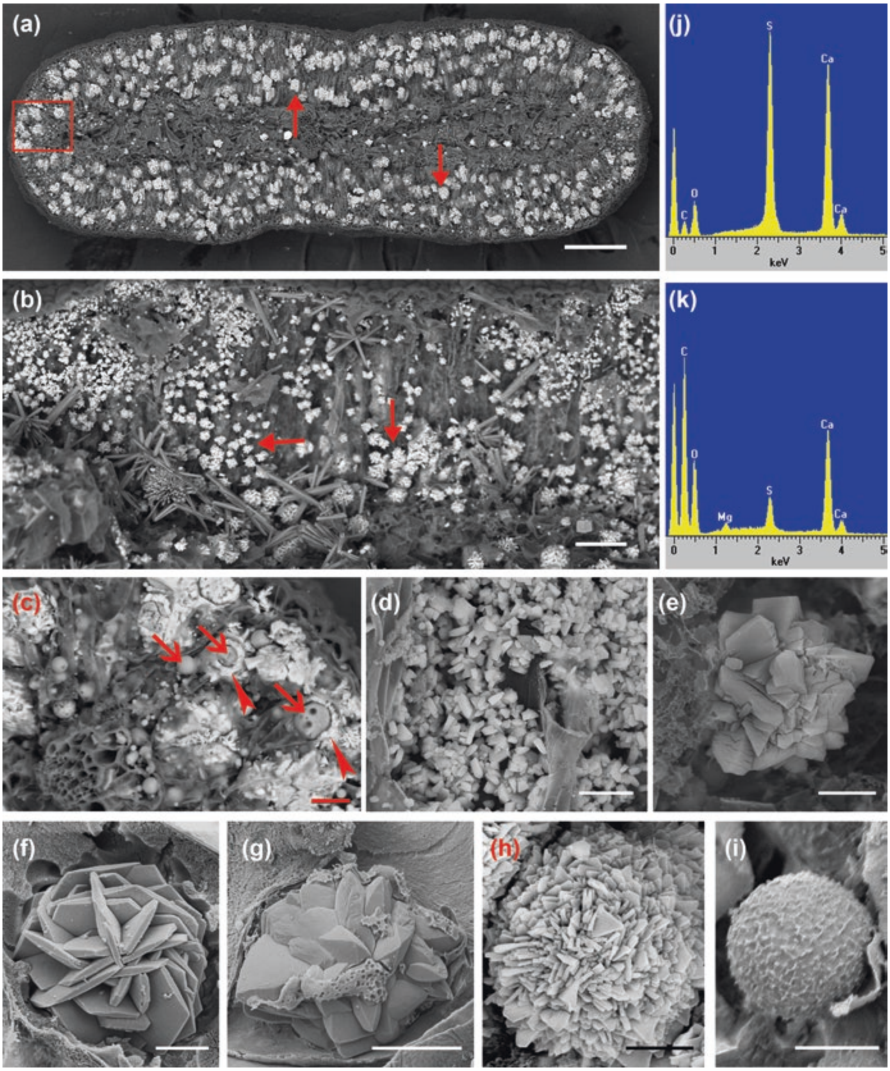


Fig. 2 Abundant sulfur (S)-rich biominerals in phyllodes of *Acacia robeorum* growing in the Telfer region of the Great Sandy Desert. (**a**) A view of a whole cross section of a phyllode with numerous biominerals. (**b**) Part of a cross section of a phyllode showing a large amount of biominerals. (**c**) An enlarged view of the area within the red rectangle in panel (**a**), showing amorphous and/or druse biominerals (filled arrow) and spherical biominerals (unfilled arrow). (**d**) Crystal sand. (**e**–**h**) Various crystal druses. (**i**) A spherical crystal. (**j**) A typical energy-dispersive X-ray microanalysis (EDX) spectrum of crystal sand, amorphous and druse biominerals. (**H**) A typical EDX spectrum of spherical biominerals. Scale bars: (**a**) 200 μm; (**b**, **d**, **g**) 10 μm; (**c**) 100 μm; (**e**) 50 μm; (**f**, **h**) 5 μm; (i) 2 μm. (Modified after He et al. 2012b, 2014)

along the Jurien Bay chronosequence, which are not rich in S, also accumulate high levels of S in their phyllodes (Hayes et al. 2014), suggesting that S accumulation in acacias may be constitutional rather than adaptive.

Non-mycotrophic Plants

The number of non-mycorrhizal species of the Proteaceae type, rather than the Brassicaceae type (Lambers and Teste 2013), is greatest when soil P concentrations are lowest, whereas mycorrhizal species dominate on less P-impoverished soils (Lambers et al. 2006, 2010). Species from the family Proteaceae are almost all non-mycorrhizal and most produce cluster (=proteoid) roots when grown in low-P soils (Shane and Lambers 2005a). Proteaceae species are abundant on the most severely P-impoverished soils in south-western Australia, where plant species diversity is greatest (Lambers et al. 2010). They are also found in the arid zone of Australia (Fig. 3), but there is very limited work on Proteaceae from the arid zone (Grigg et al. 2008a). Information on the mineral nutrition of these species comes largely from studies conducted outside the arid zone.

Some *Grevillea* species growing in an area near the Nifty Copper Operation of the Great Sandy Desert display low leaf P concentrations, e.g. the average leaf P concentration of *Grevillea eriostachya*, *Grevillea stenobotrya* and *Grevillea wickhamii* is 0.33, 0.44 and 0.33 mg g^{-1}, respectively (A.M. Grigg, *pers. comm.*). These species also show low leaf N concentrations, with the average N concentration of each species being 8.2, 9.0 and 9.8 mg g^{-1}, respectively, and the mean N:P ratio of each species is 26, 21 and 29, respectively (A.M. Grigg, *pers. comm.*), suggesting that plant productivity in the habitat of these species is P-limited (Koerselman and Meuleman 1996; Güsewell 2004; Greenwood et al. 2008). However, these species, like Proteaceae from south-western Australia, likely possess some special characteristics to function at very low soil P availability and show rapid rates of photosynthesis at very low leaf P concentrations, i.e. high photosynthetic P-use efficiency

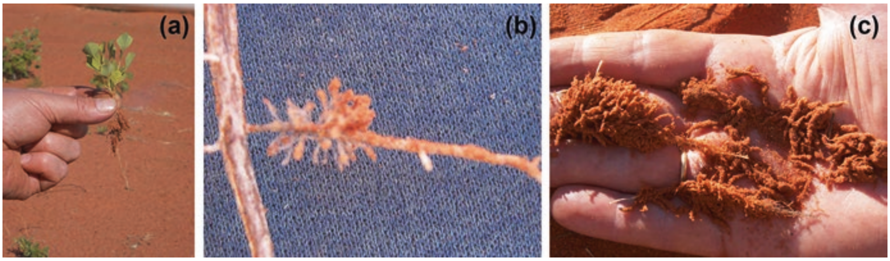


Fig. 3 Proteaceae in the arid zone of Australia. (**a**) A seedling of *Grevillea wickamii*. (**b**) Cluster root of *Grevillea wickamii*. (**c**) Cluster roots of *Grevillea wickamii* in bone-dry soil. (Photos: Hans Lambers)

(Grigg et al. 2008a), just like many south-western Australian Proteaceae (Lambers et al. 2012, 2015a).

In south-western Australia, Proteaceae species occur on the most severely P-impoverished soils where 'plant-available' (e.g. bicarbonate-extractable or resin-exchangeable) soil P concentrations are typically less than 1 μg g^{-1} soil (Lambers et al. 2013; Hayes et al. 2014). In this region, they have diversified more than anywhere else (Pate et al. 2001). Several traits related to P nutrition contribute to the success of Proteaceae on severely P-impoverished soils in south-western Australia. These include (i) releasing carboxylates from ephemeral cluster roots to 'mine' P that is sorbed onto soil particles to improve the P-acquisition efficiency; (ii) using P efficiently for photosynthesis by allocating P to photosynthetic cells and not epidermal cells, replacing phospholipids by lipids that do not contain P and investing little P in ribosomal RNA (rRNA); (iii) resorbing P very efficiently from senescing organs; and (iv) storing a high level of P in seeds (Lambers et al. 2015a; Hayes et al. 2018).

Cluster roots are ephemeral structures that only function for about 3 weeks (Shane et al. 2004a); in south-western Australia, they are predominantly produced near the surface, just under the litter layer or an ash bed after a fire in response to slightly elevated levels of P, but they are suppressed when P supply is higher (Shane and Lambers 2005a). Cluster roots of Proteaceae and Fabaceae release large amounts of carboxylates into the rhizosphere in an 'exudative burst' under P deficiency (Watt and Evans 1999; Shane et al. 2004a; Delgado et al. 2014). The released carboxylates can mobilise both inorganic and organic P that is sorbed onto soil particles, via ligand exchange, thus replacing P from the soil matrix and making P enter into the soil solution to become available for uptake by plant roots (Lambers et al. 2006; Richardson et al. 2011). The developmentally regulated release of significant amounts of carboxylates such as citrate at a fast rate has an advantage in minimising the chance of microbial degradation of the carboxylates before they can mobilise P sorbed onto soil particles (Shane et al. 2004a; Lambers et al. 2015a). Phenolic compounds such as isoflavonoids and antifungal cell wall-degrading enzymes excreted by white lupin (*Lupinus albus*) are likely also released by cluster roots of Proteaceae (Delgado et al. 2015) to inhibit microbial activity and reduce potential citrate consumption (Weisskopf et al. 2006a, b). Protons are often released before, or at the same time as the exudation of carboxylates, in order to maintain charge balance and result in rhizosphere acidification, which inhibits bacterial metabolism (Weisskopf et al. 2006a). Acidification enhances the availability of P in alkaline (calcareous) soil (Hinsinger et al. 2003; Lambers et al. 2006), but the release of protons may result in reduced P availability in acidic soils (Palomo et al. 2006; Lambers et al. 2008). Interestingly, Proteaceae from south-western Australia naturally occurring on acidic soils release other cations, possibly potassium (K^+) or sodium (Na^+), to maintain charge balance (Roelofs et al. 2001); the same has been found for white lupin, which releases both protons and other cations from its cluster roots (Zhu et al. 2005).

Leaf P concentrations of many Proteaceae in south-western Australia are extremely low, being about 0.2 mg g^{-1} dry matter (DM) (Denton et al. 2007a;

Lambers et al. 2012), much lower than the average P concentration (2 mg g^{-1}) in plant shoot dry matter sufficient for adequate crop growth (Kirkby 2012). The photosynthetic rate per unit leaf P of these species is among the highest ever recorded (Wright et al. 2004; Denton et al. 2007a; Lambers et al. 2012; A.M. Grigg *pers. comm.*). Leaf P concentrations of these species are diluted by the scleromorphic structures of the leaves but that is only a small part of the story (Lambers et al. 2015a). A preferential allocation of P to mesophyll cells, rather than to epidermal cells, partly accounts for the high photosynthetic rate per unit leaf P (photosynthetic P-use efficiency, PPUE) of Proteaceae in south-western Australia (Shane et al. 2004b; Hayes et al. 2018). Furthermore, some Proteaceae species from severely P-impoverished soils extensively replace phospholipids with galactolipids and sulfolipids that do not contain P during leaf development to achieve a high PPUE (Lambers et al. 2012). Most importantly, rRNA levels in leaves of Proteaceae species growing in their natural P-impoverished habitat are very low; these species also show a slow development of their photosynthetic apparatus, and their 'delayed greening' is associated with extremely low levels of plastidic rRNA in expanding leaves (Sulpice et al. 2014).

For many Proteaceae in south-western Australia, loss of P is minimised through efficient P resorption from senescing leaves and roots. For example, leaf P resorption efficiency of *Banksia chamaephyton* is up to 82% (Denton et al. 2007a), that of *Banksia attenuata* may exceed 90% (Hayes et al. 2014), and P concentrations in senesced leaves of *Banksia attenuata* can be as low as 19 μg P g^{-1} DM (Hayes et al. 2014). Some Proteaceae species such as harsh hakea (*Hakea prostrata*) can highly efficiently remobilise (80–90%) of P from senescing cluster roots to further enhance their ability to survive on severely P-impoverished soils (Shane et al. 2004a, 2014).

Maximising the allocation of P to seeds is another strategy to use P efficiently. Seed P content can comprise a significant proportion of the total aboveground P content in some *Banksia* species, e.g. 48% for *Banksia hookeriana*, whose seeds contain only 0.5% of all the aboveground plant biomass (Witkowski and Lamont 1996). Unlike the leaves, which contain very low concentrations of P, seeds of many south-western Australian Proteaceae species contain remarkably high P concentrations, of which the mean value is 13.2 mg P g^{-1} DM, with that in seeds of *Hakea pycnoneura* being as high as 36 mg P g^{-1} DM (Kuo 1982; Milberg and Lamont 1997; Denton et al. 2007a; Groom and Lamont 2010). In contrast, the mean value of a wide range of crop species is 3.5 mg P g^{-1} DM (Marschner 1995). Concentrations of P in seeds of a range of *Banksia* species are 20–40 times greater than those in leaves (Kuo 1982; Denton et al. 2007a). A high seed P content supports seedling establishment and early growth in P-impoverished soils, making the initial growth of these species largely independent of P acquisition from the severely P-impoverished soils in which they grow, thus giving them a strong competitive advantage over other species that contain less P in their seeds and/or use the P reserve in seeds less efficiently (Milberg and Lamont 1997). The P content of the sown seeds of nine *Banksia* species could have contributed as much as 12–70% to the total P content of 8-month-old seedlings, assuming that the transfer efficiency of P from seed to seedling was 100% and the potential contribution of seed P content to seedling P content was significantly correlated with seed size (Denton et al. 2007b). About 87–92% of P in 3-month-old seedlings of *Hakea circumalata* and *Hakea psilorrhyncha* was estimated to have been transferred from P reserves in seeds (Milberg and Lamont 1997).

Proteaceae that are endemic to P-impoverished soils show several traits related to their P economy, but many are also extremely sensitive to P toxicity, a common, but not universal phenomenon for south-western Australian Proteaceae. Plant growth will be disturbed and lethal damage may occur, even when P supply in the soil is increased only slightly (Shane et al. 2004b; Shane and Lambers 2006; Hawkins et al. 2008; de Campos et al. 2013). A low capacity of these species to downregulate their P uptake system accounts for their P sensitivity; this is correlated with a high capacity to remobilise P from senescing leaves (Shane et al. 2004c; Shane and Lambers 2006; de Campos et al. 2013).

The P-mobilising carboxylates released by cluster roots of Proteaceae also mobilise micronutrients such as Mn; as a result, Proteaceae tend to contain relatively high levels of Mn in their leaves, even when plants grow in soil with low Mn availability (Lambers et al. 2015b). Accumulation of Mn in mature leaves of *Hakea prostrata* grown at a high P supply declines as the formation of cluster roots is suppressed (Shane and Lambers 2005b). Therefore, leaf Mn concentration can be used as an easily measured aboveground trait to provide an indication of carboxylate release related to P acquisition (Shane and Lambers 2005b; Lambers et al. 2015b). Concentrations of some other micronutrients also increase when carboxylates are released by cluster roots, but not as markedly as that of Mn, whose uptake is relatively poorly controlled (Lambers et al. 2015b). However, concentrations of most other micronutrients, except Ni in *Banksia* leaves are lower than those considered sufficient for adequate growth of crops (Denton et al. 2007a; Kirkby 2012; Hayes et al. 2014). The average Mn concentration of *Grevillea eriostachya* and *Grevillea wickhamii* growing in an area near the Nifty Copper Operation of the Great Sandy Desert is 328 (ranging between 190 and 420) and 258 (ranging between 160 and 460) μg Mn g^{-1} DM, respectively, whereas that of *Grevillea stenobotrya* growing nearby is less, 60 (ranging between 30 and 94) μg Mn g^{-1} DM. The average Fe concentration is 158, 113 and 133 μg Fe g^{-1} DM for *Grevillea eriostachya*, *Grevillea stenobotrya* and *Grevillea wickhamii*, respectively. Among the three *Grevillea* species, *Grevillea eriostachya* has the highest leaf Cu concentration, which is 11.3 μg Cu g^{-1} DM, followed by that of *Grevillea stenobotrya*, which is 6.6 μg Cu g^{-1} DM, while the leaf Cu concentration of *Grevillea wickhamii* is only 3.5 μg Cu g^{-1} DM. The leaf Zn concentration of the three *Grevillea* species is low, with the mean value of each species being 3.5, 7.5 and 4.3 μg Zn g^{-1} DM (A.M. Grigg, *pers. comm.*), much less than the Zn concentration (20 μg Zn g^{-1} DM) in plant shoot dry matter sufficient for adequate crop growth (Kirkby 2012). Zinc is a cofactor for a range of enzymes (Broadley et al. 2012), and since protein levels are low in Proteaceae (Sulpice et al. 2014), low Zn levels are to be expected.

The low ribosome abundance in leaves of Proteaceae adapted to low-P soils will result in slow protein synthesis rates (Lambers et al. 2015a) and, consequently, a low N and S demand (Prodhan et al. 2016, 2017). Despite the low soil N availability

Fig. 4 *Exocarpos aphyllus*, a mistletoe species in Western Australia. This species is commonly known as a root hemiparasite belonging to a genus comprising root hemiparasites. The photos were taken near the Karara mine site in the Midwest of Western Australia. (Photos: Hans Lambers)

in the areas where the Proteaceae occur, these species have high leaf N:P ratios and plant productivity in these habitats is more severely limited by P than by N (Lambers et al. 2010; Hayes et al. 2014). Although protein concentrations on a fresh weight basis in both young and mature leaves of a few Proteaceae species in their natural habitat in south-western Australia are very low when compared with those of *Arabidopsis thaliana*, the concentrations of total free amino acids are only marginally lower (Sulpice et al. 2014). The N and S uptake and metabolism of Proteaceae species in Australia's arid zone may be tightly controlled when P is limiting, similar to what has been found for *Hakea prostrata* (Proteaceae), and such mechanisms of constrained N and S acquisition may help arid-zone Proteaceae species to survive in P-impoverished environments (Prodhan et al. 2016, 2017).

Non-mycotrophic species other than those releasing P-mobilising carboxylates include hemiparasites. Hemiparasitic mistletoes (*Amyema*, *Diplatia* and *Lysiana* species; Loranthaceae) in Australia's arid zone have received significant attention, mainly from the perspective of their water relations, which are pivotal to ensure movement of nutrients dissolved in xylem sap towards the mistletoe (Hellmuth 1971; Ehleringer et al. 1985; Ullmann et al. 1985; Reid and Lange 1988). Root hemiparasites in the arid zone include *Exocarpos aphyllus* and *Exocarpos sparteus* (Santalaceae), *Santalum acuminatum*, *Santalum lanceolatum*, *Santalum murrayanum* and *Santalum spicatum* (Santalaceae) and *Olax sparteus* (Olacaceae) (https://florabase.dpaw.wa.gov.au/). The mechanism used by these genera to acquire nutrients from the roots of their hosts is based on similar principles as those in mistletoes, i.e. a more negative water potential than that of their host (Pate et al. 1990; Tennakoon et al. 1997; Radomiljac et al. 1999; Cernusak et al. 2004). *Exocarpos aphyllus* (Fig. 4) is most remarkable in that it has been observed as a stem hemiparasite (Baird 2014; H. Lambers, *pers. obs.*), whereas this genus is known to comprise only root hemiparasites (Baird 2014).

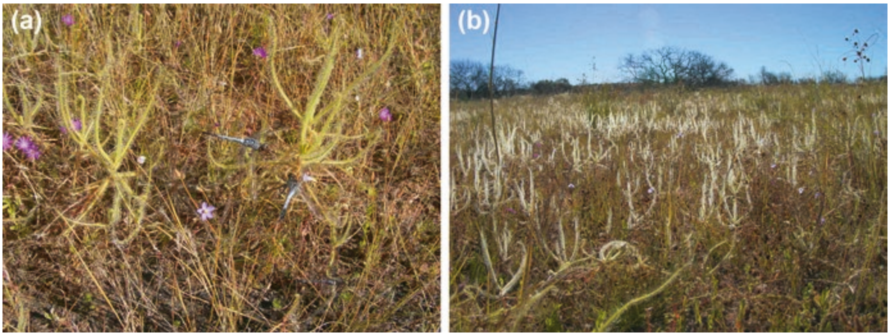


Fig. 5 *Drosera finlaysoniana*, a carnivorous species, growing at Goose Whackers in the Great Sandy Desert in Western Australia. (Photos: Hans Lambers)

Australia's arid zone may seem an unlikely place for carnivorous plants, but following heavy rain, a suitable habitat is available for *Drosera finlaysoniana* (H. Lambers, *pers. obs.*; Fig. 5). The natural distribution of other sundew (*Drosera*) and rainbow plant (*Byblis*) species also includes the arid zone (https://florabase.dpaw.wa.gov.au/).

The Role of the Desert Crust in Nutrient Cycling

Biological soil crusts are complex assemblages of mosses, lichens, liverworts, cyanobacteria, bacteria and fungi that are intimately associated with surface soils (Eldridge and Greene 1994). Biocrusts are a common component of dryland soils in southern Australia (Fig. 6), where their distribution is largely driven by rainfall distribution and soil pH (Eldridge 2003). Crusts mainly occur in the interspaces among perennial vascular plants (Weber et al. 2017), where they play substantial roles in hydrological function (Eldridge et al. 2010), soil nutrition (Weber et al. 2015; Barger et al. 2016) and soil stabilisation (Eldridge 1996; Eldridge and Leys 2003). In Australia, biocrusts are most strongly developed on highly calcareous soils in areas of winter rainfall, and as summer rainfall increases with distance northwards, lichen-dominated crusts make way to surfaces dominated by cyanobacteria and cyanolichens (Eldridge 2003). Increasing summer rainfall reduces the capacity of the lichen component of the crust to photosynthesise at high summer temperatures (Rogers 1971).

Biocrusts play substantial roles in the soil carbon (C) and N cycles (Barger et al. 2016). Their activity is closely linked to soil water availability, particularly during wet periods following rainfall when microbes are in contact with suitable substrates (Morillas and Gallardo 2015). Nitrogen-fixing cyanobacteria and cyanolichens can fix up to 6 kg N ha^{-1} $year^{-1}$ in drylands globally, accounting for about 7% of net primary productivity by terrestrial vegetation (Elbert et al. 2012). In Australian

Fig. 6 Soil biocrust. (Photo: David Eldridge)

drylands, rates of N_2 fixation by biocrusts are estimated to be about 1.3 kg N ha^{-1} $year^{-1}$ (Williams and Eldridge 2011). Although substantial amounts of N are entering the N cycle by N_2-fixing vascular plants and atmospheric N deposition, biocrusts contribute almost 50% of the biologically fixed N in global terrestrial ecosystems.

Cyanobacteria and lichens release the N they have fixed in the form of extracellular compounds and inorganic forms of N comprising NO_3^- and ammonium (NH_4^+), amides, peptides and amino acids (Barger et al. 2016). Many of these N products are subsequently available to vascular plants, with shallow-rooted plants generally benefiting more from extra N than deeper-rooted ones (Zhang and Nie 2011). The release of NH_4^+ from N_2-fixing organisms can result in rapid rates of nitrification (Strauss et al. 2012). Ammonium and NO_3^- taken up by vascular plants may be released from biological soil crusts following rainfall (Veluci et al. 2006; Dojani et al. 2007) or the breakdown of biocrust organisms. For example, Williams and Eldridge (2011) showed that the deposition of sand over biocrusts during droughts leads to cellular autolysis of the cyanobacteria and a flush of N following drought-breaking rainfall.

Cyanobacteria, either free-living or associated with crusts, are photoautotrophic and therefore contribute significant amounts of C via photosynthesis. Structures such as cyanobacterial filaments and trichomes and lichen hyphae secrete C such as polysaccharides, which are often used by heterotrophic bacteria (Baran et al. 2015). Increased C can reduce C:N ratios and increase decomposition rates, increasing the availability of other nutrients to soil organisms (Kleiner and Harper 1972). Globally, photosynthesis is predicted to increase with increasing atmospheric carbon dioxide concentrations (Maestre et al. 2013), so that net C fixation in drylands is expected to increase. Climate projections for south-eastern Australia indicate substantial reductions (20–50%) in winter rainfall (Eldridge and Beecham 2016), which will likely lead to a shrinking of crust cover and a change in composition from lichens to cyanobacteria. This could also affect C fixation, and therefore the capacity of the soils to sustain plant growth (Eldridge and Beecham 2016). The impact of these changes on C, N and other elements is largely unknown.

Biocrusts also increase the bioavailability of many macro- and micronutrients such as K, Mg, Mn and Zn, and this varies across a range of spatial scales (Bowker et al. 2005) and can lead to changes in cation-exchange capacity. Biocrusts also secrete phosphatases, which release P from organic P sources that can be used by vascular plants in P-impoverished environments (Zhang et al. 2016). Other minerals such as Cd, Li, Cu, Mo and Sr negatively affect either the abundance or diversity of algae (Starks and Shubert 1979).

Termites and Their Symbionts as a Source of N

Termite mounds are an obvious component of the ecosystems in the arid area of Australia (Fig. 7) (Coventry et al. 1988; Noble et al. 2009). Termites aid in the decomposition of wood and plant litter (Bodine and Ueckert 1975), thereby playing a significant role in nutrient cycling and sustaining plant growth in low-fertility soils of Australia's arid zone. Termites have been referred to as 'keystone species' due to their substantial effects on arid ecosystems (Coventry et al. 1988; Noble et al. 2009).

Termite mounds contain higher concentrations of nutrients such as N, P, K, Mg and Ca than the surrounding soil and act as soil nutrient reservoirs (Coventry et al.

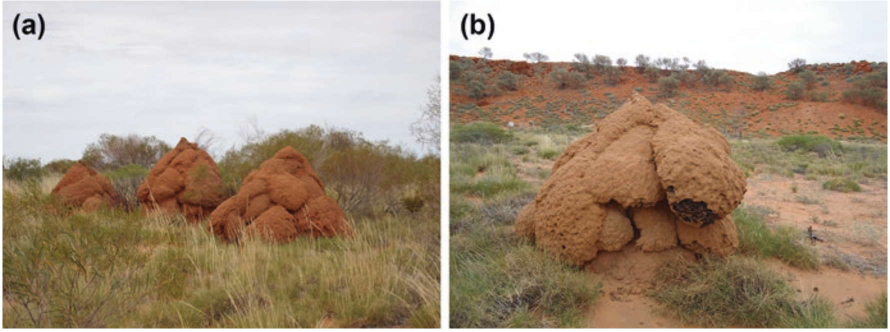


Fig. 7 Termite mounds in the Telfer region of the Great Sandy Desert. (**a**) Three neighbouring termite mounds. (**b**) A degraded and partly eroded termite mound. (Photos: Honghua He)

1988; de Bruyn and Conacher 1990, 1995; Takeshita and Araya 2004). The nutrients temporarily retained in the mounds will eventually be returned to the soil surface by erosion of abandoned mound and contribute to the development of 'Islands of Fertility' (Smith and Yeaton 1998; Takeshita and Araya 2004). Nutrient levels in the soil material turned over by termites are two to seven times that of the A1 soil horizon of some low-fertility soils in a semiarid tropical woodland in north-eastern Queensland (Coventry et al. 1988). Termites bioaccumulate, defend and gradually release mineralised N throughout the colony and contribute a substantial portion of the total N turnover in arid ecosystems (Schaefer and Whitford 1981; Takeshita and Araya 2004). There is a wealth of evidence that termites and their symbionts are a source of N in arid enviroments, including the arid zone of Australia (Barnes et al. 1992; Melchiorre et al. 2006; Whitford and Eldridge 2013).

The $\delta^{15}N$ values of termites and termite-mound material suggest that some termite colonies are capable of fixing atmospheric N (Pate et al. 1998; Melchiorre et al. 2006). Gut microbiota of wood-feeding termites are responsible for the N_2 fixation and compensate for the low availability of N in the diet of these termites (Lilburn et al. 2001; Desai and Brune 2012). The newly fixed N is converted to termite tissues and can be distributed throughout the colony by social feeding, thus contributing to the biogeochemical cycling of N in terrestrial ecosystems (Schaefer and Whitford 1981; Coventry et al. 1988; Tayasu et al. 1994). Elevated concentrations of NO_3^- and ^{15}N occur in groundwater from the arid regions of Australia, due to N_2 fixation by termites. Within a termite mound, NH_4^+ is produced by biological N_2 fixation and then bacterially oxidised to NO_3^-, which is leached out of the mound by rainfall (Barnes et al. 1992; Melchiorre et al. 2006). When the colony dies, a greater flux of NO_3^- to the substrate and groundwater for plant uptake will result from rain-induced erosion and degradation of the termite mounds, and the rate of this flux depends on the degree of erosion and on the longevity of mounds (Park et al. 1994; Melchiorre et al. 2006). For areas of high termite-mound density, the total amount of termite-fixed N is significant over geological time scales (Melchiorre et al. 2006).

Soil-feeding termites consume the humus in soil organic matter (Ngugi et al. 2011). A significant increase in NH_4^+ occurs in the nests of soil-feeding termites, possibly due to the presence of litter, and also the physicochemical and biochemical properties of the digestive system of soil-feeding termites, which can effectively catalyse the transformation of refractory soil organic N to a plant-available form (Ndiaye et al. 2004; Ji and Brune 2006). The mineralised N can leach out of the mounds and accumulate in the surrounding soil during the rainy season (Ndiaye et al. 2004). Ammonium tends to become bound to the nest soil and is less mobile than NO_3^-, which more readily leaches out of the mounds (Park et al. 1994; Ji and Brune 2006).

Termites are sensitive to moisture and temperature levels, and they are particularly active after rain (Curtis and Waller 1998; Davies et al. 2015); thus, the N_2-fixation rates of termites vary seasonally, being fastest at moderate temperatures and slowest under both extremes (Curtis and Waller 1998). Therefore, the contribution of termites and their symbionts to the N influx into the ecosystems may also show seasonal variation. In some cases, the contribution of termites to nutrient availability can be observed through the productivity of plants growing near abandoned termite mounds (Schaefer and Whitford 1981).

Metal-Accumulating Plant Species

Manganese

Manganese is an essential plant micronutrient but also one of the most important metals that may be hyperaccumulated in plants. Most plants can tolerate Mn well above their normal physiological requirements (Fernando et al. 2009). However, accumulation of Mn by some plants does not necessarily require high levels of soil Mn, and plants in the same family may show a great variation in leaf Mn concentration (Hocking 1986). As mentioned previously, *Grevillea eriostachya* and *Grevillea wickhamii* growing in the Great Sandy Desert can accumulate up to 420 and 460 μg Mn g^{-1} DM, respectively (A.M. Grigg, *pers. comm.*). It is likely that the cluster roots formed by these species play a significant role in Mn acquisition and accumulation (Shane and Lambers 2005b). However, these Proteaceae in the arid zone of Australia are not Mn-hyperaccumulators, according to the criterion of Mn concentrations for Mn hyperaccumulation, which is 10,000 μg g^{-1} (van der Ent et al. 2013). To date, almost all identified and potential Mn-hyperaccumulators are tropical rainforest species occurring in eastern Australia (Bidwell et al. 2002; Fernando et al. 2009, 2012).

Nickel

Ultramafic (or serpentine) soils typically have a high pH and are rich in Ni. Plants growing in serpentine soils are often stunted and have morphologies typical of desert perennials. Serpentine species often accumulate Ni to a very high degree, and there are usually clearly defined boundaries between serpentine and adjacent vegetation. The plant species can even serve as indicator plants for underlying serpentine deposits. Within Australia, the most extensive serpentine deposits are adjacent to the eastern goldfields of Western Australia. The *Hybanthion floribundii* Alliance, which is characterised by the Ni-hyperaccumulator *Hybanthus floribundus* and its associated species *Grevillea acuaria*, has been defined to cover the serpentine vegetation of Western Australia (Severne and Brooks 1972; Brooks et al. 1977).

The Ni-hyperaccumulator *Hybanthus floribundus* is a widely distributed dwarf to small shrub, native to Western Australia; it often occurs on ultramafic outcrops and their drainage areas. For the serpentine vegetation of Western Australia, there is a positive correlation between stand density and soil Ni concentration within the *Hybanthus floribundus* shrub communities, particularly on soils where Ni concentration exceeds 880 μg g^{-1} (Severne and Brooks 1972; Brooks et al. 1977). In the eastern goldfields of Western Australia, Severne and Brooks (1972) found that nearly all values for Ni concentration fall within a range of 400–3600 μg g^{-1} in rocks, 240–1200 μg g^{-1} in soils and 40–160 mg g^{-1} in leaf ash of *Hybanthus floribundus*. For plants growing in the soil of which the average Ni concentration is only 670 μg g^{-1}, the highest Ni concentration is over 230 mg g^{-1} in leaf ash, being over 10 mg g^{-1} (up to 14 mg g^{-1}) on a leaf dry weight basis. *Hybanthus floribundus* not only occurs in Western Australia but is also ubiquitous in Victoria, New South Wales and South Australia. However, for a specimen of *Hybanthus floribundus* growing in a substrate of unknown composition in Mildura, Victoria, the Ni concentration is only 300 μg g^{-1}, only slightly higher than normal background values, indicating that not all specimens of this species hyperaccumulate Ni (Severne and Brooks 1972). The specimens investigated in the Eastern Goldfields of Western Australia may well be ecotypes adapted to the particular substrate there (Severne and Brooks 1972). Due to its Ni-hyperaccumulating capacity, *Hybanthus floribundus* is considered a promising candidate for use in rehabilitation of Ni tailings and phytoremediation of Ni-contaminated soils (Kachenko et al. 2008).

For the Ni-hyperaccumulator *Hybanthus floribundus*, there are several mechanisms involved in Ni accumulation and tolerance. According to results of gas chromatography and mass spectrometry (GC-MS) methods, up to 95% of the Ni in leaves of *Hybanthus floribundus* is bound as an anionic citrate complex, and only about 5% is bound as a cationic aquo complex (Kersten et al. 1980). In addition to complexation, a significant proportion of the Ni in leaf tissues may be compartmentalised in the vacuole and bound to cell wall, where the Ni is made physiologically inactive (Bidwell 2001). Studies using histochemical techniques and micro-proton-induced X-ray emission (micro-PIXE) spectroscopy show that Ni is preferentially localised in epidermal cells in leaves and stems of *Hybanthus floribundus* (Severne 1974; Bidwell et al. 2004). Although high tissue Ni concentrations may play a role in drought tolerance and herbivore deterrence, the selective advantage for plant growth and reproduction from Ni hyperaccumulation is still unclear. Nickel hyperaccumulation remains an interesting topic in plant physiology and biochemistry (Severne 1974; Brooks et al. 1998).

Gold

The presence of gold (Au) in plants has been reported in a few cases, and Au concentrations and distributions shown by vegetation generally reflect those in the regolith. At three sites in the goldfields of south-western Australia, Au concentrations are <0.5 μg kg^{-1} in dried plants growing in soils with medium soil Au anomaly, poorly mineralised or in background areas but up to 11 μg kg^{-1} in those growing in soils which are well mineralised. However, there is no particular genus outstanding as an Au accumulator or indicator of mineralisation (Lintern et al. 1997).

Adjuvants such as thiocyanate- or cyanide-induced (hyper)accumulation of Au has been reported, highlighting the potential of using plants to extract Au from low-grade ore and waste products (Anderson et al. 1998, 1999; Piccinin et al. 2007). Some native Australian plants such as blue mallee (*Eucalyptus polybractea*), black wattle (*Acacia decurrens*), red grass (*Bothriochloa macra*), wallaby grass (*Austrodanthonia caespitosa*) and weeping grass (*Microlaena stipoides*) can grow in an ore body with an Au grade of 1.75 g Au ton^{-1}. When these are treated with 0.1 mg g^{-1} or 1 mg g^{-1} cyanide as aqueous sodium cyanide (NaCN), plants grown in the 1 mg g^{-1} NaCN treatment generally have higher concentrations of Au than those grown in the 0.1 mg g^{-1} NaCN treatment. Gold concentrations in stems and older leaves are higher than those in young leaves. For wallaby grass and red grass, the Au concentration is 21.6 and 23.8 g ton^{-1} in the 0.1 mg g^{-1} NaCN treatment, respectively. For blue mallee and black wattle, the Au concentration in stems is 11.1 and 14.8 g ton^{-1} in the 0.1 mg g^{-1} NaCN treatment, respectively (Piccinin et al. 2007). The use of adjuvants to induce Au (hyper)accumulation should be carefully assessed, as higher amendment levels can negatively affect the survival and vitality of plants (Anderson et al. 1998). Furthermore, limited translocation of Au from roots to shoots may be a limiting factor for the phytoextraction of Au (Piccinin et al. 2007).

Concluding Remarks

Plants in Australia's arid zone exhibit a range of strategies to survive in nutrient-impoverished soils. *Acacias* are capable of N_2 fixation and important for N cycling in arid ecosystems; they are more severely limited by P than by N, and can use P efficiently by mobilising poorly available forms of P through carboxylate exudation, and resorbing a significant proportion of P from senescing leaves. Non-mycorrhizal species such as *Grevillea* and *Hakea* (Proteaceae) are also present on P-impoverished soils, and they exhibit a range of strategies to 'mine' P, use P and resorb P efficiently. Other non-mycorrhizal species include hemiparasitic and carnivorous species. Biocrusts play a critical role in maintaining soil fertility and affect the distribution of limited nutrients, in particular N. Some termites and their symbionts can also fix N_2 and affect N cycling. Some plants can accumulate high levels of metals such as Mn and Au, and species such as *Hybanthus floribundus* can hyperaccumulate Ni. More knowledge on mineral nutrition of plants in Australia's arid zone should be gained for better ecosystem management.

References

Almeida JPF, Hartwig UA, Frehner M, Nosberger J, Luscher A (2000) Evidence that P deficiency induces N feedback regulation of symbiotic N_2 fixation in white clover (*Trifolium repens* L.). J Exp Bot 51:1289–1297

Anderson CWN, Brooks RR, Stewart RB, Simcock R (1998) Harvesting a crop of gold in plants. Nature 395:553–554

Anderson CWN, Brooks RR, Chiarucci A, LaCoste CJ, Leblanc M, Robinson BH, Simcock R, Stewart RB (1999) Phytomining for nickel, thallium and gold. J Geochem Explor 67:407–415

Austin AT, Yahdjian L, Stark JM, Belnap J, Porporato A, Norton U, Ravetta DA, Schaeffer SM (2004) Water pulses and biogeochemical cycles in arid and semiarid ecosystems. Oecologia 141:221–235

Baird IRC (2014) A novel observation of putative aerial hemiparasitism in *Exocarpus aphyllus*. Queensland Nat 52:48–52

Baran R, Brodie EL, Mayberry-Lewis J, Hummel E, Da Rocha UN, Chakraborty R, Bowen BP, Karaoz U, Cadillo-Quiroz H, Garcia-Pichel F, Northen TR (2015) Exometabolite niche partitioning among sympatric soil bacteria. Nat Commun 6:8289

Barger N, Weber B, Garcia-Pichel F, Zaady E, Belnap J (2016) Patterns and controls on nitrogen cycling of biological soil crusts. In: Weber B, Büdel B, Belnap J (eds) Biological soil crusts: an organising principle in drylands, Ecological series 226. Springer, Dordrecht, pp 257–285

Barnes CJ, Jacobson G, Smith GD (1992) The origin of high-nitrate ground waters in the Australian arid zone. J Hydrol 137:181–197

Bennett LT, Adams MA (2001) Response of a perennial grassland to nitrogen and phosphorus additions in sub-tropical, semi-arid Australia. J Arid Environ 48:289–308

Bidwell SD (2001) Hyperaccumulation of metals in Australian native plants. PhD thesis, The University of Melbourne, Australia

Bidwell SD, Woodrow IE, Batianoff GN, Sommer-Knudsen J (2002) Hyperaccumulation of manganese in the rainforest tree *Austromyrtus bidwillii* (Myrtaceae) from Queensland, Australia. Funct Plant Biol 29:899–905

Bidwell SD, Crawford SA, Woodrow IE, Sommer-Knudsen J, Marshall AT (2004) Sub-cellular localization of Ni in the hyperaccumulator, *Hybanthus floribundus* (Lindley) F. Muell. Plant Cell Environ 27:705–716

Bodine MC, Ueckert DN (1975) Effect of desert termites on herbage and litter in a shortgrass ecosystem in west Texas. Rangel Ecol Manag/J Range Manag Arch 28:353–358

Bowker MA, Belnap J, Davidson DW, Phillips SL (2005) Evidence for micronutrient limitation of biological soil crusts: importance to arid-lands restoration. Ecol Appl 15:1941–1951

Broadley M, Brown P, Cakmak I, Rengel Z, Zhao F (2012) Functions of nutrients: micronutrients. In: Marschner P (ed) Mineral nutrition of higher plants. Academic Press, London, pp 191–248

Brooks RR, Lee J, Reeves RD, Jaffre T (1977) Detection of nickeliferous rocks by analysis of herbarium specimens of indicator plants. J Geochem Explor 7:49–57

Brooks RR, Chambers MF, Nicks LJ, Robinson BH (1998) Phytomining. Trends Plant Sci 3:359–362

Cernusak LA, Pate JS, Farquhar GD (2004) Oxygen and carbon isotope composition of parasitic plants and their hosts in southwestern Australia. Oecologia 139:199–213

Coventry R, Holt J, Sinclair D (1988) Nutrient cycling by mound building termites in low fertility soils of semi-arid tropical Australia. Soil Res 26:375–390

Curtis AD, Waller DA (1998) Seasonal patterns of nitrogen fixation in termites. Funct Ecol 12:803–807

Davies AB, Eggleton P, van Rensburg BJ, Parr CL (2015) Seasonal activity patterns of African savanna termites vary across a rainfall gradient. Insect Soc 62:157–165

de Bruyn LAL, Conacher AJ (1990) The role of termites and ants in soil modification – a review. Soil Res 28:55–93

de Bruyn LAL, Conacher AJ (1995) Soil modification by termites in the central wheatbelt of Australia. Aust J Soil Res 33:179–193

de Campos MCR, Pearse SJ, Oliveira RS, Lambers H (2013) Downregulation of net phosphorus-uptake capacity is inversely related to leaf phosphorus-resorption proficiency in four species from a phosphorus-impoverished environment. Ann Bot 111:445–454

Delgado M, Suriyagoda L, Zúñiga-Feest A, Borie F, Lambers H (2014) Divergent functioning of Proteaceae species: the South American *Embothrium coccineum* displays a combination of adaptive traits to survive in high-phosphorus soils. Funct Ecol 28:1356–1366

Delgado M, Zuniga-Feest A, Almonacid L, Lambers H, Borie F (2015) Cluster roots of *Embothrium coccineum* (Proteaceae) affect enzyme activities and phosphorus lability in rhizosphere soil. Plant Soil 395:189–200

Denton MD, Veneklaas EJ, Freimoser FM, Lambers H (2007a) Banksia species (Proteaceae) from severely phosphorus-impoverished soils exhibit extreme efficiency in the use and re-mobilization of phosphorus. Plant Cell Environ 30:1557–1565

Denton MD, Veneklaas EJ, Lambers H (2007b) Does phenotypic plasticity in carboxylate exudation differ among rare and widespread *Banksia* species (Proteaceae)? New Phytol 173:592–599

Desai MS, Brune A (2012) Bacteroidales ectosymbionts of gut flagellates shape the nitrogen-fixing community in dry-wood termites. ISME J 6:1302–1313

Dojani S, Lakatos M, Rascher U, Wanek W, Luettge U, Buedel B (2007) Nitrogen input by cyanobacterial biofilms of an inselberg into a tropical rainforest in French Guiana. Flora 202:521–529

Ehleringer JR, Schulze ED, Ziegler H, Lange OL, Farquhar GD, Cowar IR (1985) Xylem-tapping mistletoes: water or nutrient parasites? Science (New York, NY) 227:1479–1481

Elbert W, Weber B, Burrows S, Steinkamp J, Budel B, Andreae MO, Poschl U (2012) Contribution of cryptogamic covers to the global cycles of carbon and nitrogen. Nat Geosci 5:459–462

Eldridge DJ (1996) Distribution and floristics of terricolous lichens in soil crusts in arid and semi-arid New South Wales, Australia. Aust J Bot 44:581–599

Eldridge DJ (2003) Biological soil crusts of Australia. In: Belnap J, Lange OL (eds) Biological soil crusts: structure, function, and management. Springer, Berlin, pp 119–132

Eldridge DJ, Beecham G (2016) The impact of climate variability on land use and livelihoods in Australia's rangelands. In: Gaur MK, Squires VR (eds) Climate variability impacts on land use and livelihoods in drylands. Springer, Dordrecht, pp 293–318

Eldridge DJ, Greene RSB (1994) Microbiotic soil crusts: a review of their roles in soil and ecological process in the rangelands of Australia. Aust J Soil Res 32:389–415

Eldridge DJ, Leys JF (2003) Exploring some relationships between biological soil crusts, soil aggregation and wind erosion. J Arid Environ 53:457–466

Eldridge DJ, Bowker MA, Maestre FT, Alonso P, Mau RL, Papadopoulos J, Escudero A (2010) Interactive effects of three ecosystem engineers on infiltration in a semi-arid mediterranean grassland. Ecosystems 13:499–510

Ernst WHO (1998) Sulfur metabolism in higher plants: potential for phytoremediation. Biodegradation 9:311–318

Erskine PD, Stewart GR, Schmidt S, Turnbull MH, Unkovich M, Pate JS (1996) Water availability – a physiological constraint on nitrate utilization in plants of Australian semi-arid mulga woodlands. Plant Cell Environ 19:1149–1159

Fernando DR, Guymer G, Reeves RD, Woodrow IE, Baker AJ, Batianoff GN (2009) Foliar Mn accumulation in eastern Australian herbarium specimens: prospecting for 'new' Mn hyperaccumulators and potential applications in taxonomy. Ann Bot 103:931–939

Fernando DR, Woodrow IE, Baker AJM, Marshall AT (2012) Plant homeostasis of foliar manganese sinks: specific variation in hyperaccumulators. Planta 236:1459–1470

Ford DJ, Cookson WR, Adams MA, Grierson PF (2007) Role of soil drying in nitrogen mineralization and microbial community function in semi-arid grasslands of north-west Australia. Soil Biol Biochem 39:1557–1569

Getzin S, Yizhaq H, Bell B, Erickson TE, Postle AC, Katra I, Tzuk O, Zelnik YR, Wiegand K, Wiegand T, Meron E (2016) Discovery of fairy circles in Australia supports self-organization theory. Proc Natl Acad Sci U S A 113:3551–3556

Goldie X, Gillman L, Crisp M, Wright S (2010) Evolutionary speed limited by water in arid Australia. Proc R Soc B Biol Sci 277:2645–2653

Gonzalez-Orozco CE, Laffan SW, Miller JT (2011) Spatial distribution of species richness and endemism of the genus *Acacia* in Australia. Aust J Bot 59:600–608

Greenwood DJ, Karpinets TV, Zhang K, Bosh-Serra A, Boldrini A, Karawulova L (2008) A unifying concept for the dependence of whole-crop N:P ratio on biomass: theory and experiment. Ann Bot 102:967–977

Grigg A (2009) An ecophysiological approach to determine problems associated with mine-site rehabilitation: a case study in the Great Sandy Desert, north-western Australia. PhD Thesis, The University of Western Australia

Grigg AM, Veneklaas EJ, Lambers H (2008a) Water relations and mineral nutrition of closely related woody plant species on desert dunes and interdunes. Aust J Bot 56:27–43

Grigg AM, Veneklaas EJ, Lambers H (2008b) Water relations and mineral nutrition of *Triodia* grasses on desert dunes and interdunes. Aust J Bot 56:408–421

Groom PK, Lamont BB (2010) Phosphorus accumulation in Proteaceae seeds: a synthesis. Plant Soil 334:61–72

Güsewell S (2004) N:P ratios in terrestrial plants: variation and functional significance. New Phytol 164:243–266

Hawkins H-J, Hettasch H, Mesjasz-Przybylowicz J, Przybylowicz W, Cramer MD (2008) Phosphorus toxicity in the Proteaceae: a problem in post-agricultural lands. Sci Hortic 117:357–365

Hayes P, Turner BL, Lambers H, Laliberte E (2014) Foliar nutrient concentrations and resorption efficiency in plants of contrasting nutrient-acquisition strategies along a 2-million-year dune chronosequence. J Ecol 102:396–410

Hayes PE, Clode PL, Oliveira RS, Lambers H (2018) Proteaceae from phosphorus-impoverished habitats preferentially allocate phosphorus to photosynthetic cells: an adaptation improving phosphorus-use efficiency. Plant Cell Environ 41:605–619

He H, Bleby TM, Veneklaas EJ, Lambers H (2011) Dinitrogen-fixing *Acacia* species from phosphorus-impoverished soils resorb leaf phosphorus efficiently. Plant Cell Environ 34:2060–2070

He H, Bleby TM, Veneklaas EJ, Lambers H (2012a) Arid-zone *Acacia* species can access poorly soluble iron phosphate but show limited growth response. Plant Soil 358:119–130

He H, Bleby TM, Veneklaas EJ, Lambers H, Kuo J (2012b) Morphologies and elemental compositions of calcium crystals in phyllodes and branchlets of *Acacia robeorum* (Leguminosae: Mimosoideae). Ann Bot 109:887–896

He H, Veneklaas EJ, Kuo J, Lambers H (2014) Physiological and ecological significance of biomineralization in plants. Trends Plant Sci 19:166–174

Hellmuth EO (1971) Eco-physiological studies on plants in arid and semi-arid regions in Western Australia: IV. Comparison of the field physiology of the host, *Acacia gasbyi* and its hemiparasite, *Amyema nestor* under optimal and stress conditions. J Ecol 59:351–363

Hingston F, Malajczuk N, Grove T (1982) Acetylene reduction (N_2-fixation) by jarrah forest legumes following fire and phosphate application. J Appl Ecol 19:631–645

Hinsinger P, Plassard C, Tang CX, Jaillard B (2003) Origins of root-mediated pH changes in the rhizosphere and their responses to environmental constraints: a review. Plant Soil 248:43–59

Hocking P (1986) Mineral nutrient composition of leaves and fruits of selected species of *Grevillea* from southwestern Australia, with special reference to *Grevillea leucopteris* Meissn. Aust J Bot 34:155–164

Islam M, Turner DW, Adams MA (2000) Regeneration of the legumes *Acacia ancistrocarpa* and *Senna notabilis* in the Pilbara region of Western Australia: mineral nutrition and carbon fractions. Aust J Bot 48:435–444

Ji R, Brune A (2006) Nitrogen mineralization, ammonia accumulation, and emission of gaseous NH_3 by soil-feeding termites. Biogeochemistry 78:267–283

Kachenko AG, Singh B, Bhatia NP, Siegele R (2008) Quantitative elemental localisation in leaves and stems of nickel hyperaccumulating shrub *Hybanthus floribundus* subsp floribundus using micro-PIXE spectroscopy. Nucl Instrum Methods Phys Res Sect B Beam Interact Mater Atoms 266:667–676

Kersten WJ, Brooks RR, Reeves RD, Jaffré A (1980) Nature of nickel complexes in *Psychotria douarrei* and other nickel-accumulating plants. Phytochemistry 19:1963–1965

Kirkby E (2012) Introduction, definition and classification of nutrients. In: Marschner P (ed) Mineral nutrition of higher plants. Academic Press, London, pp 3–5

Kleiner EF, Harper KT (1972) Environment and communiy organization in grasslands of Canyonlands National Park. Ecology 53:299–309

Koerselman W, Meuleman AFM (1996) The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. J Appl Ecol 33:1441–1450

Kouas S, Louche J, Debez A, Plassard C, Drevon JJ, Abdelly C (2009) Effect of phosphorus deficiency on acid phosphatase and phytase activities in common bean (*Phaseolus vulgaris* L.) under symbiotic nitrogen fixation. Symbiosis 47:141–149

Kuo J (1982) Nutrient reserves in seeds of selected Proteaceous species from south-western Australia. Aust J Bot 30:231–249

Lambers H, Teste FP (2013) Interactions between arbuscular mycorrhizal and non-mycorrhizal plants: do non-mycorrhizal species at both extremes of nutrient availability play the same game? Plant Cell Environ 36:1911–1915

Lambers H, Shane MW, Cramer MD, Pearse SJ, Veneklaas EJ (2006) Root structure and functioning for efficient acquisition of phosphorus: matching morphological and physiological traits. Ann Bot 98:693–713

Lambers H, Thijs LP, Chapin FS (2008) Plant physiological ecology. Springer, New York

Lambers H, Brundrett MC, Raven JA, Hopper SD (2010) Plant mineral nutrition in ancient landscapes: high plant species diversity on infertile soils is linked to functional diversity for nutritional strategies. Plant Soil 334:11–31

Lambers H, Cawthray GR, Giavalisco P, Kuo J, Laliberte E, Pearse SJ, Scheible W-R, Stitt M, Teste F, Turner BL (2012) Proteaceae from severely phosphorus-impoverished soils extensively replace phospholipids with galactolipids and sulfolipids during leaf development to achieve a high photosynthetic phosphorus-use-efficiency. New Phytol 196:1098–1108

Lambers H, Ahmedi I, Berkowitz O, Dunne C, Finnegan PM, Hardy GESJ, Jost R, Laliberte E, Pearse SJ, Teste FP (2013) Phosphorus nutrition of phosphorus-sensitive Australian native plants: threats to plant communities in a global biodiversity hotspot. Conserv Physiol 1:cot010

Lambers H, Clode PL, Hawkins H-J, Laliberte E, Oliveira RS, Reddell P, Shane MW, Stitt M, Weston P (2015a) Metabolic adaptations of the non-mycotrophic Proteaceae to soil with a low phosphorus availability. In: Plaxton WC, Lambers H (eds) Phosphorus metabolism in plants. Wiley, Chichester, pp 289–335

Lambers H, Hayes PE, Laliberte E, Oliveira RS, Turner BL (2015b) Leaf manganese accumulation and phosphorus-acquisition efficiency. Trends Plant Sci 20:83–90

Lilburn TC, Kim KS, Ostrom NE, Byzek KR, Leadbetter JR, Breznak JA (2001) Nitrogen fixation by symbiotic and free-living spirochetes. Science 292:2495–2498

Lintern MJ, Butt CRM, Scott KM (1997) Gold in vegetation and soil – three case studies from the goldfields of southern Western Australia. J Geochem Explor 58:1–14

Maestre FT, Escolar C, Ladron De Guevara M, Quero JL, Lazaro R, Delgado-Baquerizo M, Ochoa V, Berdugo M, Gozalo B, Gallardo A (2013) Changes in biocrust cover drive carbon cycle responses to climate change in drylands. Glob Chang Biol 19:3835–3847

Marschner H (1995) Mineral nutrition of higher plants. Academic Press, London

Marsudi NDS, Glenn AR, Dilworth MJ (1999) Identification and characterization of fast- and slow-growing root nodule bacteria from South-Western Australian soils able to nodulate Acacia saligna. Soil Biol Biochem 31:1229–1238

Melchiorre EB, Williams PA, Rose TP, Talyn BC (2006) Biogenic nitrogen from termite mounds and the origin of gerhardtite at the great Australia mine, Cloncurry, Queensland, Australia. Can Mineral 44:1447–1455

Milberg P, Lamont BB (1997) Seed/cotyledon size and nutrient content play a major role in early performance of species on nutrient-poor soils. New Phytol 137:665–672

Morillas L, Gallardo A (2015) Biological soil crusts and wetting events: effects on soil N and C cycles. Appl Soil Ecol 94:1–6

Morton SR, Smith DMS, Dickman CR, Dunkerley DL, Friedel MH, McAllister RRJ, Reid JRW, Roshier DA, Smith MA, Walsh FJ, Wardle GM, Watson IW, Westoby M (2011) A fresh framework for the ecology of arid Australia. J Arid Environ 75:313–329

Ndiaye D, Lepage M, Sall CE, Brauman A (2004) Nitrogen transformations associated with termite biogenic structures in a dry savanna ecosystem. Plant Soil 265:189–196

Ngugi DK, Ji R, Brune A (2011) Nitrogen mineralization, denitrification, and nitrate ammonification by soil-feeding termites: a ^{15}N-based approach. Biogeochemistry 103:355–369

Noble JC, Müller WJ, Whitford WG, Pfitzner GH (2009) The significance of termites as decomposers in contrasting grassland communities of semi-arid eastern Australia. J Arid Environ 73:113–119

Orians GH, Milewski AV (2007) Ecology of Australia: the effects of nutrient-poor soils and intense fires. Biol Rev 82:393–423

Palomo L, Claassenb N, Jones DL (2006) Differential mobilization of P in the maize rhizosphere by citric acid and potassium citrate. Soil Biol Biochem 38:683–692

Park HC, Majer JD, Hobbs RJ (1994) Contribution of the Western Australian wheatbelt termite, *Drepanotermes tamminensis* (Hill), to the soil nutrient budget. Ecol Res 9:351–356

Pate JS, Davidson NJ, Kuo J, Milburn JA (1990) Water relations of the root hemiparasite *Olax phyllanthi* (Labill) R.Br. (Olacaceae) and its multiple hosts. Oecologia 84:186–193

Pate JS, Unkovich MJ, Erskine PD, Stewart GR (1998) Australian mulga ecosystems – ^{13}C and ^{15}N natural abundances of biota components and their ecophysiological significance. Plant Cell Environ 21:1231–1242

Pate JS, Verboom WH, Galloway PD (2001) Co-occurrence of Proteaceae, laterite and related oligotrophic soils: coincidental associations or causative inter-relationships? Aust J Bot 49:529–560

Piccinin RCR, Ebbs SD, Reichman SM, Kolev SD (2007) A screen of some native Australian flora and exotic agricultural species for their potential application in cyanide-induced phytoextraction of gold. Miner Eng 20:1327–1330

Pillans B (2018) Seeing red: some aspects of the geological and climatic history of the Australian arid zone. In: Lambers H (ed) On the ecology of Australia's arid zone. Springer, Dordrecht

Prodhan MA, Jost R, Watanabe M, Hoefgen R, Lambers H, Finnegan PM (2016) Tight control of nitrate acquisition in a plant species that evolved in an extremely phosphorus-impoverished environment. Plant Cell Environ 39:2754–2761

Prodhan MA, Jost R, Watanabe M, Hoefgen R, Lambers H, Finnegan PM (2017) Tight control of sulfur assimilation: an adaptive mechanism for a plant from a severely phosphorus-impoverished habitat. New Phytol 215:1068–1079

Radomiljac AM, McComb JA, Pate JS (1999) Gas exchange and water relations of the root hemi-parasite *Santalum album* L. in association with legume and non-legume hosts. Ann Bot 83:215–224

Reid N, Lange RT (1988) Host specificity, dispersion and persistence through drought of two arid zone mistletoes. Aust J Bot 36:299–313

Reid N, Robson TC, Radcliffe B, Verrall M (2016) Excessive sulphur accumulation and ionic storage behaviour identified in species of *Acacia* (Leguminosae: Mimosoideae). Ann Bot 117:653–666

Richardson AE, Lynch JP, Ryan PR, Delhaize E, Smith FA, Smith SE, Harvey PR, Ryan MH, Veneklaas EJ, Lambers H, Oberson A, Culvenor RA, Simpson RJ (2011) Plant and microbial strategies to improve the phosphorus efficiency of agriculture. Plant Soil 349:121–156

Robson T, Stevens J, Dixon K, Reid N (2017a) Foliar gypsum formation and litter production in the desert shrub, *Acacia bivenosa*, influences sulfur and calcium biogeochemical cycling in arid habitats. Plant Soil 417:1–16

Robson T, Stevens J, Dixon K, Reid N (2017b) Sulfur accumulation in gypsum-forming thiophores has its roots firmly in calcium. Environ Exp Bot 137:208–219

Roelofs RFR, Rengel Z, Cawthray GR, Dixon KW, Lambers H (2001) Exudation of carboxylates in Australian Proteaceae: chemical composition. Plant Cell Environ 24:891–903

Rogers RW (1971) Distribution of the lichen *Chondropsis semiviridis* in relation to its heat and drought resistance. New Phytol 70:1069–1077

Schaefer DA, Whitford WG (1981) Nutrient cycling by the subterranean termite *Gnathamitermes tubiformans* in a Chihuahuan desert ecosystem. Oecologia 48:277–283

Schortemeyer M, Atkin OK, McFarlane N, Evans JR (2002) N_2 fixation by *Acacia* species increases under elevated atmospheric CO_2. Plant Cell Environ 25:567–579

Severne BC (1974) Nickel accumulation by *Hybanthus floribundus*. Nature 248:807–808

Severne BC, Brooks RR (1972) A nickel-accumulating plant from Western Australia. Planta 103:91–94

Shane MW, Lambers H (2005a) Cluster roots: a curiosity in context. Plant Soil 274:101–125

Shane MW, Lambers H (2005b) Manganese accumulation in leaves of *Hakea prostrata* (Proteaceae) and the significance of cluster roots for micronutrient uptake as dependent on phosphorus supply. Physiol Plant 124:441–450

Shane MW, Lambers H (2006) Systemic suppression of cluster-root formation and net P-uptake rates in *Grevillea crithmifolia* at elevated P supply: a proteacean with resistance for developing symptoms of 'P toxicity'. J Exp Bot 57:413–423

Shane MW, Cramer MD, Funayama-Noguchi S, Cawthray GR, Millar AH, Day DA, Lambers H (2004a) Development physiology of cluster-root carboxylate synthesis and exudation in harsh hakea. Expression of phosphoenolpyruvate carboxylase and the alternative oxidase. Plant Physiol 135:549–560

Shane MW, McCully ME, Lambers H (2004b) Tissue and cellular phosphorus storage during development of phosphorus toxicity in *Hakea prostrata* (Proteaceae). J Exp Bot 55:1033–1044

Shane MW, Szota C, Lambers H (2004c) A root trait accounting for the extreme phosphorus sensitivity of *Hakea prostrata* (Proteaceae). Plant Cell Environ 27:991–1004

Shane MW, Stigter K, Fedosejevs ET, Plaxton WC (2014) Senescence-inducible cell wall and intracellular purple acid phosphatases: implications for phosphorus remobilization in *Hakea prostrata* (Proteaceae) and Arabidopsis thaliana (Brassicaceae). J Exp Bot 65:6097–6106

Skopp J, Jawson MD, Doran JW (1990) Steady-state aerobic microbial activity as a function of soil water content. Soil Sci Soc Am J 54:1619–1625

Smith FR, Yeaton RI (1998) Disturbance by the mound-building termite, Trinervitermes trinervoides, and vegetation patch dynamics in a semi-arid, southern African grassland. Plant Ecol 137:41–53

Starks TL, Shubert LE (1979) Algal colonization on a reclaimed surface mined area in western North Dakota. In: Wali MK (ed) Ecology and coal resource development. Pergamon Press, New York, pp 652–660

Strauss SL, Day TA, Garcia-Pichel F (2012) Nitrogen cycling in desert biological soil crusts across biogeographic regions in the Southwestern United States. Biogeochemistry 108:171–182

Sulpice R, Ishihara H, Schlereth A, Cawthray GR, Encke B, Giavalisco P, Ivakov A, Arrivault S, Jost R, Krohn N, Kuo J, Laliberte E, Pearse SJ, Raven JA, Scheible W-R, Teste F, Veneklaas EJ, Stitt M, Lambers H (2014) Low levels of ribosomal RNA partly account for the very high photosynthetic phosphorus-use efficiency of Proteaceae species. Plant Cell Environ 37:1276–1298

Takeshita M, Araya T (2004) Soil nutrient loss caused by intensive land use and the retention of nutrients inside termite mounds in Niger, Africa. Jpn J Ecol (Otsu) 54:117–124

Tayasu I, Sugimoto A, Wada E, Abe T (1994) Xylophagous termites depending on atmospheric nitrogen. Naturwissenschaften 81:229–231

Tennakoon KU, Pate JS, Arthur D (1997) Ecophysiological aspects of the woody root hemiparasite *Santalum acuminatum* (R Br) A DC and its common hosts in south western Australia. Ann Bot 80:245–256

Tongway DJ, Ludwig JA (1994) Small-scale resource heterogeneity in semi-arid landscapes. Pac Conserv Biol 1:201–208

Tongway DJ, Ludwig JA, Whitford WG (1989) Mulga log mounds: fertile patches in the semi-arid woodlands of eastern Australia. Aust J Ecol 14:263–268

Ullmann I, Lange OL, Ziegler H, Ehleringer J, Schulze ED, Cowan IR (1985) Diurnal courses of leaf conductance and transpiration of mistletoes and their hosts in Central Australia. Oecologia 67:577–587 van der Ent A, Baker AJM, Reeves RD, Pollard AJ, Schat H (2013) Hyperaccumulators of metal and metalloid trace elements: facts and fiction. Plant Soil 362:319–334

van Etten EJB, Burrows ND (2018) Fire regimes and ecology of arid Australia. In: Lambers H (ed) On the ecology of Australia's arid zone. Springer, Dordrecht

Veluci RM, Neher DA, Weicht TR (2006) Nitrogen fixation and leaching of biological soil crust communities in mesic temperate soils. Microb Ecol 51:189–196

Watt M, Evans JR (1999) Proteoid roots. Physiology and development. Plant Physiol 121:317–323

Weber B, Wu D, Tamm A, Ruckteschler N, Rodriguez-Caballero E, Steinkamp J, Meusel H, Elbert W, Behrendt T, Soergel M, Cheng Y, Crutzen PJ, Su H, Poeschi U (2015) Biological soil crusts accelerate the nitrogen cycle through large NO and HONO emissions in drylands. Proc Natl Acad Sci U S A 112:15384–15389

Weber B, Büdel B, Belnap J (2017) Biological soil crusts: an organising principle in drylands, Ecological series 226. Springer, Dordrecht

Weisskopf L, Abou-Mansour E, Fromin N, Tomasi N, Santelia D, Edelkott I, Neumann G, Aragno M, Tabacchi R, Martinoia E (2006a) White lupin has developed a complex strategy to limit microbial degradation of secreted citrate required for phosphate acquisition. Plant Cell Environ 29:919–927

Weisskopf L, Tomasi N, Santelia D, Martinoia E, Langlade NB, Tabacchi R, Abou-Mansour E (2006b) Isoflavonoid exudation from white lupin roots is influenced by phosphate supply, root type and cluster-root stage. New Phytol 171:657–668

Whitford W, Eldridge DJ (2013) Effects of ants and termites on soil and geomorphological processes. In: Schroder JF (ed) A treatise on geomophology, Methods in geomorphology, vol 14. Academic Press, San Diego

Williams WJ, Eldridge DJ (2011) Deposition of sand over a cyanobacterial soil crust increases nitrogen bioavailability in a semi-arid woodland. Appl Soil Ecol 49:26–31

Winkworth R (1967) The composition of several arid spinifex grasslands of central Australia in relation to rainfall, soil water relations, and nutrients. Aust J Bot 15:107–130

Witkowski ETF, Lamont BB (1996) Disproportionate allocation of mineral nutrients and carbon between vegetative and reproductive structures in Banksia hookeriana. Oecologia 105:38–42

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets U, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R (2004) The worldwide leaf economics spectrum. Nature 428:821–827

Zhang YM, Nie HL (2011) Effects of biological soil crusts on seedling growth and element uptake in five desert plants in Junggar Basin, western China. Chin J Plant Ecol 35:380–388

Zhang Y, Aradottir AL, Serpe M, Boeken B (2016) Interactions of biological soil crusts with vascular plants. In: Weber B, Büdel B, Belnap J (eds) Biological soil crusts: an organizing principle in drylands. Springer, Dordrect, pp 385–406

Zhu YY, Yan F, Zorb C, Schubert S (2005) A link between citrate and proton release by proteoid roots of white lupin (*Lupinus albus* L.) grown under phosphorus-deficient conditions? Plant Cell Physiol 46:892–901

Ecophysiology of Australian Arid-Zone Marsupials

S. Don Bradshaw

> *Short-sighted indeed are the Anglo-Australians, or they would long ere this have made laws for the preservation of their highly singular, and in many cases noble, indigenous animals: and doubly short-sighted are they for wishing to introduce into Australia the production of other climes…. Let me then urge them to bestir themselves, ere it be too late, to establish laws for the preservation of the large kangaroos, the Emu and other conspicuous indigenous animals: without such protection the remnant that is left will soon disappear, to be followed by unavailing regret for the apathy with which they have been previously regarded.*
> (Gould 1863)

Introduction

The suite of marsupials now found inhabiting the arid zone is vastly reduced compared with that which confronted the first European settlers in the late eighteenth and early nineteenth centuries (Woinarski et al. 2015; Burbidge 2009). Early explorers of the arid zone described how they needed to erect barriers around their tents to prevent marauding 'rat kangaroos' from raiding their stores of biscuits and other provisions. The situation is vastly different today. In the Little Sandy Desert in Western Australia, for example, of the 43 mammal species present at the time of European settlement, 19 are still present, but a further 19 marsupial species and 6 rodents once collected are now regionally extinct (Start et al. 2013; Burbidge et al. 2007).

The loss of species has not been uniform but focuses on marsupials in what has become known as the 'critical weight range' (CWR) of 35 g–5.5 kg (Burbidge and McKenzie 1989). Why species in this particular weight range are more vulnerable than others remains a subject of continued interest and debate, with some arguing the correlation reflects simply the fact that the majority of recent Australian mam-

---

S. D. Bradshaw (✉)
School of Biological Sciences, The University of Western Australia,
Crawley (Perth), Australia
e-mail: Don.Bradshaw@uwa.edu.au

H. Lambers (ed.), *On the Ecology of Australia's Arid Zone*,
https://doi.org/10.1007/978-3-319-93943-8_5

mals fall within this size range (Cardillo and Bromham 2001), with another phylogenetic analysis failing to find any effect of body mass on the pattern of decline among marsupials (Fisher et al. 2003).

A recent careful analysis has shown that the form of the CWR relationship differs for ground-dwelling versus tree-dwelling species and for species from low- versus high-rainfall areas (Johnson and Isaac 2009). Australian mainland marsupials in the CWR were found to be most extinction prone, and the effect was most pronounced in ground-dwelling species from areas with low annual rainfall (i.e. the arid zone). This conclusion has also been reinforced by a broad analysis of extinction factors showing that faunal losses have been greatest in arid regions and lowest in high-rainfall areas (McKenzie et al. 2007) and by a recent analysis arguing that the CWR is also relevant for species in tropical areas of Australia (Murphy and Davies 2014).

As was the case when considering arid-zone reptiles in Chap. 6 arid-zone marsupials must contend with the same environmental contingencies characteristic of arid environments, viz.:

(a) High day temperatures that must be tolerated, regulated or avoided
(b) A shortage of available free water that renders difficult
(c) The regulation of water and electrolyte balance
(d) Seasonal deficiencies of nitrogen (protein) and energy (carbohydrate and fat) essential for growth and reproduction

The accepted explanation for the vulnerability of CWR species in the arid zone is that they are prime targets for the two major marsupial predators, feral cats and foxes (Burbidge and McKenzie 1989). Some or all of the factors listed above, however, may also be involved, as failure to deal adequately with one of these may predispose an individual to enhanced levels of predation. It is thus important to be able to discern whether a given species is ever exposed to stressful environmental conditions (e.g. heat and drought) that reduce its physiological condition and make it an easy target for predators.

The Nature of Stress

Documenting the incidence and measuring the intensity of stress responses in free-ranging marsupials should be a conservation priority but is as yet a field in its infancy (Bradshaw 2007, 2010, 2017). One of the main difficulties is clarifying what is meant by stress after it was first defined, somewhat poetically, by Hans Selye as *a state of non-specific tension in living matter* (Selye 1946, 1952). An essential step is to distinguish ‘stressors’, emanating from the environment, from ‘stress’, which is the impact of these on the organism, thus avoiding meaningless contradictions such as ‘the stress of reproduction’.

The medical concept of ‘allostasis’ or ‘maintaining stability through change’ (Sterling and Eyer 1988) was adopted by McEwen (1998), who proposed that animals experience an ‘allostatic load’ divided into three levels: A = baseline cortico-

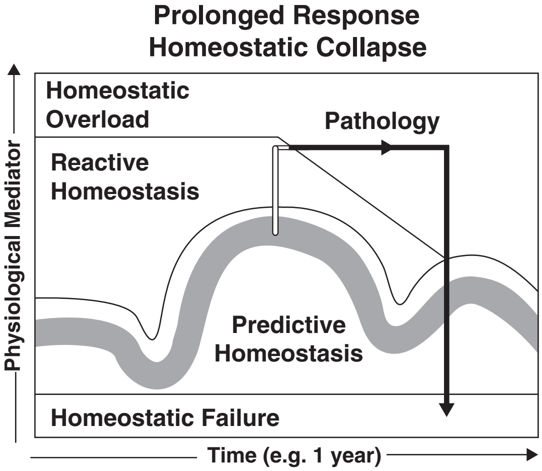


Fig. 1 The 'Reactive Scope Model' of stress. Diagrammatic representation of the impact of prolonged stressors on 'wear and tear' as depicted by a progressive decrease in the threshold between reactive homeostasis and homeostatic overload or stress. (From Romero et al. 2009 with permission)

steroid levels, B = daily and seasonal changes in levels and C = 'allostatic overload' leading to chronic stress if not alleviated (McEwen and Wingfield 2003). The use of the balance between energy expenditure and intake as a measure of allostatic load has been criticised by Walsberg (2003), and Michael Romero has countered with an innovative 'reactive scope model' of stress (Romero et al. 2009; Romero 2012). This is based on the concept that reacting to a stress (reactive homeostasis or level B in the allostatic system) involves 'wear and tear' and erodes the safety gap between B and C, leading with chronic exposure to allostatic overload (Fig. 1).

Whatever system one uses, it is obviously important to be able to discern when individuals in natural populations cross the threshold between homeostatic adaptive responses to environmental stressors and experience 'allostatic overload' or stress. A recent review of factors influencing the stress response in Australian marsupials, for example, documents studies that have measured either plasma or faecal levels of glucocorticoids (Hing et al. 2014). Elevated steroid levels alone, however, are not necessarily an index of stress (Johnstone et al. 2012) as they form part of the animal's normal adaptive response to the stressor (Angelier and Wingfield 2013). Opinion is also still divided on whether total levels or non-protein-bound 'free' levels of corticosteroids are what should be measured in studies of stress (Breuner et al. 2013; Schoech et al. 2013, Desantis et al. 2013).

An Operational Definition of Stress

An early simple operational definition proposed for stress, which avoids some of the difficulties referred to above, is 'the physiological resultant of demands that exceed an animal's homeostatic capacities' (Bradshaw 1997, 1986, 2003). This allows one to both discern the incidence of stress and measure its severity. Inherent in the definition is the understanding that the animal has maximally deployed whatever defences it has against the stressor and that, despite this, its internal state or 'milieu intérieur' has been significantly perturbed. By simultaneously monitoring the extent of the animal's adaptive response to a stressor (e.g. levels of adrenocortical hormones, antidiuretic hormone) along with measures of its internal state (e.g. total body water content, plasma osmolality, body temperature), one can effectively detect individuals that are in stress. The primary aim of this review is to use ecophysiological data to identify, where possible, instances of arid-zone marsupials evincing stress response to environmental stressors.

High temperatures and lack of water characterise the arid zone, and when considering the relative impact of the four environmental constraints experienced by marsupials listed above, these two would appear to be the most relevant as loss of CWR species has been highest in the arid zone since European colonisation.

Temperature Regulation

'Adaptive Heterothermy'

There have been few studies of thermoregulation of free-ranging marsupials in the Australian arid zone, but adaptive heterothermy, described for eutherian mammals, has been suggested as a response helping to ameliorate high diurnal temperatures (McCarron and Dawson 1989; Brown and Dawson 1977; McCarron et al. 2001). Pioneering research by Knut Schmidt-Nielsen with camels (Schmidt-Nielsen et al. 1956) and Richard Taylor on East African ungulates (Taylor 1970) established the paradigm of large arid-zone mammals using heterothermy to conserve water by storing heat in the body during the day, which it then lost by radiation at night (Bradshaw 2003). Added to this were studies suggesting that in those species possessing a carotid rete, such as the eland, selective brain cooling operates to protect cerebral function from high core body temperatures (Taylor and Lyman 1972). Recent studies, however, incorporating body temperature recording from free-ranging animals in desert conditions (bio-logging) have questioned this established view. Body temperatures of African antelopes, for example, are higher at night than during the day (Mitchell et al. 2002). Selective brain cooling as an adaptive response has also been questioned. It has never been observed in free-living mammals and may be a response restricted to captive animals exposed to heat or exercising on a treadmill (Fuller et al. 2014). In a relatively recent review, the authors comment that 'With the possible exception of the camel, we doubt that arid-zone mammals use adaptive heterothermy at all.' (Mitchell et al. 2002).

There have been a number of studies of changes in diurnal body temperatures of resting arid-zone kangaroos carried out by Terry Dawson and colleagues at the Fowlers Gap research station in northern New South Wales. These enable us to pose the question of whether these large macropods ever give evidence of stress resulting from high environmental temperatures. Using the operational definition of stress

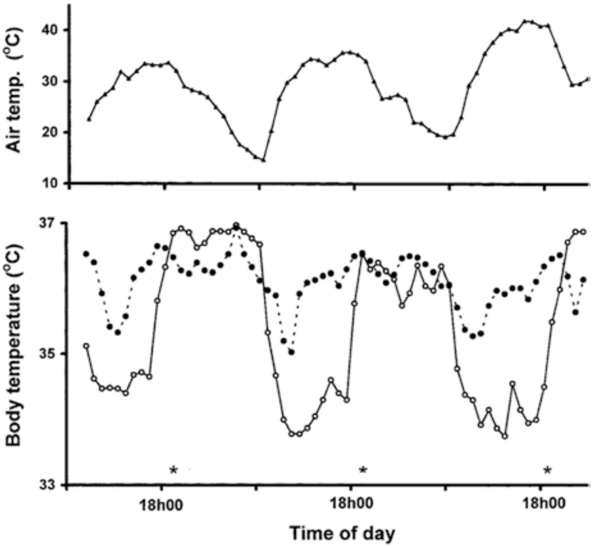


Fig. 2 Diel changes in air temperature and the comparison of the nychthermal cycle in deep body temperature under ad libitum conditions for a representative eastern grey kangaroo (open circles) and red kangaroo (solid circles). The asterisk indicates the time of day at which eastern grey kangaroos went to drink. (From McCarron et al. 2001 with permission)

above, this would mean finding evidence of a significant elevation of the body temperature above what is considered to be the normal range, despite the deployment by the kangaroo of its full suite of physiological and behavioural defences (e.g. shade seeking, sweating, saliva spreading). Thermoregulatory responses of mesic eastern grey (*Macropus giganteus*) and arid red kangaroos (*Macropus rufus*), held in small pens, to ambient temperatures ranging from –5 to 45 °C were compared by Dawson et al. (2000). Both species maintained their body temperature within the normal range of 36.5–37 °C; the only difference was the slightly lower rates of respiratory evaporative water loss of the red kangaroo at 45 °C. Somewhat different results were obtained when the same two species were compared while ‘free-ranging’ in an 8 ha enclosure with access to water (McCarron et al. 2001). Body temperatures of the eastern grey kangaroos were approximately 2 °C lower than those of red kangaroos during the middle of the day and 0.3 °C higher at night (Fig. 2). The daily body temperature range of the mesic grey kangaroos was thus higher than that of red kangaroos with access to water (2.76 °C vs 1.72 °C) and much higher when denied access to water (4.70 °C vs 2.29 °C). Even so, the mean body temperature of the eastern greys when denied access to water was still only 36.55 ± 0.40 °C, which would not appear to be above its ‘normal’ range and thus not supporting a case for thermal stress. The eastern grey, which is normally thought of as a ‘mesic’ species, has recently extended its range into the arid zone (Dawson 1995; Dawson et al. 2006), but the adequacy of its thermoregulatory response would appear to enable it to do this without experiencing stress responses or ‘allostatic overload’.

A major and obvious difference between eutherians and marsupials is that the latter, with one exception (the numbat), are essentially all nocturnal, or at most crepuscular. This means that they are not normally exposed to the full onslaught of the arid situation as they are typically active and forage at dawn and dusk and throughout the night. Although there are few data on the subject, it seems likely that adaptive heterothermy in the 'classical' context (i.e. as a response to high diurnal temperatures) is absent in arid-zone marsupials, but what is very clear is that heterothermy is very important in the group as a response to low, rather than high, temperatures. Hibernation and daily torpor (i.e. temporal heterothermy) have been reported in approximately 15% of all marsupials with data from 41 species included in a recent review (Riek and Geiser 2014). Deserts and arid zones are rather cold at night, because of the lack of cloud cover and the high levels of radiation to the sky, and temperature ranges between night and day may be as high as 60 °C (Monod 1973). Nocturnal animals, such as marsupials inhabiting the arid zone, must thus contend with potential heat losses during their prime activity period.

Torpor

Although it might be thought that mammals do not need to utilise torpor in a 'warm' country such as Australia, there is in fact a large body of literature on the incidence and intensity of torpor in Australian marsupials, and it is clear that arid-zone species, especially small insectivorous dasyurids, employ it routinely (Geiser 2004; Riek and Geiser 2014). Known heterothermic dasyurids range in body size from 6 g planigales (*Planigale* spp.) to the western quoll, *Dasyurus geoffroii*, weighing almost a kilogram (Geiser and Kortner 2010). Minimum body temperatures during torpor range from 11 to 15 °C in the smaller species (<100 g) and from 15 to 23 °C in larger species (>100 g) with the metabolic rate typically falling to 30–50% of the basal metabolic rate (Geiser 2004). Torpor also has a considerable impact on the water economy of arid-zone marsupials, with a reduction in absolute evaporative water loss (EWL) from 23.5 to 42.3% of normothermic values reported for the stripe-faced dunnart, *Sminthopsis macroura*, in a recent laboratory study (Fig. 3) (Cooper et al. 2005).

It is perhaps not surprising that arid-zone species using torpor are primarily small carnivores that depend on food sources such as grasshoppers, termites and alates that often fluctuate in availability. In captivity, torpor can be readily induced in dasyurids by reducing the ambient temperature but also by withholding food (Geiser 2003). Field data from *Pseudantechinus macdonnellensis*, *Planigale gilesi* and the mulgara, *Dasycercus blythi*, add weight to this. Long torpor bouts of 20 h were initiated in up to 100% of days during winter in these free-ranging desert dasyurids when food supplies were low (Geiser and Pavey 2007; Pavey and Geiser 2008; Kortner et al. 2008b; Warnecke and Geiser 2009). Torpor bouts in the field may vary from a little as 2 h to as long as 26 h in the stripe-faced dunnart (*Sminthopsis macroura*) (Kortner and Geiser 2011). Female brush-tailed mulgara (*Dasycercus*

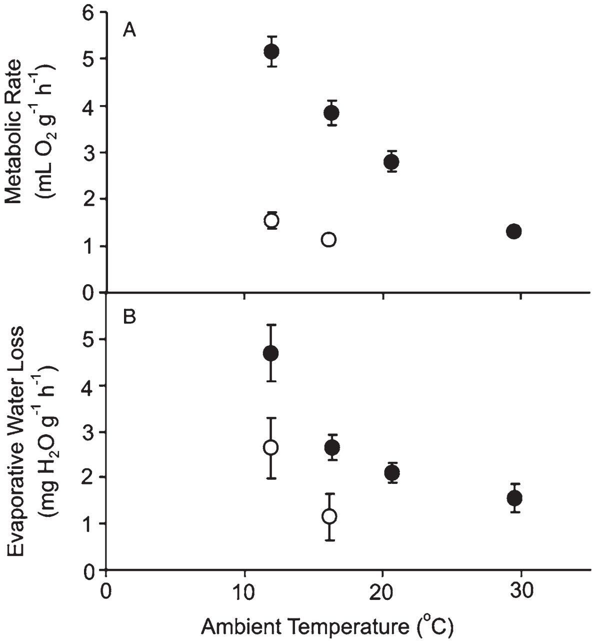


Fig. 3 Metabolic rate (**a**) and evaporative water loss EWL (**b**) of normothermic (dots) and torpid (circles) stripe-faced dunnarts (*Sminthopsis macroura*) at various ambient temperatures. Values are mean ± SE and n = number of observations. For normothermic dunnarts, $n = 6$ at $T_a = 11–20$ °C and $n = 10$ at $T_a = 30$ °C; for torpid dunnarts, $n = 6$ at $T_a = 11$ and $n = 10$ at $T_a = 16$ °C. (From Cooper et al 2005 with permission)

blythi) employ torpor throughout most of their pregnancy, but not during lactation (Kortner et al. 2008a). These studies on free-ranging individuals, equipped with temperature-sensitive radio-transmitters, have shown that daily torpor is a crucial survival strategy for small dasyurids in the arid zone during the cold months of the year and contributes to their long-term persistence in these habitats (Kortner and Geiser 2009; Masters and Dickman 2012; Dickman et al. 2001). A recent study on the 27 g kaluta (*Dasykaluta rosamondae*) in the Pilbara region of Western Australia has revealed that, during the colder winter months, animals were essentially diurnal and retreated into burrows overnight (Kortner et al. 2010). Torpor also differed between males and females, with females torpid at body temperatures of 21 °C throughout the night, whereas males entered multiple short and shallow bouts during the night (Fig. 4). The sandy inland mouse, *Pseudomys hermannsburgensis*, also displays an unusual response to low environmental temperatures, falling into torpor but apparently lacking the ability to arouse spontaneously (Tomlinson et al. 2007). As spontaneous arousal forms part of the accepted definition of ‘torpor’ (Lyman et al. 1982), this appears to be an instance of ‘adaptive hypothermia’ in an arid-zone marsupial, rather than torpor.

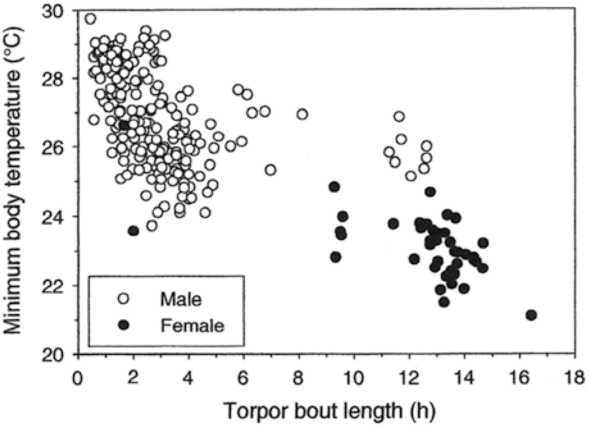


Fig. 4 Relationship between minimum T_b during torpor and torpor bout length in free-ranging male and female Kaluta (*Dasykaluta rosamondae*). (From Kortner et al. 2010 with permission)

Given the substantial change in the milieu intérieur of the torpid animal (i.e. the dramatic fall in body temperature and reduced metabolic rate), it is reasonable to ask whether torpor is a stress response. Our 'operational definition' of stress 'the physiological resultant of demands that exceed an animal's homeostatic capacities' mandates, however, that the animal is 'attempting' to maintain its normal level of homeostasis, despite the stressor. In the case of torpor, the animal clearly 'abandons' the normal physiological processes that maintain its body temperature within a narrow range, allowing it to fall close to ambient levels. Recent work on the endocrinological and molecular mechanisms underlying torpor in mammals has identified leptin as a key factor in initiating recovery from torpor bouts. Leptin, a peptide hormone, is produced by lipid tissue and is thought to relay nutritional status from peripheral fat stores to sites within the hypothalamus, especially the arcuate nucleus (Sahu 2003). The other hormone that has been implicated is ghrelin, secreted by the stomach which activates neuropeptide Y neurones (NPY) in the arcuate nucleus, leading to increased food intake and rate of metabolism (Swoap 2008). Thyroidectomy has also long been known to disrupt torpor in mammals by uncoupling mitochondrial heat production (Bechtold and Loudon 2007), and recent research has found that type 3 deiodinase reduces the availability of tri-iodothyronine (T_3, the active form of the hormone thyroxine) in the hypothalamus, initiating torpor in Siberian hamsters (Murphy et al. 2011). Recent studies implicate the melatonin-expressing cells in the pars tuberalis of the pituitary as the source of the information passed to hypothalamic tanycytes, where the deiodinase is expressed (Scherbarth and Steinlechner 2010). All this research has been undertaken in eutherian mammals, but data suggesting that leptin levels may also be involved in the initiation of torpor in marsupials is supported by a study with the stripe-faced dunnart, *Sminthopsis macroura*, in which leptin treatment halved the duration of torpor bouts in animals deprived of food for 24 h (Geiser et al. 1998).

Torpor in marsupials is thus not a stress response[1] but an apparently adaptive regulated response to an unfavourable energy balance, whereby normal homeostatic maintenance of body temperature by increased metabolism is temporarily uncoupled, allowing the body temperature to fall with significant savings in energy expenditure. Marsupials also lack brown fat, the metabolically highly active tissue in eutherian mammals that is used to restore body temperature from torpor bouts, and a number of studies have identified the importance of solar basking and huddling behaviour in rewarming of marsupials (Geiser and Pavey 2007; Pavey and Geiser 2008; Warnecke and Geiser 2009; Tomlinson et al. 2014). Basking during rewarming from torpor has been reported in at least four small dasyurids (*Planigale gilesi* (8 g), *Sminthopsis crassicaudata* (10 g), *Sminthopsis macroura* (15 g) and *Pseudantechinus macdonnellensis* (31 g)) with basking commencing approximately 3 h after sunrise when their body temperatures range from 13.8 to 19.3 °C (Warnecke and Geiser 2009, Geiser and Kortner 2010). The significant saving of energy expenditure by these small arid-zone marsupials through the reduction in metabolic rate and access to solar energy during passive rewarming from daily torpor has been estimated at 80% (Warnecke et al. 2008).

Water and Electrolyte Balance

Low availability of free water is the other primary factor characterising the arid zone, and animals living there must contend with this potential stressor. Rates of water turnover in free-ranging marsupials have been measured using tritiated water (^{3}HHO) in a wide range of species and vary allometrically with body mass (Nagy and Peterson 1988; Nagy 1994). The exponent of the relationship in macropodid marsupials varies from 0.82 to 0.87 (Green 1997), which is higher than 0.75, the exponent for metabolic rate of eutherian mammals, and also much higher than the exponent for the field metabolic rate (FMR) of marsupials at 0.69. This means that, as body mass increases, water turnover does not decrease on a mass-specific basis as rapidly as metabolic rate. This discrepancy between the two exponents, with respect to water, means that larger marsupials require relatively more water for a given energy intake than smaller animals and thus may have more difficulty obtaining their daily water requirements from their food. This question was explored in an early paper with data from two species of kangaroos, the red kangaroo and the euro, *Macropus robustus*, in the Pilbara region of Western Australia (Main and Bakker 1981). Males are twice the size of females in both species, and, with the onset of the dry season, males were found to lose body mass in contrast to females, which retained their initial mass. The authors interpreted this as evidence of differential dehydration in the larger males, which was supported by the first field study of euros by Tim Ealey (Ealey 1967; Ealey and Main 1967; Main 1970).

---

[1] To date plasma corticosteroid levels during torpor have not been reported in any marsupial, but they would be of interest.

The Quokka

Evidence of stress due to lack of water is difficult to establish in these kangaroo species, because of the lack of information on regulatory hormonal responses, and a case study of a small macropodid wallaby, the quokka (*Setonix brachyurus)* (Fig. 5), is informative as an example, providing details of the nature of the data required. The quokka is originally a forest dweller, not an arid-zone species but a relictual population that survives on Rottnest Island 20 km off the coast of Perth in Western Australia, where there is no free water and the environment is severely degraded due to fire and overgrazing (Bradshaw 1983; Pen and Green 1983). There are a number of hypersaline lakes on the island, formed by intrusions from the ocean, and seeps into these lakes are all brackish. Quokkas living close to the lakes drink at these soaks, and a study was undertaken in late summer to determine whether this marginal intake of water would benefit lakeside dwellers compared with quokkas living on the dry West End of the island (Jones et al. 1990).

Table 1 compares rates of water and sodium turnover of quokkas living in the two habitats – both rates are substantially lower in the West End animals. Table 2 gives information on the body mass and condition of the two populations, along with plasma levels of antidiuretic hormone (ADH, lysine rather than arginine vasopressin in these marsupials), plasma osmolality and urine function. What is evident is that the West End animals are in poorer condition, have very high levels of ADH and have a significantly elevated plasma osmolality. They thus exemplify our operational definition of stress: a significant perturbation of the milieu intérieur (raised plasma osmolality), despite the maximal deployment of regulatory responses (the

Fig. 5 Adult female marsupial quokka wallaby (*Setonix brachyurus*), drinking at a brackish seep that flows into one of the hypersalline lakes, on Rottnest Island, 20 km off the coast of Perth in Western Australia

Table 1 Rates of turnover of water and sodium measured as influx in quokkas (*Setonix brachyurus*) from two locations in late summer on Rottnest Island, Western Australia

Turnover	Lake Baghdad	West End	Significance
Water influx (mL.Kg^{-1}.day^{-1})	133.5 ± 12.1	55.7 ± 15.5	$P < 0.005$
Sodium influx (mmol.Kg^{-1}.day^{-1})	34.5 ± 5.0	10.2 ± 2.9	$P < 0.001$

Modified from Jones et al. (1990)

Table 2 Comparison between body mass, condition and plasma levels of antidiuretic hormone (lysine vasopressin) and kidney function in quokkas (*Setonix brachyurus*) from two locations in late summer on Rottnest Island in Western Australia

Parameter	Lake Baghdad	West End	Significance
Body mass (kg)	2.66 ± 0.13	2.09 ± 0.15	$P < 0.01$
Condition index	6.45 ± 0.25	5.33 ± 0.26	$P < 0.01$
Lysine vasopressin $pg.mL^{-1}$	35.6 ± 15.8	89.2 ± 19.5	$P < 0.05$
Urine production ($mL.Kg^{-1}.day^{-1}$)	58.18 ± 13.79	20.35 ± 2.75	$P < 0.02$
Urine osmolality ($mOsm.Kg^{-1}$)	968.7 ± 101.3	1253.1 ± 44.7	$P < 0.02$
Plasma osmolality ($mOsm.Kg^{-1}$)	279.8 ± 2.4	301.3 ± 6.0	$P < 0.005$
U/P_{osm}	3.46	4.16	$P < 0.02$

Modified from Jones et al. (1990)

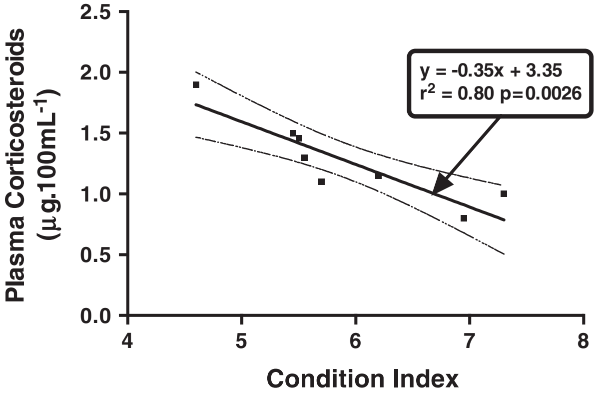


Fig. 6 Regression of plasma corticosteroid concentrations against body condition index in quokkas (*Setonix brachyurus*) in late summer on Rottnest Island in Western Australia. (Modified from Miller and Bradshaw 1979)

highest levels of ADH yet recorded in a marsupial). Measurement of plasma corticosteroid levels of quokkas in late summer also shows that the HPA axis is chronically stimulated, with a highly significant negative correlation with body condition (Fig. 6) (Miller and Bradshaw 1979).

Barrow Island Macropods

A long-term study of the ecophysiology of a suite of marsupials on Barrow Island, some 1400 km north of Perth in the Pilbara region of Western Australia, has provided valuable insights into the level of adaptation of arid-zone species (Bradshaw 1992). Barrow Island is Australia's foremost A-Class Reserve, harbouring 13 mammal species, 8 of them marsupial, of which 4 are either extinct on the mainland of Australia or virtually so (Moro and Lagdon 2013). Normally when rates of water turnover and FMR are measured in free-ranging animals, the study involves only single species, with perhaps a seasonal component. The study of Barrow Island, however, involved 12 vertebrate species (including a lizard and a bird) all measured simultaneously in different seasons over a 4-year period. Rates of metabolism in the field can then be used as 'metabolic currency' to compare the differential impact on available resources of the many vertebrates inhabiting this 234 km^2 arid island. Six marsupial species were included in the study, and variation in rates of water turnover was assessed using doubly-labelled water. An earlier study on the spectacled hare-wallaby, *Lagorchestes conspicillatus*, on Barrow Island had already established that this species has an extremely slow rate of water turnover in the driest part of the year, averaging 47.1 ± 4.1 mL.kg$^{-0.82}$.day^{-1}, which equates to only 5.1 ± 0.6% of its total body water content per day (Bakker and Bradshaw 1989).

An allometric comparison of rates of water turnover and FMR of Australian marsupials, using the doubly-labelled water method, shows that both parameters are substantially lower in arid-zone marsupials than in species inhabiting mesic habitats (Fig. 7) (Nagy and Bradshaw 2000). Rates of water turnover were compared in four species of macropodids on Barrow Island in the wet season (summer/autumn with cyclonic rains) and the dry winter season over a 5-year period in the 1990s (King and Bradshaw 2008). The species were the dwarf Barrow Island euro kangaroo, *Macropus robustus isabellinus*; the spectacled hare-wallaby; the black-footed rock wallaby, *Petrogale lateralis*; and Lesueur's bettong or 'boodie', *Bettongia lesueur*. Water influx rates were highest in bettongs during the dry season at 79.6 ± 6.1 mL.kg$^{-0.82}$.day^{-1} and lowest in the hare wallaby, averaging 28.2 ± 6.1 mL.kg$^{-0.82}$.day^{-1}, with the other two species intermediate between these values (Fig. 8). The water turnover has also been expressed as the percentage of the animal's total body water content exchanged per day, and the high fraction for the bettongs (13.98 ± 0.6%) contrasts with that for the hare wallabies (3.51 ± 0.4%). The latter is an extraordinarily slow rate of water turnover for a desert mammal. Rates of water turnover in summer in desert rodents from southern Tunisia, for example, average between 15.3 and 21.8% of the total body water content per day (Bradshaw et al. 1976). There were no significant differences between plasma osmolality recorded in the dry and wet seasons for any of the macropods on Barrow Island; urine osmolality, however, was significantly elevated in hare wallabies in the dry season, averaging 2256 mOsm.kg^{-1}.

In evaluating the impact of the many vertebrate species that inhabit Barrow Island, and measuring the way in which they share scarce resources, the FMR can be used as 'metabolic currency' to compare the environmental cost of different lifestyles. If one takes the FMR of a single euro kangaroo (approximately 96 L of CO_2 per animal per day) as our unit of measurement, then multiplying this by the estimate number of euros on the island[2] gives total energy turnover by euros in

---

[2] There are no accurate population estimates for Barrow Island marsupials, but available data from transects have been aggregated and then extrapolated, based on the area surveyed. As this assumes that animals are uniformly distributed across the island, the estimates generated are thus upper limits. SHORT, J. & TURNER, B. 1991. Distribution and abundance of Spectacled hare-wallabies and euros on Barrow Island. *Wildlife Research,* 18**,** 421–429, SHORT, J. & TURNER, B. 1993.

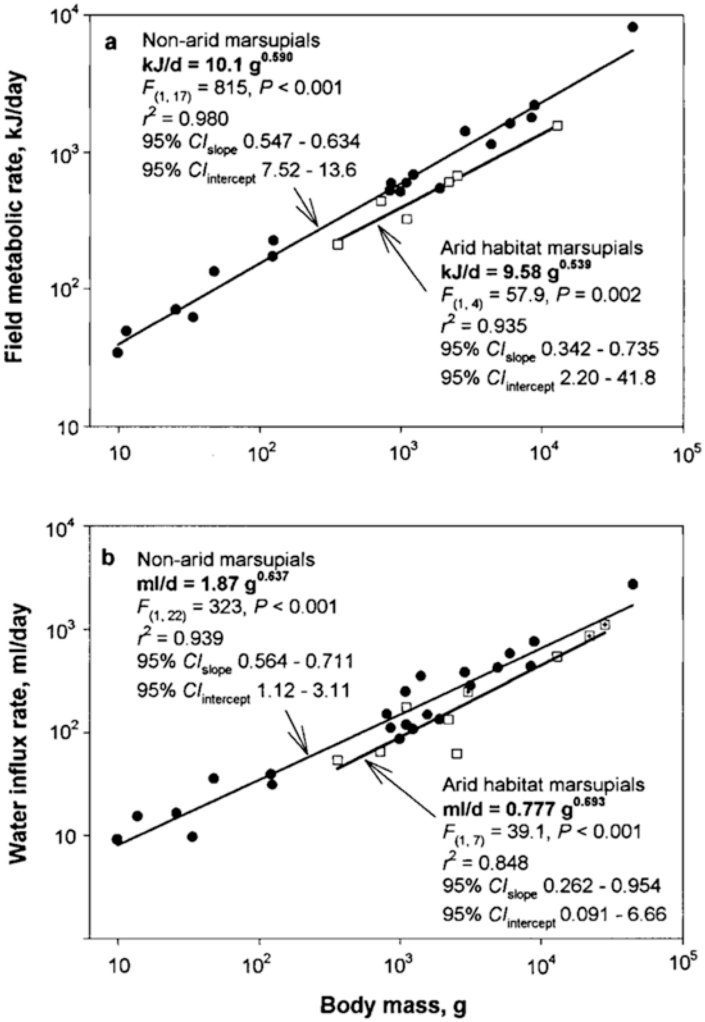


Fig. 7 Allometric regressions of (**a**) field metabolic rate (FMR) against body mass (g) for free-ranging marsupials from arid (open squares) and non-arid habitats (black circles) and (**b**) water influx rate against body mass for free-ranging marsupials from arid (open squares) and non-arid habitats (black circles). (From Nagy and Bradshaw 2000, with permission)

'Kangaroo Equivalents'. FMR data are available for a wide range of other Barrow Island vertebrates from which one can estimate their energy usage and express this

---

The distribution and abundance of the Burrowing bettong (Marsupialia: Macropodoidea). *Wildlife Research,* 20**,** 525–534, LAGDON, R. 1988. Barrow Island Environmental Review: 1963–1988. Perth, Western Australia: West Australian Petroleum Pty. Limited.

A.A. Burbidge (pers. com.).

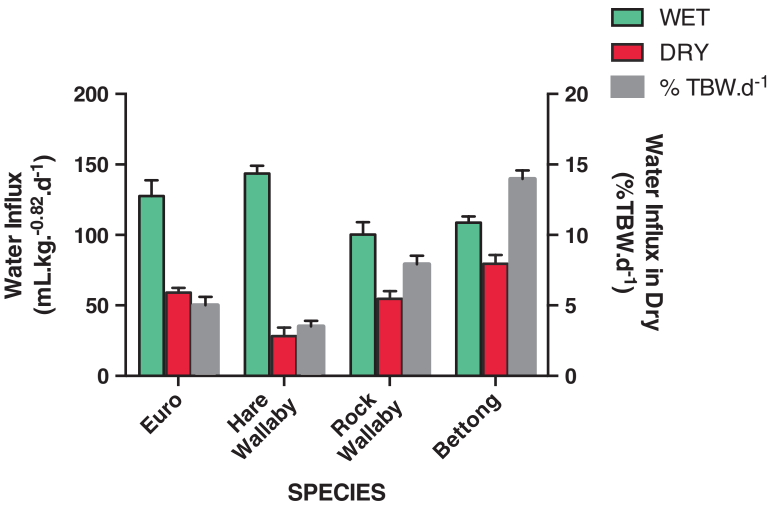


Fig. 8 Comparison between rates of water influx in mL.kg$^{-0.82}$.day^{-1} in wet and dry seasons in four marsupial species on Barrow Island in the arid Pilbara region of Western Australia. Species are the Barrow Island euro, *Macropus robustus isabellinus;* spectacled hare-wallaby, *Lagorchestes conspicillatus*; black-flanked rock wallaby, *Petrogale lateralis*; and the Burrowing bettong, *Bettongia lesueur*. Rates of water loss in the dry season are also expressed on the right-hand ordinate as a percentage of the total body water content exchanged per day (% of total body water content.day^{-1}) (calculated with data from King and Bradshaw 2008, 2010)

in 'Kangaroo Equivalents' (Fig. 9). Interestingly, the much smaller but very abundant golden bandicoots have an energetic impact larger than the euros, followed by hare wallabies, then the giant varanid lizard, the perentie, and then burrowing bettongs. The energetic impact of other small vertebrates, including native rodents, dragon lizards and the spinifex bird, is trivial in comparison.

The Barrow Island Euro

Seasonal variation in water and electrolyte balance were studied over a 5-year period in the euro, and plasma levels of ADH (lysine vasopressin) were also measured for the first time in this species (King and Bradshaw 2008). Plasma ADH levels increased with plasma osmolality and were negatively correlated with total body water content. Mean concentrations ranged from 2.1 ± 0.6 pg.mL^{-1} in June 1995, the wettest year of the study, to 16.7 ± 4.6 pg.mL^{-1} in November 1994, following an 8-month drought, when total rainfall for that year was only 54 mm. This was composed of 50 mm in February and 4 mm in December. The average annual rainfall for Barrow Island is 320 mm (Moro and Lagdon 2013).

A detailed analysis of changes in body condition, haematology and hormone levels of Barrow Island euros in November 1994 found significantly elevated

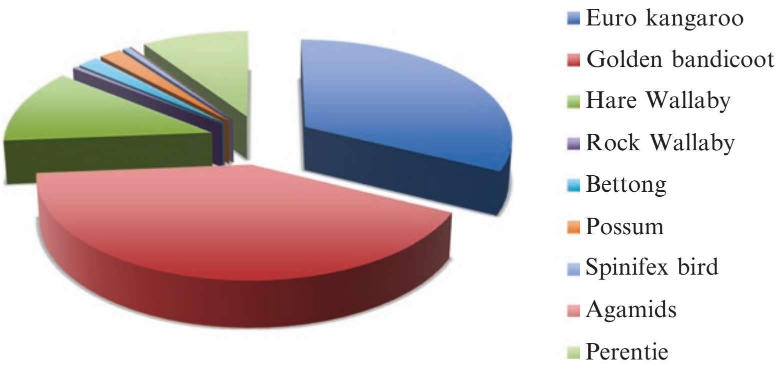
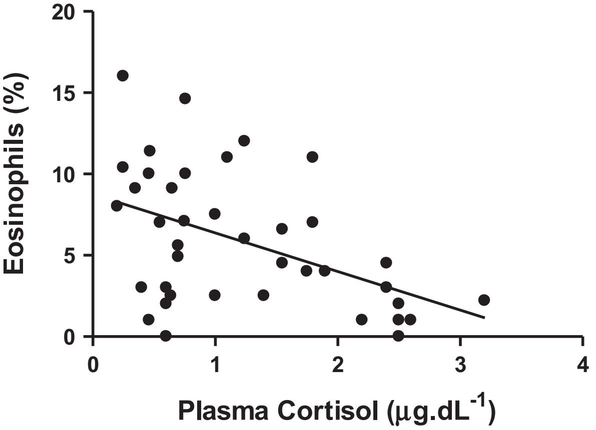


Fig. 9 Partitioning of energy turnover by a suite of vertebrate taxa on Barrow Island in the Pilbara region of Western Australia. Field metabolic rates (FMR) of the various taxa, measured in CO_2 production in litres per animal, have been normalised to 'Kangaroo Equivalents' (KE) with 1 KE = daily CO_2 production of the euro, *Macropus robustus isabellinus*, and then multiplied by the population estimate for each species. (Produced with data from Nagy and Bradshaw 2000; Short and Turner 1991, 1993; A.A. Burbidge (pers. com.), Ambrose et al. 1996; Green et al. 1986)

Fig. 10 Regression of eosinophil counts, expressed as a percentage of total leucocytes, against plasma cortisol levels in μg.dL^{-1} in the Barrow Island euro, *Macropus robustus isabellinus*. The negative regression is statistically significant with $r^2 = 0.201$ and $P = 0.0037$. (Adapted from King and Bradshaw 2010)



plasma osmolality, plasma cortisol levels and plasma ADH and a reduced eosinophil count (King and Bradshaw 2010). Plasma cortisol levels and eosinophil counts were also significantly negatively correlated (Fig. 10), suggesting that the exposure was chronic and compromising the euros' immune capabilities (Sapolsky et al. 2000; Davis et al. 2008). Euros suffered from a regenerative normative hypochromic anaemia, not found in mainland animals, compromising their respiratory capacities and severely limiting any sustained activity (Billiards et al. 1999). Despite their small body size, and high surface/volume ratio, the euros have a low rate of water turnover in the dry time of the year and a water economy index (WEI = water influx/FMR) characteristic of arid-adapted marsupials (Nagy and Bradshaw 2000). Unfortunately, rates of water influx were not measured on the November 1994 field trip, but the body mass and condition index of the euros was not decreased, suggesting that the increased plasma osmolality may not have been the result of simple dehydration. Levels of ADH, although elevated, were nowhere near as high as those measured in quokkas from the West End of Rottnest Island, suggesting that the euros were experiencing a very high ‘allostatic load’ but had not yet reached ‘allostatic overload’ (King and Bradshaw 2010).

Desert Wallabies

Seasonal changes in water and electrolyte balance and kidney function have been studied in two species of wallabies in the arid Pilbara region of Western Australia: the spectacled hare-wallaby, *Lagorchestes conspicillatus*, again on Barrow Island, and Rothschild’s rock wallaby, *Petrogale rothschildi*, on Enderby Island in the Dampier Archipelago (Fig. 11) (Bradshaw et al. 2001). Although both species are nocturnal feeders, they differ markedly in the nature of their daytime refugia. The hare wallaby shelters in large clumps of spinifex (*Triodia* spp.) during the day, whereas the rock wallaby shelters in caves and rock piles. Temperatures in the spinifex clumps often exceed 40 °C during the summer months, and the air is very dry, whereas cave sites are much cooler, with high constant humidity.

Data on rates of water turnover and water and electrolyte homeostasis for the two wallabies during the driest part of the year are presented in Table 3. There are no significant differences between plasma electrolyte concentrations, plasma osmolality and total body water content for the two species, indicating that they are both effectively maintaining homeostasis at this time. Rates of water influx, however, differ substantially, and the figure of 27.5 ± 2.0 mL.kg$^{-0.82}$day^{-1} is the lowest rate of water turnover yet reported for any mammal worldwide.

A comparison of kidney function in the field during the dry and the wet months of the year revealed major differences between the two species (Fig. 12) (Bradshaw et al. 2001; Bakker and Bradshaw 1989). Hare wallabies show a pronounced antidiuresis in the dry season, accompanied by a large increase in urine concentration (U/P$_{OSM}$) and a very significant increase in plasma ADH levels. This is a standard response from a mammal and what one would expect when challenged by water deprivation. The rock wallabies, on the other hand, respond with an antidiuresis (not as effective), but there is no change in the concentration of the urine being elaborated (U/P$_{osm}$) nor any significant increase in plasma ADH levels. A detailed analysis of kidney function, involving measurement of rates of glomerular filtration and renal plasma flow (RPF), revealed that the rock wallabies in the dry season were reducing rates of blood flow to the kidney and hence reducing glomerular filtration (GFR) rather than increasing the rate of water reabsorption from the renal tubules (Bradshaw et al. 2001). This marked difference in renal function between the two species is shown in Fig. 13.

Rothschild’s rock wallaby is unique in being the first mammalian species in which the lack of a hormonal antidiuretic response to water deprivation has been

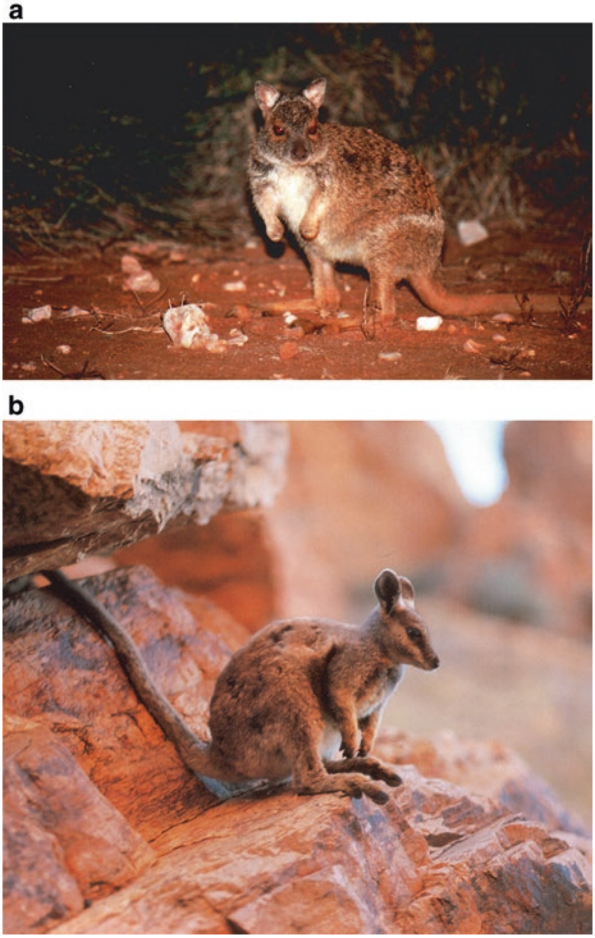


Fig. 11 Photographs of (**a**) the spectacled hare-wallaby, *Lagorchestes conspicillatus*, on Barrow Island and (**b**) Rothschild's rock wallaby, *Petrogale rothschildi*, on Enderby Island in the Pilbara region of Western Australia

Table 3 Water metabolism and homeostasis during the dry season of spectacled hare-wallabies (*Lagorchestes conspicillatus*) on Barrow Island and Rothschild's rock wallaby (*Petrogale rothschildi*) on Enderby Island in the arid Pilbara region of Western Australia

Species	Body mass (kg)	Total body water (%)	Water influx (mL.kg$^{-0.82}$.day^{-1})	Plasma sodium (mmol.L^{-1})	Plasma potassium (mmol.L^{-1})	Plasma osmolality (mOsm.kg^{-1})
Hare wallaby	2.31 ± 0.06	76.4 ± 1.60	27.5 ± 2.0	151.9 ± 1.1	5.6 ± 0.2	287.3 ± 2.1
Rock wallaby	3.32 ± 0.12	78.2 ± 1.69	68.9 ± 5.2	145 ± 0.86	5.17 ± 0.2	291.3 ± 2.5

Adapted from Bradshaw et al. (2001)

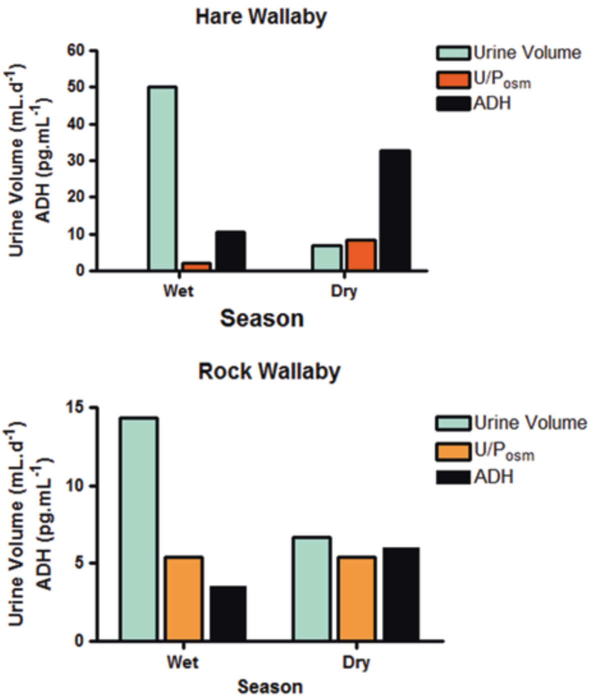


Fig. 12 Renal function in wet and dry seasons in arid-zone wallabies in the Pilbara region of Western Australia. Rates of urine production in mL.day^{-1}, urinary concentrations in U/P$_{OSM}$ and plasma levels of antidiuretic hormone (ADH = lysine vasopressin) in pg.mL^{-1} are shown for spectacled hare-wallabies (*Lagorchestes conspicillatus*) on Barrow Island and Rothschild's rock wallaby (*Petrogale rothschildi)* on Enderby Island. (Adapted from Bradshaw et al. 2001)

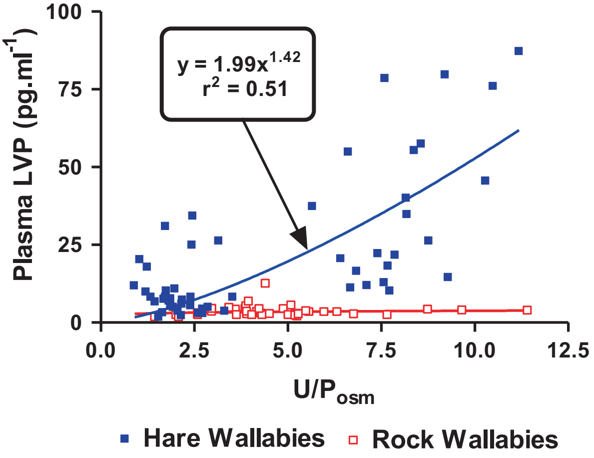


Fig. 13 Variation in circulating levels of lysine vasopressin (LVP) in hare wallabies and rock wallabies as a function of the concentrating activity of the kidney (U/P$_{osm}$). (Adapted from Bradshaw et al. 2001)

detected. Despite this, it is clear that the species is able to deal effectively with the challenges of its arid environment and it owes this to the protection provided by its cave or rockpile habitat. Its response to water deprivation is reminiscent of that often seen in reptiles, with a reduction in glomerular filtration, rather than an increase in reclamation of filtered water (Dantzler and Bradshaw 2009; Ford and Bradshaw 2006). Lysine vasopressin is present in the plasma of the rock wallaby, but further work is needed to establish whether it acts via cyclic-AMP to increase water permeability of the renal tubules in this species or whether it has lost this primary function (Morel 1983). There is no evidence that either species of wallaby experiences 'allostatic overload' or stress, even during the longest drought recorded in 1994 on Barrow Island. The vital role of habitat in enabling the rock wallaby to persist in this arid habitat is paramount, however, and without a cool, humid refuge to which it can retreat during daylight hours, it would be unable to survive. By way of contrast, the hare wallaby provides another example of the extent to which physiological adaptations can facilitate survival and persistence in challenging environments (Bradshaw 1992, 2007).

Seasonal Deficiencies of Nitrogen, Phosphorus and Energy

The last of the major factors confronting animals that inhabit the arid zone is the one least documented, despite its importance. It is primarily a concern of herbivorous species, as the food of carnivores is generally much more nitrogen, phosphorus and energy-dense than plant products (Prosser et al. 1950; Withers 1992). Nitrogen in the form of protein varies seasonally in most plants, falling to extremely low levels in arid-zone species. By reconstituting the diet of free-ranging macropods from faecal analysis of epidermal fragments (Storr 1963), the nitrogen concentration as percent dry weight of the diet of euro (*Macropus robustus)* and red kangaroos (*Macropus rufus*), for example, was found to range from 1.6 to as low as 0.8% (Main 1970). Nitrogen levels in spinifex grasses (*Triodia* spp.) fall to even lower levels and present a major challenge for the maintenance of nitrogen balance and growth in arid-zone marsupials.

A series of studies on the energetics of arid-zone kangaroos, carried out at the Fowlers Gap research station in New South Wales, has highlighted the large difference between marsupial and eutherian herbivores. Both the basal metabolic rate and field metabolic rate (FMR) of kangaroos are lower than those of similar-sized eutherian mammals, such as sheep, and a 'dry sheep equivalent' (DSE) of 0.7 is usually used when calculating rates of resource utilisation (Munn et al. 2009; Dawson and Munn 2007). This difference has usually been attributed to the significantly lower basal metabolic rate of marsupials, compared with that of eutherian mammals (Dawson and Hulbert 1970), but has been tempered somewhat by the compilation of data on the field metabolic rate (FMR) of free-ranging marsupials. Whereas the allometric exponent of FMR with body mass in eutherians is 0.75 (similar to that of basal metabolic rate), in marsupials the exponent for FMR is much lower at 0.69

(Nagy 2005; Nagy et al. 1999; Riek and Bruggeman 2013). This means that the FMR of small marsupials is higher than that of equivalent-sized eutherian mammals but substantially lower in the case of large marsupials, such as kangaroos. A recent analysis of FMR in Australian marsupials revealed strong phylogenetic correlations, with macropods having significantly lower FMRs than carnivorous marsupials (Riek and Bruggeman 2013). FMR also scales positively with body mass in marsupials, in contrast to the situation in eutherian mammals where total population energy use is independent of species' body mass (Munn et al. 2013).

As well as having lower rates of energy turnover in the field, it has also been suggested that marsupials have lower protein requirements in their diet than eutherians, because there should be a close relationship between basal metabolic rate and rates of whole-body protein synthesis (Hume 1999). Few species have been studied to date, but rates of protein synthesis in the tammar wallaby (*Macropus eugenii*), the Parma wallaby (*M. parma*) (White et al. 1988), the wombat (*Vombatus ursinus*) (Barboza et al. 1993) and the honey possum (*Tarsipes rostratus*) (Bradshaw and Bradshaw 2001) are all well below levels reported in eutherians (Waterlow 1984). Nitrogen cycling to the fermentative foregut of macropods has also been posited as one of the mechanisms employed by arid-zone herbivores to offset the low levels of protein in plants available in summer (Kinnear et al. 1979).

Laboratory studies with a number of species of macropods have shown that they are resistant to the usual nitrogen-mobilising diabetogenic effect of the steroid hormone cortisol (Griffiths et al. 1969; McDonald and Bradshaw 1981). This is not a general marsupial characteristic, however, as cortisol injections increase nitrogen excretion and elevate blood glucose levels in brush-tailed possums (*Trichosurus vulpecula*) (McDonald and Than 1976; McDonald 1977). Cortisol is a catabolic steroid released in response to stressors, such as starvation, and stimulates gluconeogenesis through the breakdown of tissue protein with the release of nitrogen that is normally excreted. In the case of arid-zone macropods, however, the nitrogen would appear to be reabsorbed through the kidney, rather than excreted, and redirected to the microbial population in the animal's foregut, where it is synthesised into bacterial protein and subsequently digested (Kinnear and Main 1975). This would appear to be a very effective adaptation that may have evolved in these species to offset the problem of seasonal deficiencies in dietary protein (Kinnear and Main 1979). Little is known of the precise mechanism of urea recycling, however, although a study of the effects of dehydration and protein deficiency in the spectacled hare-wallaby found that relative urea clearance (C_{UREA}/C_{IN}) is positively correlated with the rate of urine production (Bakker and Bradshaw 1983). Both dehydration and protein deficiency resulted in a decrease in the glomerular filtration rate (measured as inulin clearance C_{IN}) and a decrease in urea clearance with a fall in nitrogen excretion. Exposure to high-protein diets in this desert wallaby resulted in a 'protein diuresis', and the authors of the study suggest that urea recycling in this macropodid is obligatory and reflects the low level of protein in its spinifex-dominated diet (Bakker and Bradshaw 1983).

Another important discovery is the major difference in nitrogen metabolism of marsupials compared with that of eutherian mammals involving endogenous urinary

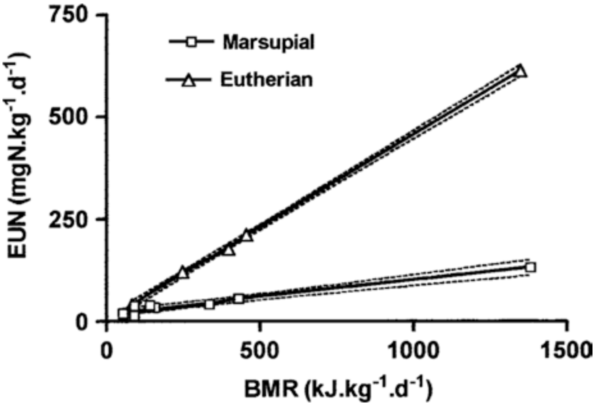


Fig. 14 Relationship between endogenous urinary nitrogen (EUN in mg N $kg^{-1}d^{-1}$) excretion and heat production (kJ kg^{-1} day^{-1}) in eutherian (open squares) and marsupial (open triangles) mammals. Data for eutherians are taken from Smuts (1935) and data for marsupials from Hume (1999) and Bradshaw and Bradshaw (2001). The linear regression equation for eutherians is EUN = 0.45BMR + 4.44, r2 = 0.999 and for marsupials is EUN = 0.08BMR + 19.24, r2 = 0.96. (Adapted from Bradshaw and Bradshaw 2001)

nitrogen excretion (EUN). EUN is estimated by regressing urinary nitrogen excretion against truly digestible nitrogen intake and extrapolating the curve to zero intake, where the measured loss is taken as obligatory. In eutherian mammals it is well established that approximately 2 mg of EUN is excreted for each kcal (4.184 kJ) of basal heat production (Smuts 1935), and it has been assumed that the lower EUN found in marsupials is a direct consequence of their lower basal metabolic rate (Hume 1999). When data from a range of marsupials are examined, however, a highly significant, but very different, relationship from that observed in eutherian mammals is found (Fig. 14). When expressed per kcal of heat production, marsupials excrete only 0.34 mg of nitrogen, not 2 mg, and this figure is, of course, corrected for the difference in basal metabolic rate (Bradshaw and Bradshaw 2001). Such a fundamental biochemical difference between marsupials and eutherian mammals is unexpected, and its mechanism and significance remain to be explored, but it does suggest that the separate dictates of marsupial evolution have resulted in a different balance between energy and nitrogen metabolism from that in eutherians.

Conclusion

Ecophysiology is the study of the physiological responses of organisms to the ecological dictates of their environment. It involves the study of animals in their natural environment, rather than in the confines of laboratories. An operational definition of stress as ‘the physiological resultant of demands that exceed an animal’s homeostatic capacities' has been used to search for instances of stress in arid-zone marsupials due to high temperatures and lack of water. The recent use of body temperature loggers in free-ranging animals has shown that 'adaptive heterothermy' and selective brain cooling, first described in camels and African ungulates, do not occur in kangaroos, which maintain normothermia over a wide range of ambient temperatures. Torpor, on the other hand, is widely employed by arid-zone marsupials, especially those with low body mass, to offset the low night temperatures also characteristic of the arid zone. Torpor in marsupials, however, is not a stress but an adaptive regulated response to an unfavourable energy balance, whereby normal homeostatic maintenance of body temperature is uncoupled, allowing body temperature to fall with significant savings in energy expenditure. Significant perturbations of water and electrolyte balance in arid-zone marsupials are also rare, and, even in the driest year ever recorded on Barrow Island, only one species, the Barrow Island euro *Macropus robustus isabellinus*, showed signs of an increased allostatic load, but not 'allostatic overload', or stress. The spectacled hare-wallaby, *Lagorchestes conspicillatus*, serves as an exemplar of the level of adaptation by some arid-zone marsupials, having the lowest rate of water loss yet recorded for any mammal worldwide. This contrasts with the Rothschild's rock wallaby, *Petrogale rothschildi*, which lacks hormonal control over water loss by the kidney but survives in a similar habitat to that of the hare wallaby by its reliance during daylight hours on cool and humid caves and rockpile shelters to conserve water. Nutritional adaptations are also evident; these aid with seasonal deficiencies of nitrogen and energy in herbivorous species. The lower field metabolic rate of arid-zone compared with mesic species of marsupials, especially macropods, results in lower levels of food intake, and urea recycling helps offset exceptionally low protein levels in the diet. Rates of protein turnover also appear to be lower in marsupial than in eutherian mammals, and the linkage between obligatory nitrogen loss from the body in the form of endogenous urinary excretion and basal energy production is almost six times lower in marsupials. Arid-zone marsupials thus appear physiologically and behaviourally well buffered to withstand the rigours of their habitat, but the environmental changes wrought by European colonisation of the continent increasingly put these adaptations to the test. If the predications of current climate change scenarios do eventuate, stress responses seen in species such as the Rottnest Island quokka will likely in the not-too-distant future be observed in arid-zone species.

Acknowledgements Acknowledgement is made to the Australian Research Council (ARC) and The University of Western Australia for financial support of much of the research carried out by the author. My especial thanks to Felicity Bradshaw whose expertise in the laboratory ensured the success of these studies. Many graduate students have also contributed to these studies of Australian animals in their natural environment, and their important contribution is acknowledged.

Glossary

CWR The critical weight range of 35 g–5.5 kg for which Australian marsupials have been found most vulnerable to extinction.

Stress An unfavourable body condition originally defined by Hans Selye as ‘a state of non-specific tension in living matter’.

Stressor An environmental factor that will provoke stress if sustained.

Allostasis Originally conceived as ‘maintaining stability through change’ and introduced into the medical literature to deal with situations, such as fever, where the body changes to a new regulated state, with a change in the set point for body temperature. The concept has been developed by biologists who have introduced the concept of ‘allostatic load’, which can be monitored through changes in circulating levels of adrenal corticosteroids.

Glucocorticoids Steroid hormones secreted by the adrenal glands in vertebrates that are released under stressful conditions and act to mobilise glucose reserves in the body.

Allostatic overload A condition equivalent to chronic stress.

‘milieu intérieur’ The ‘internal environment’ of animals identified by the French physiologist, Claude Bernard in 1878, as the closely regulated condition common to all vertebrate animals and on which their independence from the external environment depends.

Homeostasis (also homoiostasis) The term introduced by the American physiologist, Walter Cannon in 1929, to describe the process by which the ‘internal environment’ of vertebrates is protected from change.

ADH Antidiuretic hormone, which is secreted by the posterior lobe of the pituitary gland and, when released into the blood, stimulates reabsorption of water from the kidney of vertebrates, reducing urine production and assisting in coping with water deprivation and dehydration.

Heterothermy Significant variation throughout the day in body temperature – as opposed to homeothermy in which body temperature is maintained between narrow limits.

Adaptive heterothermy The process originally described in desert camels whereby they contend with excessive heat by allowing their body temperature to rise, thus storing heat that may then be lost at night by radiation.

Carotid rete A group of specialised blood vessels in the base of the brain of some mammals that operates to cool warmed blood flowing to the brain by countercurrent exchange.

Crepuscular Animals that commence their activity at dawn and dusk.

Torpor A condition in which an animal ceases activity for a period of time and is associated with a significant fall in both body temperature and metabolic rate. Torpor may last for hours or days and is truncated by spontaneous arousal of the animal with a rapid rise in its body temperature back to normal levels.

Leptin Often known as the ‘satiety hormone’, is a hormone produced by fat cells that helps to regulate energy balance by inhibiting hunger.

Ghrelin Also called the 'hunger hormone' is a peptide hormone, made up of a small number of amino acids, that is produced by cells in the intestinal tract and acts on the central nervous system to increase appetite.

Arcuate nucleus A group of nerve cell bodies in the hypothalamus of the brain that contain important neurotransmitters involved in controlling hormone release from the pituitary gland.

Neuropeptide Y Neurones (NPY) are also located in the arcuate nucleus and are important in the regulation of appetite.

Tanycytes Special cells found in the brain and on the floor of the fourth ventricle, which have processes extending deep into the hypothalamus. It is thought that their function is to transfer chemical signals from the cerebrospinal fluid to the central nervous system.

Thyroidectomy Removal of the thyroid gland.

Deiodinase Specific enzymes that break down the hormone thyroxin (T_4) by successively removing iodine molecules.

Iodothyronine (T_3) The active form of the hormone thyroxin, which has three molecules of iodine instead of four.

Pars tuberalis A group of cells located around the stalk of the pituitary gland that contain hormone-secreting cells.

Brown fat Highly metabolically active tissue found in eutherian mammals that produces heat to restore the normal body temperature of torpid mammals. Brown fat is not found in marsupials, which recover from torpor by shivering.

ADH (anti-diuretic hormone) A hormone secreted by the posterior lobe of the pituitary gland, which acts on the kidney to enhance reabsorption of water from the urine when animals are dehydrated or water deprived.

HPA axis (hypothalamo-pituitary-adrenal axis) Many of the hormones secreted by the pituitary gland (e.g. growth hormone, thyroid-stimulating hormone, adrenocorticotropic hormone (ACTH), etc.) are controlled by small molecule 'releasing factors' elaborated in the hypothalamus of the brain and transported to the pituitary gland by a dedicated portal blood supply. Stressors act via the HPA to activate secretion of hormones, firstly from the pituitary gland, which then go on to stimulate other glands in the body, such as the adrenals.

Doubly-labelled water This is water where the heavy isotope of oxygen (^{18}O) replaces normal oxygen (^{16}O) and hydrogen is replaced by either deuterium (^{2}H) or radioactive tritium (^{3}H). When injected into animals, the differential turnover of the two isotopes enables one to measure the rate of carbon dioxide production in free-ranging animals and hence their field metabolic rate (FMR).

Macropodids Marsupial species belonging to the family Macropodidae (large foot) which includes the kangaroos and wallabies.

Osmolality The osmotic pressure of a liquid that is a function the number of molecular components dissolved in the fluid (e.g. plasma or urine).

Water economy index (WEI) The ratio of water influx to FMR and a measure of animal's adaptation to low water regimes.

Eosinophil One type of white-blood cell and one of the immune system's components responsible for combating multicellular parasites and certain infections in vertebrates. Their numbers are often used as a measure of the competence of the animal's immune system.

Anaemia A reduction in the number of red cells in the blood, and its haemoglobin content, resulting in a lowering of the oxygen-carrying capacity of the blood.

U/P_{OSM} The ratio of the osmotic pressure of the urine relative to the plasma is a measure of the concentrating capacity of the kidney and increases when animals are water deprived.

Renal plasma flow (RPF) The rate at which blood flows through the kidneys.

Glomerular filtration rate (GFR) The rate at which blood is filtered in the kidney to produce urine. GFR is usually measured by the rate of clearance of inulin, a plant polysaccharide, and expressed as $C_{IN.}$

C_{OSM}/C_{IN} Relative osmolar clearance.

Dry sheep equivalent (DSE) The amount of energy that a marsupial requires per day compared with a similar-sized sheep. The figure of 0.7 is usually quoted and reflects the fact that the basal metabolic rate (BMR) of marsupials is approximately 30% lower than that of eutherian mammals.

'Diabetogenic' effect of steroid hormones So-called because steroids such as cortisol and corticosterone increase blood sugar levels when injected.

C_{UREA}/C_{IN} Relative urea clearance and the amount of urea cleared from the blood relative to the rate of glomerular filtration.

References

Ambrose SJ, Bradshaw SD, Withers PC, Murphy DP (1996) Water and energy balance of captive and free-ranging Spinifexbirds (Eremiornis carteri)North (Aves: Sylviidae) on Barrow Island, Western Australia. Aust J Zool 44:107–117

Angelier F, Wingfield JC (2013) Importance of glucocorticoid stress response in a changing world: theory, hypotheses and perspectives. Gen Comp Endocrinol 190:118–128

Bakker HR, Bradshaw SD (1983) Renal function in the spectacled Hare Wallaby (*Lagorchestes conspicillatus*): effects of dehydration and protein deficiency. Aust J Zool 31:101–108

Bakker HR, Bradshaw SD (1989) Water turnover and electrolyte balance of the spectacled Hare Wallaby (*Lagorchestes conspicillatus*) on Barrow Island. Comp Biochem Physiol 92A:521–529

Barboza PS, Hume ID, Nolan JV (1993) Nitrogen metabolism and requirements of nitrogen and energy in wombats (Marsupialia:Vombatidae). Physiol Zool 66:807–828

Bechtold DA, Loudon ASI (2007) Hypothalamic thyroid hormones: mediators of seasonal physiology. Endocrinology 148:3605–3607

Billiards SS, King JM, Agar NS (1999) Comparative erythrocyte metabolism in three species of marsupials from Western Australia. Comp Haematol Int 9:86–91

Bradshaw FJ, Bradshaw SD (2001) Maintenance nitrogen requirement of an obligate nectarivore, the honey possum, *Tarsipes rostratus*. J Comp Physiol B 171:59–67

Bradshaw SD (1983) Research on Rottnest Island. J Roy Soc West Aust 66:1–61

Bradshaw SD (1986) Ecophysiology of desert reptiles. Academic Press, Sydney

Bradshaw SD (1992) L'Ecophysiologie d'une île désertique en Australie: études de bilans énergétiques et homéostasie de vertébrés terrestres dans un milieu aride. Bulletin de la Société d'Ecophysiologie (Paris) 17:83–92

Bradshaw SD (1997) Homeostasis in desert reptiles. Springer, Berlin/Heidelberg

Bradshaw SD (2003) Vertebrate ecophysiology: an introduction to its principles and applications. Cambridge University Press, Cambridge

Bradshaw SD (2007) Environmental endocrinology. Gen Comp Endocrinol 152:125–141

Bradshaw SD (2010) Ecophysiology and conservation of wildlife in Western Australia. J R Soc West Aust 93:153–164

Bradshaw SD (2017) A state of non-specific tension in living matter? Stress in Australian Animals. Gen Comp Endocrinol 244:118–129

Bradshaw SD, Cheniti T, Lachiver F (1976) Echanges hydriques chez deux rongeurs désertiques, *Meriones shawii* et *Meriones libycus* étudiés dans leur environnement naturel en Tunisie. Bulletin de la Société d'Ecophysiologie (Paris) 1:30–31

Bradshaw SD, Morris KD, Bradshaw FJ (2001) Water and electrolyte homeostasis and kidney function of desert-dwelling marsupial wallabies in Western Australia. J Comp Physiol B 171:23–32

Breuner C, Delahanty B, Boonstra R (2013) Evaluating stress in natural populations of vertebrates: total CORT is not enough. Funct Ecol 27:24–36

Brown GD, Dawson TJ (1977) Seasonal variations in the body temperatures of unrestrained kangaroos (Macropodidae: Marsupialia). Comp Biochem Physiol A 56:59–67

Burbidge A (2009) Extinction, decline and recovery in Australia's terrestrial mammal fauna. In: Knott B, O'shea JE (eds) Art, science and the environment: a Festchrift for Emeritus Professor Don Bradshaw. UWA Press, Perth

Burbidge AA, Mckenzie NL (1989) Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. Biol Conserv 50:143–198

Burbidge AA, Short J, Fuller PJ (2007) Relict *Bettongia lesueur* warrens in Western Australian deserts. Aust Zool 34:97–103

Cardillo M, Bromham L (2001) Body size and risk of extinction in Australian mammals. Biol Conserv 15:1435–1439

Cooper CE, Mcallan BM, Geiser F (2005) Effect of torpor on the water economy of an arid zone marsupial, the stripe-faced dunnart (*Sminthopsis macroura)*. J Comp Physiol B 175:323–328

Dantzler WH, Bradshaw SD (2009) Reptiles. In: Evans D (ed) Osmotic and ionic regulation: cells and animals. CRC Press (Taylor & Francis Group), New York

Davis AK, Maney D, Maerz JC (2008) The use of leucocyte profiles to measure stress in vertebrates: a review for ecologists. Funct Ecol 22:760–772

Dawson TJ (1995) Kangaroos: the biology of the largest marsupials. University of New South Wales Press, Sydney

Dawson TJ, Munn A (2007) How much to kangaroos of differing age and size eat relative to domestic stock? Implications for the arid rangelands. In: Dickman CR, Lunney D, Burgin S (eds) Animals of arid Australia: out on their own. Sydney, Royal Zoological Society of New South Wales

Dawson TJ, Blaney CE, Munn A, Krockenberger AK, Maloney SK (2000) Thermoregulation by kangaroos from mesic and arid habitats: influence of temperature on routes of heat loss in eastern grey kangaroos (*Macropus giganteus*) and red kangaroos (*Macropus rufus*). Physiol Biochem Zool 73:374–381

Dawson TJ, Hulbert AJ (1970) Standard metabolism, body temperature and surface areas of Australian marsupials. Am J Physiol 218:1233–1238

Dawson TJ, Mctavish KJ, Munn A, Holloway JC (2006) Water use and the thermoregulatory behaviour of kangaroos in arid regions: insights into the colonisation of rangelands in Australia by the Eastern Grey kangaroo (*Macropus giganteus*). J Comp Physiol 176:45–53

Desantis LN, Delahanty B, Weir JT, Boonstra R (2013) Mediating free glucocorticoid levels in blood of vertebrates: are corticosteroid-binding proteins always necessary? Funct Ecol 27:107–119

Dickman CR, Haythornthwaite AS, Mcnaught GH, Mahon PS, Tamayo B, Letnic M (2001) Population dynamics of dasyurid marsupials in arid central Australia: a 10-year study. Wildl Res 28:493–506

Ealey EHM (1967) Ecology of the euro, *Macropus robustus* (Gould) in North-Western Australia. CSIRO Wildl Res 12:67–80

Ealey EHM, Main AR (1967) Ecology of the euro, *Macropus robustus* (Gould) in North-Western Australia. III seasonal changes in nutrition. CSIRO Wildl Res 12:53–65

Fisher DO, Blomberg SO, Owens IPF (2003) Extrinsic vs intrinsic factors in the decline and extinction of Australian marsupials. Proc R Soc Biol Sci Ser B 270:1801–1808

Ford SS, Bradshaw SD (2006) Kidney function and the rôle of arginine vasotocin (AVT) in three agamid lizards from differing habitats in Western Australia. Gen Comp Endocrinol 147:62–69

Fuller A, Hetem RS, Maloney SK, Mitchell D (2014) Adaptation to heat and water shortage in large, arid-zone mammals. Physiology 29:159–167

Geiser F (2003) Thermal biology and energetics of carnivorous marsupials. In: Jones M, Dickman CR, Archer M (eds) Predators with pouches: the biology of carnivorous marsupials. CSIRO Publications, Melbourne

Geiser F (2004) The role of torpor in the life of Australian arid zone mammals. Aust Mammal 26:125–134

Geiser F, Kortner G (2010) Hibernation and daily torpor in Australian mammals. Aust Zool 35:204–215

Geiser F, Kortner G, Schmidt I (1998) Leptin increases energy expenditure of a marsupial by inhibition of daily torpor. Am J Physiol:R1627–R1632

Geiser F, Pavey CR (2007) Basking and torpor in a rock-dwelling marsupial: survival strategies in a resource-poor environment. J Comp Physiol B 177:885–892

Gould J (1863) Kangaroos, Vol. II. Reprinted as the mammals of Australia (1973). In: Dixon JM (ed) Macmillan. Macmillan, Melbourne

Green B, King D, Butler WH (1986) Water, sodium and energy turnover in free-living Perenties, *Varanus giganteus*. Aust Wildl Res 13:589–595

Green B (1997) Field energetics and water fluxes in marsupials. In: Saunders N, Hinds L (eds) Marsupial biology: recent research, new perspectives. University of New South Wales Press, Sydney

Griffiths M, Mcintosh DL, Leckie RMC (1969) The effects of cortisone on nitrogen balance and glucose metabolism in diabetic and normal kangaroos, sheep and rabbits. J Endocrinol 44:1–12

Hing S, Narayan E, Thompson RCA, Godfrey S (2014) A review of factors influencing the stress response in Australian marsupials. Conserv Physiol 2:1–17

Hume ID (1999) Marsupial nutrition. Cambridge University Press, Cambridge

Johnson CN, Isaac JL (2009) Body mass and extinction risk in Australian marsupials: the ‘critical weight range’ revisited. Austral Ecol 34:35–40

Johnstone CP, Reina RD, Lill A (2012) Interpreting indices of physiological stress in free-living vertebrates. J Comp Physiol B 182:861–879

Jones MEE, Bradshaw SD, Fergusson B, Watts R (1990) The effect of available surface water on levels of anti-diuretic hormone (lysine vasopressin) and water and electrolyte metabolism of the Rottnest Island quokka (*Setonix brachyurus*). Gen Comp Endocrinol 77:75–87

King JM, Bradshaw SD (2008) Comparative water metabolism in Barrow Island macropodid marsupials: hormonal *versus* behavioural-dependent mechanisms of body water conservation. Gen Comp Endocrinol 155:378–385

King JM, Bradshaw SD (2010) Stress in an Island kangaroo? The Barrow Island euro, *Macropus robustus isabellinus*. Gen Comp Endocrinol 167:60–67

Kinnear JE, Cockson A, Christensen P, Main AR (1979) The nutritional biology of the ruminants and non-ruminant-like mammals – a new approach. Comp Biochem Physiol 64A:357–365

Kinnear JE, Main AR (1975) The recycling of urea nitrogen by the wild tammar wallaby (*Macropus eugenii*) – a “ruminant-like” marsupial. Comp Biochem Physiol 51A:793–810

Kinnear JE, Main AR (1979) Niche theory and macropodid nutrition. J R Soc West Aust 62:65–74

Kortner G, Geiser F (2009) The key to winter survival: daily torpor in a small arid-zone marsupial. Naturwissenschaften 96:525–530

Kortner G, Geiser F (2011) Activity and torpor in two sympatric Australian desert marsupials. J Zool 283:249–256

Kortner G, Pavey CR, Geiser F (2008a) Ecological physiology of a small arid zone marsupial in relation to its thermal environment. In: Lovegrove BG, Mckechnie AE (eds) Hypometabolism in animals: hibernation, torpor and cryobiology. University of KwaZulu-Natal, Pietermaritzburg

Kortner G, Pavey CR, Geiser F (2008b) Thermal biology, torpor, and activity in free-living mulgaras in arid zone Australia during the winter reproductive season. Physiol Biochem Zool 81:442–451

Kortner G, Rojas AD, Geiser F (2010) Thermal biology, torpor use and activity patterns of a small diurnal marsupial from a tropical desert: sexual differences. J Comp Physiol B 180:869–876

Lagdon R (1988) Barrow Island environmental review: 1963–1988. West Australian Petroleum Pty. Limited, Perth

Lyman CP, Willis SS, Malan A, Wang LCH (1982) Hibernation and torpor in mammals and birds. Acadaemic Press, London

Main AR (1970) Measures of wellbeing in populations of herbivorous macropod marsupials. In: Den Boer PJ, Gradwell GR (eds) Dynamics in populations. Centre for Agricultural Publishing and Documentation, Wageningen

Main AR, Bakker HR (1981) Adaptation of macropod marsupials to aridity. In: Keast A (ed) Ecological biogeography of Australia. Dr. W. Junk, The Hague

Masters P, Dickman CR (2012) Population dynamics of *Dasycercus blythi* (Marsupialia: Dasyuridae) in central Australia: how does the mulgara persist? Wildl Res 39:419–428

Mccarron CK, Dawson TJ (1989) Thermal relations of the Macropodoidea in hot environments. In: Grigg G, Jarman P, Hume I (eds) Kangaroos, wallabies and rat-kangaroos. Sydney, Surrey Beatty & Sons

Mccarron HCK, Buffenstein R, Fanning FD, Dawson T (2001) Free-ranging heart rate, body temperature and energy metabolism in eastern grey kangaroos (*Macropus giganteus)* and red kangaroos (*Macropus rufus*) in the arid regions of South East Australia. J Comp Physiol B 171:401–411

Mcdonald IR (1977) Adrenocortical functions in marsupials. In: Stonehouse B, Gilmore D (eds) The biology of marsupials. Macmillan Press, London

Mcdonald IR, Bradshaw SD (1981) Resistance to the nitrogen-mobilising, diabetogenic action of cortisol in a small wallaby (*Setonix brachyurus*). Gen Comp Endocrinol 43:39–41

Mcdonald IR, Than KA (1976) Effect of cortisol on utilisation and hepatic release of glucose in the marsupial brush-tailed possum *Trichosurus vulpecula*. J Endocrinol 68:31–41

Mcewen BS (1998) Stress, adaptation, and disease: allostasis and allostatic load. Ann N Y Acad Sci 840:33–44

Mcewen BS, Wingfield JC (2003) The concept of allostasis in biology and biomedicine. Horm Behav 43:2–15

Mckenzie NL, Burbidge AA, Baynes A, Brereton RN, Dickman CR, Gordon GB, Gibson LA, Menkhorst PW, Robinson AC, Williams MR, Woinarski CZ (2007) Analysis of factors implicated in the recent decline of Australia's mammal fauna. J Biogeogr 34:597–611

Miller T, Bradshaw SD (1979) Adrenocortical function in a field population of a macropodid marsupial (*Setonix brachyurus*, Quoy & Gaimard). J Endocrinol 82:159–170

Mitchell D, Maloney SK, Jessen C, Laburn HP, Kamerman PR, Michell G, Fuller A (2002) Adaptive heterothermy and selective brain cooling in arid-zone mammals. Comp Biochem Physiol B-Biochem Mol Biol 131:571–585

Monod T (1973) Les Déserts. Editions Horizons de France, Paris

Morel F (1983) Regulation of kidney functions by hormones: a new approach. Recent Prog Horm Res 39:271–304

Moro D, Lagdon R (2013) History and environment of Barrow Island. Rec West Aust Mus 83:1–8

Munn A, Dawson TJ, Mcleod SR, Croft DB, Thompson MB, Dickman CR (2009) Field metabolic rate and water turnover of red kangaroos and sheep in arid rangeland: an empirically derived dry-sheep-equivalent for kangaroos. Aust J Zool 57:23–28

Munn A, Dunne C, Muller DWH, Clauss M (2013) Energy in-equivalence in Australian marsupials: evidence for disruption of the continent's mammal assemblage, or are rules meant to be broken? PLoS One 8:e57449

Murphy BP, Davies HF (2014) There is a critical weight range for Australia's declining tropical mammals. Glob Ecol Biogeogr 23:1058–1061

Murphy M, Jethwa PH, Warner A, Barrett P, Nilaweera KN, Brameld JM, Ebling FJP (2011) Effects of manipulating hypothalamic triiodothyronine concentrations on seasonal body weight and torpor cycles in Siberian hamsters. Endocrinology 153:101–112

Nagy KA (1994) Seasonal water, energy and food use by free-living, arid-habitat mammals. Aust J Zool 42:55–63

Nagy KA (2005) Field metabolic rate and body size. J Exp Biol 208:1621–1625

Nagy KA, Bradshaw SD (2000) Scaling of energy and water fluxes in free-living arid-zone Australian marsupials. J Mammal 81:962–970

Nagy KA, Girard IA, Brown TK (1999) Energetics of free-ranging mammals, reptiles, and birds. Annu Rev Nutr 19:247–277

Nagy KA, Peterson CC (1988) Scaling of water flux rate in animals. Univ Calif Publ Zool 120:1–172

Pavey CR, Geiser F (2008) Basking and diurnal foraging in the dasyurid marsupial *Pseudantechinus macdonnellensis*. Aust J Zool 56:129–135

Pen LJ, Green JW (1983) Botanical exploration and vegetational changes on Rottnest Island. In: Bradshaw SD (ed) Research on Rottnest Island. The Royal Society of Western Australia, Perth

Prosser CL, Bishop DW, Brown FA, Jahn TL, Wulff VJ (1950) Comparative animal physiology. W.B. Saunders Company, Philadelphia

Riek A, Bruggeman J (2013) Estimating field metabolic rates for Australian marsupials using phylogeny. Comp Biochem Physiol 164:598–604

Riek A, Geiser F (2014) Heterothermy in pouched mammals – a review. J Zool 292:74–85

Romero LM (2012) Using the reactive scope model to understand why stress physiology predicts survival during starvation in Galapagos marine iguanas. Gen Comp Endocrinol 176:296–299

Romero LM, Dickens MJ, Cyr NE (2009) The reactive scope model – a new model integrating homeostasis, allostasis and stress. Horm Behav 55:375–389

Sahu A (2003) Leptin signaling in the hypothalamus: emphasis on energy homeostasis and leptin resistance. Front Neuroendocrinol 24:225–253

Sapolsky RM, Romero LM, Munck AU (2000) How do corticoids influence stress responses? Integrating permissive, suppressive, stimulatory and preparative actions. Endocr Rev 21:55–89

Scherbarth F, Steinlechner S (2010) Endocrine mechanisms of seasonal adaptation in small mammals: from early results to present understanding. J Comp Physiol 180:935–952

Schmidt-Nielsen B, Schmidt-Nielsen K, Houpt TR, Jarnum SA (1956) Water balance of the camel. Am J Physiol 185:185–194

Schoech SJ, Romero LM, Moore IT, Bonier F (2013) Constraints, concerns and considerations about the necessity of estimating free glucocorticoid concentrations for field endocrine studies. Funct Ecol 27:1100–1106

Selye H (1946) The general adaptation syndrome and the diseases of adaptation. J Clin Endocrinol Metab 6:117–230

Selye H (1952) The story of the adaptation syndrome. Acta Incorporated, Montreal

Short J, Turner B (1991) Distribution and abundance of spectacled hare-wallabies and euros on Barrow Island. Wildl Res 18:421–429

Short J, Turner B (1993) The distribution and abundance of the Burrowing Bettong (Marsupialia: Macropodoidea). Wildl Res 20:525–534

Smuts DB (1935) The relationship between the basal metabolism and the endogenous nitrogen metabolism, with particular reference to the estimation of the maintenance requirement of protein. J Nutr 9:403–433

Start AN, Burbidge AA, Kendrick PG, Mckenzie NL (2013) Terrestrial mammals of the south-western Little Sandy Desert, Western Australia. Aust Mammal 35:54–64

Sterling P, Eyer J (1988) Allostasis: a new paradigm to explain arousal pathology. In: Fisher K, Reason J (eds) Handbook of life stress, cognition and health. Wiley, New York

Storr GM (1963) Estimation of dry matter intake in wild herbivores. Nature (Lond) 197:307–308

Swoap S (2008) The pharmacology and molecular mechanisms underlying temperature regulation and torpor. Biochem Pharmacol 76:817–824

Taylor CR (1970) Strategies of temperature regulation: effect on evaporation in East African ungulates. Am J Physiol 219:1131–1135

Taylor CR, Lyman CP (1972) Heat storage in running antelopes: independence of brain and body temperatures. Am J Physiol 222:114–117

Tomlinson S, Withers PC, Cooper CE (2007) Hypothermia *versus* torpor in response to cold stress in the native Australian mouse, *Pseudomys hermannsburgensis* and the introduced house mouse *Mus musculus*. Comp Biochem Physiol 148:645–650

Tomlinson S, Withers PC, Maloney SK (2014) Huddling behaviour and energetics in *Sminthopsis* spp. (Marsupialia, Dasyuridae) in response to environmental challenge. Physiol Behav 128:9–15

Walsberg GE (2003) How useful is energy balance as an overall index of stress in animals? Horm Behav 43:16–17

Warnecke L, Geiser F (2009) Basking behaviour and torpor in free-ranging *Planigale gilesi*. Aust J Zool 57:373–375

Warnecke L, Turner JM, Geiser F (2008) Torpor and basking in a small arid zone marsupial. Naturwissenschaften 95:73–78

Waterlow JC (1984) Protein turnover with special reference to man. Q J Exp Physiol 69:409–438

White RG, Hume ID, Nolan JV (1988) Energy expenditure and protein turnover in three species of wallabies (Marsupialia: Macropodidae). J Comp Physiol B 158:237–246

Withers PC (1992) Comparative animal physiology. Saunders College Publishing, Fort Worth

Woinarski CZ, Burbidge AA, Harrison PL (2015) Ongoing unraveling of a continental fauna: decline and extinction of Australian mammals since European settlement. Proc Natl Acad Sci U S A 112:4531–4540

Ecophysiology of Australian Arid-Zone Reptiles

S. Don Bradshaw

Introduction

The Australian arid zone supports a diverse lizard and snake fauna that is significantly more species-rich than that of other arid regions in the world (Pianka 1986; Morton and James 1988; Powney et al. 2010). The precise origins of this fauna are, however, still the subject of research and some dispute. There is clear evidence for a Gondwanan origin for many components of the Australian fauna, e.g., monotremes, marsupials, passerine birds, parrots, ratites and chelid turtles, but the case for lizards and snakes is less clear. The arid zone was also not always arid, and it is only since the early Miocene that it started to take its present form (Martin 2006). A case for the Gondwanan origin of agamid lizards, with a 150-million-year divergence date between Southeast Asian and Australasian agamids based on mitochondrial DNA, was made by Schulte et al. (2003). The study was criticised, however, for methodological flaws, and a reanalysis of their data, along with the addition of nuclear (c-*mos*) sequences, pushed the date of this implied separation back to approximately 30 MYA (Hugall and Lee 2004). This would make an Asian origin for the Australian agamids by rafting and island hopping plausible, as the Australasian tectonic plate approached the Asian continent. Amongst the Australian agamids, two species stand out as being basal to the radiation and much older than other groups: the chameleon dragon, *Chelosonia brunnea*, and the mountain devil, *Moloch horridus* (Hugall et al. 2008), with the latter invading the developing arid zone long before any other agamid. The current consensus is in favour of an Asian origin for the agamids, dating to the early Miocene, which was followed by an extensive adaptive radiation of the group in the arid zone. There is one group of

---

S. D. Bradshaw (✉)
School of Biological Sciences, The University of Western Australia,
Crawley (Perth), Australia
e-mail: Don.Bradshaw@uwa.edu.au

H. Lambers (ed.), *On the Ecology of Australia's Arid Zone*,
https://doi.org/10.1007/978-3-319-93943-8_6

lizards, however, where a case for Gondwanan origin is compelling: the geckos and pygopodids (Oliver and Sanders 2009; Oliver and Bauer 2011). Molecular phylogenies indicate that at least five Australian lineages of diplodactyloid gecko, with wide distributions in the arid zone, are as old or older than elapid snakes and agamids. The snake-like pygopodids appear to have radiated before Australia was occupied by snakes, and recent research suggest that the Australian elapids have evolved from primitive sea kraits (*Laticaudia*) that may have swum the sea gap from Asia and come ashore in a snake-deficient continent (Scanlon and Lee 2004; Underwood 1957).

A strong case for an Asian, rather than Gondwanan origin, can also be made for the varanid lizards (Fuller et al. 1998). Molecular analyses reveal the existence of three monophyletic clades: an African, Indo-Asian and an Indo-Australian clade. Within the Indo-Australia clade, the endemic dwarf monitors (*Odatria*) form a clade sister to the large Australian monitors (the *gouldii* group) (Ast 2001). These studies thus indicate that the squamate fauna of the Australian arid zone is composed of both old Gondwanan (geckos and pygopodids) and more recent Asian elements (agamid lizards, skinks, elapid snakes and varanids).

Despite this wide diversity displayed in their phylogenetic origins, all of the reptiles inhabiting the Australian arid zone must contend with the same environmental contingencies that characterise arid environments worldwide, viz.:

(a) High day temperatures through summer that must be tolerated, regulated, or avoided
(b) A deficiency of available free water that renders difficult
(c) The regulation of water and electrolyte balance
(d) Seasonal deficiencies of nitrogen (protein), phosphorus and energy (carbohydrate) essential for growth and reproduction

Temperature Regulation

Following the pioneering study of Cowles and Bogert on North American desert lizards (Cowles and Bogert 1944), early publications on Australian lizards in the arid zone focused on thermoregulation. The concept of 'ectotherms' with an 'eccritic' or 'preferred body temperature' (PBT), resulting from active choice on the part of the animal in a thermal gradient, was established, and early surveys compared mean body temperatures of lizards active in the field (MBT) with their PBT determined in the laboratory (Licht et al. 1966; Heatwole 1970; Bradshaw and Main 1968). Although originally thought to be an unvarying and conservative feature of the thermal biology of different reptilian taxa, detailed field studies showed that the MBT actually represents a compromise between physiological preferences and ecological opportunities (Avery 1982; Cogger 1974). Various studies aimed at measuring the accuracy of thermoregulation of arid-zone species have shown, however, that this can be quite precise. A single specimen of Australia's largest terrestrial reptile, the perentie, *Varanus giganteus*, which is widespread in the arid zone, was radio-tracked for a period of 7 days by King et al. (1989) on Barrow Island. The authors found that its body temperature during the day was relatively constant, averaging 35.8 °C when active, similar to that of other varanid species (Pianka 1986). The body temperature did not fall below 30 °C at night, however, due to the thermal buffering of its large body mass (8.8 kg).

Thermoregulatory precision in monitor lizards was studied by Christian and Weavers (1996), who developed an index of thermal exploitation (Ex), based on an earlier study on North American reptiles (Hertz et al. 1993). The Ex parameter is a ratio calculated by dividing the time that a lizard spends within its set-point range by the time available for the animal to exploit this temperature range and describes the thermoregulatory characteristics of ectotherms in a heterogeneous thermal environment. In their study of three species of varanids, Ex varied from 1.0 (perfect regulation) to negative (no thermoregulation) with the most active species, *Varanus panoptes*, being the 'better' regulator over all seasons. *Varanus gouldii*, a species whose range also extends into the arid zone, was a perfect regulator in the wet season of the year, but Ex became negative in the dry season, when all activity ceased and they remained in their burrows (Christian and Weavers 1996). A more recent attempt to correlate active body temperatures and microhabitat occupation in central Australian agamids is that of Melville and Schulte II (2001), with thermal factors playing a considerable role.

A critical question is whether arid-zone reptiles are ever forced to endure body temperatures significantly above their PBT, and, therefore, likely to induce stress responses leading to decreased fitness (Bradshaw 1997, 2017). An early analysis with a range of agamids of the genus *Ctenophorus* (then *Amphibolurus*) established that increasing aridity of the habitat was associated with MBTs significantly above the PBT, and this was attributed to the greater amount of time more arid-living species were forced to spend in high-temperature-avoidance behaviour patterns (Bradshaw 1988). This repetitive exposure to higher than 'preferred' body temperatures entrained an increased thermal resistance, measured as the critical thermal maximum (CTMax), which was lost after acclimation to laboratory conditions. Greer (1980, 1990) found that the CTMax of arid-living species of scincid lizards was also higher than that of mesic species, assuming these differences to be genetic, but the effect of acclimation was not investigated. Today, one also needs to consider the possibility of epigenetic effects (Hoppeler 2015). When considered in relation to the CTMax for each species, however, the highest body temperatures recorded in the field are invariably some 5–6 °C below the CTMax, and lizards (both in Australia and in North America) thus experience wide safety margins in the field (Huey 1982; Bradshaw 1988). Many reptiles commence 'panting' with a gaping mouth when apparently suffering from heat stress, and the panting threshold (PT) is positively correlated with the CTMax in 14 species of North American lizards (Whitfield and Livezey 1973). Panting thresholds for the few species of Australian lizards that have been studied are, however, well above the maximum body temperature ever recorded in the field (Stebbins and Barwick 1968; Heatwole 1976). Dehydration and increases in plasma osmolality, however, have a significant impact on the PT of the North American desert iguana (Dupré and Crawford 1985a) and also impact on its thermoregulation (Dupré and Crawford 1985b). Hypernatraemia (see glossary) also significantly depresses the PBT of the rock-living agamid, *Ctenophorus ornatus*, operating through the pituitary peptide hormone, arginine vasotocin (AVT) (Bradshaw et al. 2007).

So far as I am aware, there has been no study to date on the thermoregulation of any snake inhabiting the Australian arid zone. It is thus not possible to reach any conclusions regarding their thermoregulatory abilities and potential exposure to thermal stress. An early paper documented PBTs in a number of Australian snakes in the laboratory, ranging from 29.6 to 34.5 °C (Lillywhite 1980). Only one of these, the Western brown snake *Pseudonaja nuchalis*, is common in the arid zone, and its PBT was 34.0 ± 1.2 °C. Suggestions in the literature that the PBT of snakes is generically invariant (Rosen 1990) have been contested by careful studies involving telemetry. A 4-year study, for example, of the Australian blacksnake, *Pseudechis porphyriacus* (not an arid-zone species, however) showed excellent thermoregulatory capacities, maintaining a body temperature between 28 and 31 °C over a variety of seasons (Shine 1987). Available CTMax data for North American snakes also show a 6.8 °C differential when compared with maximum-recorded body temperatures in the field (Bradshaw 1988; Huey 1982), suggesting that thermal stress is never a problem. The most notable feature about snakes in the arid zone is their behavioural use of nocturnality as a means of avoiding high day temperatures (Greer 2000). Dehydration and hypernatraemia also depress the PBT by some 6–7 °C of the Western tiger snake, *Notechis scutatus* (also not an arid-zone species) operating also through AVT and lowering rates of evaporative water loss (Ladyman and Bradshaw 2003; Ladyman et al. 2003, 2006). There are some chelid species that occur in the arid zone (e.g. the flat-shelled turtle, *Chelodina steindachneri*), but nothing is known of their ecophysiology or how they survive for long periods in dry river beds (Kuchling 1999).

Water Turnover and Osmoregulation

Reptiles possess a metanephric kidney but lack the countercurrent multiplier mechanism of birds and mammals needed to elaborate an hyperosmotic urine (Dantzler and Bradshaw 2009; O’Shea et al. 1993). This renders them particularly vulnerable to significant perturbations of their *milieu intérieur* should they be faced with high electrolyte intakes or lack sufficient free water needed to excrete dietary salts (Cooper 2017). Some species possess cephalic salt-secreting glands that help in the maintenance of osmotic homeostasis (e.g. most varanids and many scincid lizards (Bradshaw 1986)), but they are absent in Australian agamids and terrestrial snakes (Saint Girons and Bradshaw 1987; Saint Girons et al. 1981).

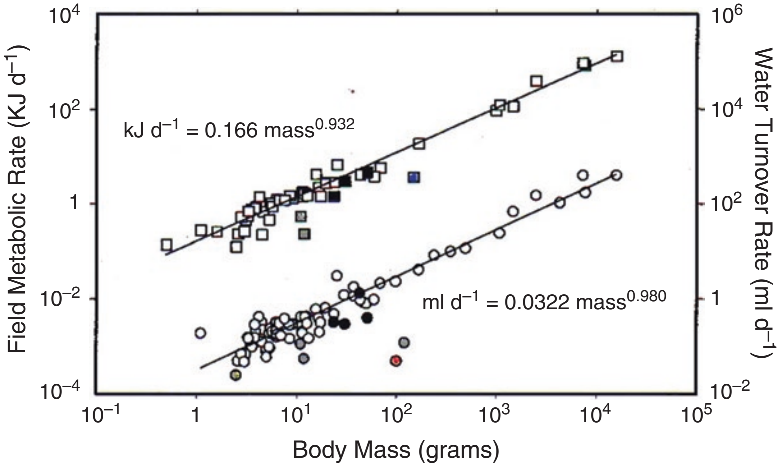


Fig. 1 Allometric relationship between body mass and field metabolic rate in kJ.d^{-1} (FMR, squares) and water turnover rate in mL.d^{-1} (circles) for semiarid- and arid-zone lizards. (Adapted from Withers and Bradshaw, 1995)

The increased availability of tritiated water and liquid scintillation counters in the 1970s and '80s led to the first measurements of rates of water turnover of free-living lizards in North America, followed soon after by those of Australian arid-zone species. When compared with rates in tropical and subtropical species, those in arid-zone species were significantly lower, reflecting their overall enhanced water economy (Nagy 1982). Water turnover increases virtually linearly with body mass, and Nagy's regression for arid-zone species of mL.d^{-1} = 20.5 kg$^{0.91}$ was updated to 32.2 kg$^{0.98}$ by Withers and Bradshaw (1995) and is close to the allometric relationship for free-ranging varanids with mL.d^{-1} = 38 kg$^{1.19}$ (Bradshaw 1997). In all three cases, the exponent of the equation does not differ significantly from 1.0 (Fig. 1).

Interspecific regression equations such as these, which are based on average values for a wide range of species, can, however, mask more subtle differences between species that may only be apparent when intraspecific regression equations are compared. A comparative study of the relationship between body mass and rate of evaporative water loss in several skinks, geckos and an agamid lizard found large and significant differences in the values of 'a' and 'b' in the allometric relationship $y = ax^b$ where y is water loss and x is body mass in grammes (Fig. 2). These data from an early preliminary study suggest that there are substantial differences in the value of the constant 'a', which represents the rate of water loss of a 1 g (or 1 kg) animal depending on the scale. The gecko *Gehyra variegata* has a very high 'a' value of 8.71 and thus will have a high rate of water loss when small, but the low value of the exponent 'b' of 0.26 means that its rate of evaporative water loss will decrease, relative to its body mass, as it grows in size. The barking gecko, *Underwoodisaurus milii*, on the other hand, with $b = 0.97$, does not benefit from any relative increase in its water economy as it grows. The agamid, *Ctenophorus*

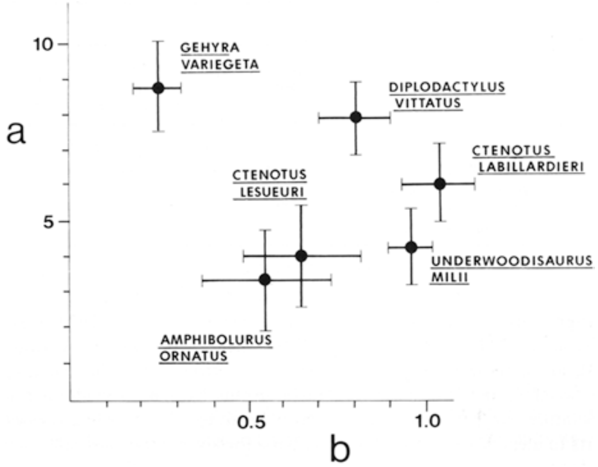


Fig. 2 A plot of mean values for 'a' and 'b' from the respective allometric equations ($y = ax^b$) describing the relationship between body mass (x) and rate of evaporative water loss (y) for six species of Australian lizards from three families. (Adapted from Bradshaw, 1986, and references therein. NB *Ctenotus lesueuri* = *C. australis*)

(formerly *Amphibolurus*) *ornatus*, is the 'best' adapted in terms of water economy, with $a = 3.16$ and $b = 0.55$, and it is evident that lizards such as *Ctenotus labillardieri* and *Diplodactylus vittatus* must, if they are to survive, restrict their movements to moist habitats because of their coupled high 'a' and 'b' values and potential for desiccation.

In the absence of a renal concentrating system, increases in water economy in reptiles can only be achieved by either reducing intake of water or by limiting losses. Under extreme conditions of salt loading, some lizards close down kidney function, cease filtering and become temporarily anuric (Bradshaw 1997), but reduction in rates of respiratory and cutaneous water loss underpins their enhanced water economy (Lillywhite 2006; Zucher 1980).

The role of the pituitary hormone arginine vasotocin (AVT) in controlling kidney function in three species of agamid lizards was investigated by Ford and Bradshaw (2006) who posited an 'adaptationist' scenario (sensu Gould and Lewontin (1979)), testing whether desert species would display enhanced renal responses to dehydration and salt loading when compared with mesic species. In fact, they found little support for this hypothesis, apart from a primarily glomerular rather than tubular response to salt loading in the mesic species, *Pogona minor*. Surprisingly, AVT levels in the desert species, *Ctenophorus nuchalis*, showed no significant correlation with changes in plasma osmolality, although increasing levels of AVT were associated with a marked antidiuresis that was both glomerular and tubular in nature. This study thus supports the conclusion that desert-living reptiles are 'exapted' rather than adapted to the exigencies characteristic of the arid zone (Bradshaw 1986, 1988).

The Western netted dragon, *Ctenophorus nuchalis*, is widespread in sandy areas of the arid zone in Australia and was the subject of a long-term ecophysiological and population study at Shark Bay in Western Australia (Bradshaw 1986). An unexpected discovery to emerge from mark-and-recapture data with this large (up

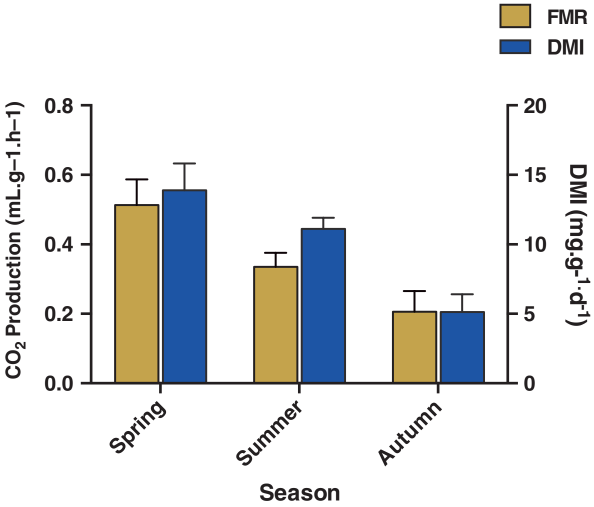


Fig. 3 Seasonal changes in field metabolic rate (FMR) measured as CO_2 production in mL.g^{-1}.h^{-1} and estimated dry matter intake (DMI) in mg.g^{-1}.d^{-1} in the Western netted dragon, *Ctenophorus nuchalis*, in Shark Bay, Western Australia. (Adapted from Nagy and Bradshaw, 1995)

to 60 g), fast-growing lizard is that it is an annual species, along with many other species in the genus. Following winter rains, they breed and lay eggs in spring, then progressively lose condition and die during summer such that, by autumn, few if any adults in the population survive and the young emerge to colonise what is an 'empty' environment (Bradshaw 1981). A detailed study of seasonal changes in body condition, with modelling of daily changes in thermoregulatory activity, established that coping with high environmental temperatures in summer precludes the lizards from feeding adequately (even though food is available) and thus leads to their demise (Bradshaw and De'ath 1991). Their gradual slide into negative water balance as summer progresses, with a corresponding catastrophic decline in field metabolic rate (FMR) and dry matter intake (DMI), measured with doubly labelled water, is shown in Fig. 3.

A closely related species, the ringtail dragon, *Ctenophorus caudicinctus*, is a rock-dweller and lives sympatrically with *C. nuchalis* in the arid Pilbara region of Western Australia. This species breeds invariably in autumn, following cyclonic rains, and a study of the two species together found that *C. nuchalis* deferred breeding in spring in some years when winter rains failed, survived the summer period and bred in autumn with *C. caudicinctus* (Bradshaw et al. 1991). This implies that the summer death seen with *C. nuchalis* at Shark Bay is a post-reproductive phenomenon, and both *C. nuchalis* and *C. caudicinctus*, like *C. fordi* (Cogger 1978), are thus semelparous species (Henle 1991; Dickman et al. 1999). The reasons why there is a breakdown in the ability to maintain homeostasis following reproduction in

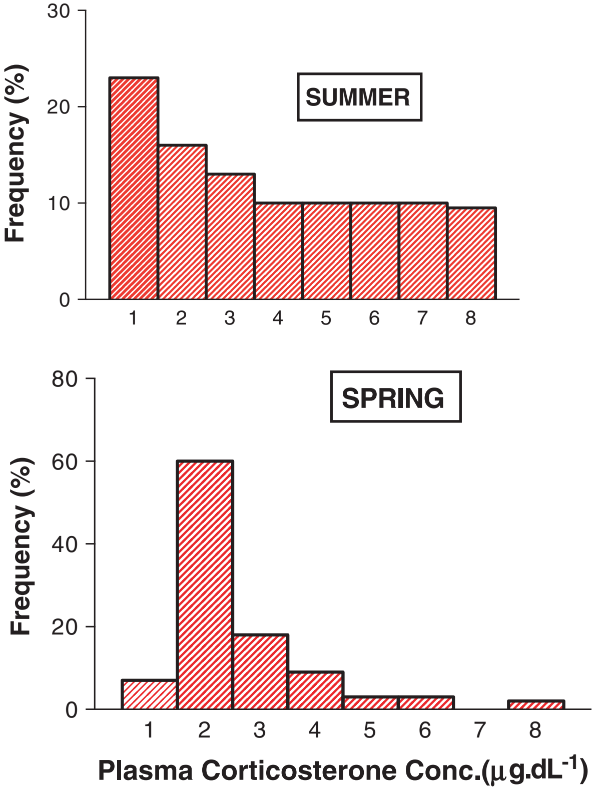


Fig. 4 Frequency distribution of plasma corticosteroid concentrations in the agamid lizard *Ctenophorus nuchalis* injected with adrenocorticotrophic hormone (ACTH) after dexamethasone blockade in spring and summer at Shark Bay in Western Australia. The aberrant, non-Gaussian response of the lizards in late summer to the ACTH challenge is evident. (Adapted from Bradshaw 1986)

these lizards is not clear, although parallels with small semelparous dasyurid marsupials are obvious (Bradley 2003). Changes in circulating levels of corticosteroid-binding globulin (CBG) and free and bound concentrations of the adrenal steroid, corticosterone, have been implicated in stress reactivity studies of the North American lizard, *Urosaurus ornatus* (Jennings et al. 2000), but have yet to be measured in these Australian species. What has been documented in *C. nuchalis* is a marked change in the normal adrenal response in spring to the stress of confinement, or injections of adrenocorticotrophic hormone (ACTH), when repeated after breeding in late summer at Shark Bay, with the majority of individuals failing to respond, whilst others show an aberrant overresponse to the stressor (Bradshaw 1997, 2017) (Fig. 4).

A number of studies have been conducted in the wet/dry tropics of Australia, using doubly-labelled water to document the energetics of agamid and varanids lizards which are very informative, linking activity, thermoregulation and foraging patterns. Two species of varanid lizards, for example, were studied along the South Alligator River in the Northern Territory of Australia and displayed divergent patterns of activity and resource exploitation (Christian et al. 1995). Rates of energy expenditure and water turnover were faster in *Varanus gouldii* than in *V. panoptes*, but levels were higher in both species in the wet/dry tropics than in other varanids, such as *Varanus giganteus* occupying the arid zone (Green et al. 1986). *Varanus gouldii*, for example, with an average water influx of 50.7 $mL.kg^{-1}.d^{-1}$, was turning over approximately 8% of its total body water content per day (TBW), compared with only 3.9% for *V. giganteus* on Barrow Island (King and Green 1999). The frilled-neck lizard, *Chlamydosaurus kingii*, is a large 600 g agamid that is common in the tropical north of Australia. It ceases activity in the dry season of the year, spending it perched on tree trunks. Rates of water turnover are rapid, as would be expected in the wet season with a mean annual rainfall of 1600 mm in Darwin, but water turnover rates fall to 13.6 $mL.kg^{-1}.d^{-1}$ in the early dry season which is only approximately 2% of the TBW per day; later in the dry season, this falls even further to 5.6 $mL.kg^{-1}.d^{-1}$ (2.9 $mL.d^{-1}$) (Christian and Green 1994). This is, however, still substantially greater than the rate of metabolic water production for a lizard of this size (ca. 0.3 $mL.d^{-1}$), showing that whilst apparently inactive, the lizards are still feeding sporadically. The only other study of an arid-living varanid is that of the small (12 g) arboreal *Varanus caudolineatus* in the Murchison region of Western Australia (Thompson et al. 1997). Water influx in summer averaged 31.6 $mL.kg^{-1}.d^{-1}$, and FMR was 0.46 mL $CO_2.g^{-1}.h^{-1}$, which enables a calculation of the 'Water Economy Index' (WEI) of 0.14 (Nagy and Peterson 1988). This is considerably less than that reported for any other varanid species.

There is a single published study of energetics and water flux rates of a free-ranging gecko, the marbled velvet gecko, *Oedura marmorata*, in both tropical regions and in central Australia (Christian et al. 1998). As would be expected, both FMR and rates of water influx are much lower in the arid population than in the geckos from the tropical locations. The FMR of arid geckos in spring was 40.1 $kJ.d^{-1}$, compared with FMRs ranging from 109.8 to 148.9 $kJ.d^{-1}$ for the tropical geckos. The authors do raise the possibility that the two populations may not in fact be from the one species, and a recent paper on the systematics of the *Oedura* complex confirms this with the arid population currently listed as *Oedura aff. Marmorata* (P Doughty pers. comm.). Rates of metabolism and water flux have been reported in the northern death adder, *Acanthophis praelongus*, again not an arid-zone species, with a similar tropical pattern of reduced rates in the dry season compared with that in the wet (Christian et al. 2007).


© Jordan Vos
© Jordan Vos
© Jordan Vos
© Jordan Vos
© Jordan Vos

Conclusion

This short review serves to highlight how little we actually know of the ecophysiology of arid-zone reptiles in Australia. Despite having a reptilian fauna that is at least three times as rich in number of species as that of other desert regions of the world, ecophysiology has been little studied, and we only have speculations and hypotheses to account for reptile abundance and diversity (Morton and James 1988; Pianka 1986, 1989, 2014; Byrne et al. 2008). Although rates of water and energy turnover of arid-zone species are slower than those occurring in tropical regions of Australia, this does not appear to be the result of any specific adaptations of the former. In fact some species, such as the semelparous lizard *Ctenophorus nuchalis,* typically 'avoid' the exigencies of the arid zone by what may be thought of as the bizarre habit of breeding and depositing eggs in spring, only to die in the oncoming summer. The population thus survives during the hottest period of the year in the egg phase, and juveniles emerge each autumn to a habitat devoid of adults. Natural selection also does not operate to enhance summer survival as the lizards are then post-reproductive. Longer-living lizards, such as the many varanids, have to survive during the summer months and, in most cases, do this by drastically reducing their activity and often retreating below ground. In common with reptiles living in other regions of the world, the reason for their abundance and diversity in desert areas is linked to their ectothermy and slow rates of resource utilisation, compared with those of birds and mammals, and better described as 'exaptations' (Gould and Vrba 1982), rather than adaptations (Bradshaw 1988).

Glossary

Ectotherm An animal that derives its body heat from an external source, such as the sun.

Eccritic or preferred body temperature (PBT) The mean body temperature maintained behaviourally by a reptile when placed in a thermal gradient.

Mean body temperature (MBT) The average body temperature of a reptile when active, which may differ from the PBT because of a lack of thermal resources.

Agamid A lizard belonging to the family Agamidae, also called dragon lizard, e.g. the ornate dragon lizard, *Ctenophorus ornatus*.

Varanid A lizard belonging to the family Varanidae, also called monitor lizards, e.g. the perentie, *Varanus giganteus*.

Index of thermal exploitation (Ex) A ratio calculated by dividing the time that a lizard spends within its set-point range by the time available for the animal to exploit this temperature range and describes the thermoregulatory characteristics of ectotherms in a heterogeneous thermal environment.

CTMax The critical thermal maximum, or highest body temperature, above which the animal is unable to recover.

FMR Field metabolic rate. The rate of metabolism of a free-ranging animal in its natural habitat measured as either the rate of oxygen consumption or carbon dioxide production, usually with the doubly-labelled water method.

Scincid A lizard belonging to the family Scincidae, also called skinks, e.g., the bobtail goanna, *Tiliqua rugosa*.

Vasotocin (AVT, arginine vasotocin) A peptide hormone released from the posterior lobe of the pituitary gland of reptiles that enhances water reabsorption from the kidney and also lowers the PBT.

Hypernatraemia An increase in the concentration of sodium ions in the blood above normal hydrated levels.

PT (panting threshold) The body temperature at which some lizards open their mouth (gape) and increase their respiratory rate (panting).

Metanephric kidney The structurally more complex kidney of higher vertebrates, which in the case of birds and mammals, is capable of producing an hyperosmotic urine (i.e. one with an osmotic pressure greater than the plasma).

Cephalic salt glands Specialised glands found in many reptiles that assist in osmoregulation by secreting a concentrated salt solution rich in either sodium or potassium. All are located in the head (nose, eye or tongue) and hence called ‘cephalic’.

Anuric Ceasing to produce urine; seen in many lizards when feeding on diets rich in salt.

Semelparous Animals, such as salmon, that die after breeding only once. Named after the unfortunate Semelae, mother of Bacchus, who succumbed after a night of passion with the Greek God Zeus.

References

Ast JC (2001) Mitochondrial DNA evidence and evolution in Varanoidae (Squamata). Cladistics 17:211

Avery RA (1982) Field studies of body temperature temperatures and thermoregulation. In: Gans C, Pough FH (eds) Biology of the Reptilia. Academic Press, New York, pp 211–226

Bradley AJ (2003) Stress, hormones and mortality in small carnivorous marsupials. In: Jones ME, Dickman CR, Archer M (eds) Predators with pouches: the biology of carnivorous marsupials. CSIRO, Collingwood

Bradshaw SD (1981) Ecophysiology of Australian desert lizards: studies on the genus *Amphibolurus*. In: Keast A (ed) Biogeography and ecology in Australia. Junk, Den Haag

Bradshaw SD (1986) Ecophysiology of desert reptiles. Academic Press, Sydney

Bradshaw SD (1988) Desert reptiles: a case of adaptation or pre-adaptation? J Arid Environ 14:155–174

Bradshaw SD (1997) Homeostasis in desert reptiles. Springer, Berlin/Heidelberg

Bradshaw SD (2017) A state of non-specific tension in living matter? Stress in Australian animals. Gen Comp Endocrinol 244:118–129

Bradshaw SD, De’ath G (1991) Variation in condition indices due to climatic and seasonal factors in an Australian desert lizard, *Amphibolurus nuchalis*. Aust J Zool 39:373–385

Bradshaw SD, Main AR (1968) Behavioural attitudes and regulation of temperature in *Amphibolurus* lizards. J Zool (Lond) 154:193–221

Bradshaw SD, Saint Girons H, Bradshaw FJ (1991) Patterns of breeding in two species of agamid lizards in the arid sub-tropical Pilbara region of Western Australia. Gen Comp Endocrinol 82:407–424

Bradshaw SD, Ladyman M, Stewart T (2007) Effect of hypernatraemia and the neurohypophysial peptide, arginine vasotocin (AVT), on behavioural thermoregulation in the agamid lizard, *Ctenophorus ornatus*. Gen Comp Endocrinol 150:34–40

Byrne M, Yeates DK, Joseph L, Kearney M, Bowler J, Williams AJ, Cooper S, Donnellan SC, Keogh S, Leys R, Melville J, Murphy DJ, Porch N, Wyrwoll KH (2008) Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. Mol Ecol 17:4398–4417

Christian KC, Green B (1994) Seasonal energetics and water turnover of the Frillneck Lizard, *Chlamydosaurus kingii*, in the wet-dry tropics of Australia. Herpetologica 50(3):274–281

Christian KA, Weavers BW (1996) Thermoregulation of monitor lizards in Australia: an evaluation of methods in thermal biology. Ecol Monogr 66(2):139–157

Christian CS, Corbett LK, Green B (1995) Seasonal activity and energetics of two species of varanid lizards in tropical Australia. Oecologia 103:349–357

Christian K, Bedford GS, Green B, Schultz T, Newgrain K (1998) Energetics and water flux of the marbled velvet gecko (*Oedura marmorata)* in tropical and temperate habitats. Oecologia 116:336–342

Christian K, Webb JK, Schultz T, Green B (2007) Effects of seasonal variation in prey abundance on field metabolism, water flux, and activity of a tropical ambush foraging snake. Physiol Biochem Zool 80:522–533

Cogger HG (1974) Thermal relations of the mallee dragon, *Amphibolurus fordii* (Lacertilia: Agamidae). Aust J Zool 22:319–339

Cogger HG (1978) Reproductive cycles, fat body cycles, and sociosexual behaviour in the Mallee dragon, *Amphibolurus fordi* (Lacertilia: Agamidae). Aust J Zool 26:653–672

Cooper CE (2017) Endocrinology of osmoregulation and thermoregulation of Australian desert tetrapods: a historical perspective. Gen Comp Endocrinol 244:186–200

Cowles RB, Bogert CM (1944) A preliminary study of the thermal requirements of desert reptiles. Bull Am Mus Nat Hist 83:265–296

Dantzler WH, Bradshaw SD (2009) Reptiles. In: Evans D (ed) Osmotic and ionic regulation: cells and animals. CRC Press (Taylor & Francis Group), New York

Dickman CR, Letnic M, Mahon PS (1999) Population dynamics of two species of dragon lizards in arid Australia: the effect of rainfall. Oecologia 119:357–366

Dupré KR, Crawford EC (1985a) Control of panting in the desert iguana: roles for peripheral temperatures and the effect of dehydration. J Exp Zool 235:341–347

Dupré RK, Crawford EC (1985b) Behavioral thermoregulation during dehydration and osmotic loading of the desert iguana. Physiol Zool 58:357–363

Ford SS, Bradshaw SD (2006) Kidney function and the rôle of arginine vasotocin (AVT) in three agamid lizards from differing habitats in Western Australia. Gen Comp Endocrinol 147:62–69

Fuller S, Baverstock PR, King D (1998) Biogeographic origins of goannas (Varanidae): a molecular perspective. Mol Phylogenet Evol 9:294–307

Gould SJ, Lewontin RC (1979) The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proc R Soc Lond B 205:581–598

Gould SJ, Vrba ES (1982) Exaptation – a missing term in the science of form. Paleobiology 8:4–15

Green B, King D, Butler WH (1986) Water, sodium and energy turnover in free-living Perenties, *Varanus giganteus*. Aust Wildl Res 13:589–595

Greer AE (1980) Critical thermal maximum temperatures in Australian scincid lizards: their ecological and evolutionary significance. Aust J Zool 28:98–102

Greer AE (1990) The biology and evolution of Australian lizards. Surrey Beatty & Sons, Sydney

Greer AE (2000) The biology and evolution of Australian snakes. Q Rev Biol 75:67–68

Heatwole H (1970) Thermal ecology of the desert dragon, *Amphibolurus inermis*. Ecol Monogr 40:425–457

Heatwole H (1976) Reptile ecology. University of Queensland Press, Queensland

Henle K (1991) Life history patterns in lizards of the arid and semiarid zone of Australia. Oecologia 88:347–358

Hertz PE, Huey RB, Stevenson RD (1993) Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. Am Nat 142:796–818

Hoppeler H (2015) Epigenetics in comparative physiology. J Exp Biol 218:6

Huey RB (1982) Temperature, physiology, and the ecology of reptiles. In: Gans C, Pough FH (eds) Biology of the Reptilia. Academic Press, New York

Hugall AF, Lee SY (2004) Molecular claims of Gondwanan age for Australian agamid lizards are untenable. Mol Biol Evol 21:2102–2110

Hugall AF, Foster R, Hutchinson M, Lee SY (2008) Phylogeny of Australasian agamid lizards based on nuclear and mitochondrial genes: implications for morphological evolution and biogeography. Biol J Linn Soc 93:343–358

Jennings DH, Moore MC, Knapp R, Matthews L, Orchinick M (2000) Plasma steroid-binding globulin mediation of differences in stress reactivity in alternate male phenotypes in tree lizards, *Urosaurus ornatus*. Gen Comp Endocrinol 120:289–299

King D, Green B (1999) Goannas. UNSW Press, Sudney

King D, Green B, Butler H (1989) The activity pattern, temperature regulation and diet of *Varanus giganteus* on Barrow Island, Western Australia. Wildl Res 16:41–47

Kuchling G (1999) The reproductive biology of the Chelonia. Springer, Heidelberg

Ladyman M, Bradshaw SD (2003) The influence of dehydration on the thermal preferences of the Western Tiger snake, Notechis scutatus. J Comp Physiol B 173:239–246

Ladyman M, Bradshaw SD, Bradshaw FJ (2003) Hypernatraemia and its effect on temperature regulation and levels of the hormone aginine vasotocin in the Western Tiger snake, *Notechis scutatus*. J Comp Physiol B

Ladyman MT, Bradshaw SD, Bradshaw FJ (2006) Physiological and hormonal control of thermal depression in the Tiger snake, *Notechis scutatus*. J Comp Physiol B 176:547–557

Licht P, Dawson WR, Shoemaker VH, Main AR (1966) Observations on the thermal relations of Western Australian lizards. Copeia 1966:97–110

Lillywhite HB (1980) Behavioural thermoregulation in Australian elapid snakes. Copeia 1980:452–458

Lillywhite H (2006) Water relations of tetrapod integument. J Exp Biol 209:200–226

Martin HA (2006) Cenozoic climatic change and the development of the arid vegetation in Australia. J Arid Environ 66:533–563

Melville J, Schulte Ii JA (2001) Correlates of active body temperatures and microhabitat occupation in nine species of central Australian agamid lizards. Austral Ecol 26:660–669

Morton SR, James CD (1988) The diversity and abundance of lizards in arid Australia: a new hypothesis. Am Nat 132:237–256

Nagy KA (1982) Field studies of water relations. In: Gans C, Pough H (eds) Biology of the Reptilia. Academic Press, New York

Nagy KA, Bradshaw SD (1995) Energetics, osmoregulation and food consumption by free-living desert lizards, *Ctenophorus (=Amphibolurus) nuchalis*. Amphibia-Reptilia 16:25–35.

Nagy KA, Peterson CC (1988) Scaling of water flux rate in animals. Univ Calif Publ Zool 120:1–172

Oliver PM, Bauer AM (2011) Systematics and evolution of the Australian knobtail geckos (*Nephrurus,* Carphodactylidae, Gekkota): pleisomorphic grades and progressive biome shifts through the Miocene. Mol Phylogenet Evol 59:664–674

Oliver PM, Sanders KL (2009) Molecular evidence for Gondwanan origins of multiple lineages within a diverse gecko radiation. J Biogeogr 36:2044–2055

O'shea JE, Bradshaw SD, Stewart T (1993) The renal vasculature and excretory system of the agamid lizard *Ctenophorus ornatus*. J Morphol 217:287–299

Pianka ER (1986) Ecology and natural history of desert lizards. Princeton University Press, Princeton

Pianka E (1989) Desert lizard diversity: additional comments and some data. Am Nat 134:344–364

Pianka E (2014) Rarity in Australian desert lizards. Austral Ecol 13:214–224

Powney GD, Grenyer, Orme CDL, Owens IPF, Meiri S (2010) Hot, dry and different: Australian lizard richness is unlike that of mammals, amphibians and birds. Glob Ecol Biogeogr 19:386–396

Rosen PC (1990) Comparative field study thermal preferenda in garter snakes (*Thamnophis*). J Herpetol 25:301–312

Saint Girons H, Bradshaw SD (1987) Aspects of variation in histology and cytology of the external nasal glands of Australian lizards. J R Soc West Aust 69:117–121

Saint Girons H, Rice GE, Bradshaw SD (1981). Histologie comparée et ultrastructure de la glande nasale externe de quelques Varanidae (Reptilia, Lacertilia). Annales Scientifiques et Naturelles en Zoologie de Paris, 3, 13ème Ser.:15–21

Scanlon JD, Lee MSY (2004) Phylogeny of Australasian venomous sea snakes (Colubridae, Elapidae, Hydrophiinae) based on phenotypic and molecular evidence. Zool Scr 33:335–366

Schulte J, Melville J, Larson A (2003) Molecular phylogenetic evidence for ancient divergence of lizard taxa on either side of Wallace's line. Proc R Soc Lond B 270:597–603

Shine R (1987) Intraspecific variation thermoregulation, movements and habitat use by Australian blacksnakes, *Pseudechis porophyriacus* (Elapidae). J Herpetol 21:165–177

Stebbins RC, Barwick RE (1968) Radiotelemetric study of thermoreulation in a lace monitor. Copeia 1968:541–547

Thompson GG, Bradshaw SD, Withers PC (1997) Energy and water turnover rates of a free-living and captive goanna, *Varanus caudolineatus* (Lacertilia: Varanidae). Comp Biochem Physiol 116A:105–111

Underwood G (1957) On lizards of the family Pygopodidae: a contribution to the morphology and phylogeny of the Squamata. J Morphol 100:207–268

Whitfield CL, Livezey RL (1973) Thermoregulatory patterns in lizards. Physiol Zool 46:285–296

Withers PC, Bradshaw SD (1995) Water and energy balance of the mountain devil *Moloch horridus*: is the devil a sloth? Amphibia-Reptilia 16:47–54

Zucher A (1980) Procedural and anatomical considerations of the determination of cutaneous water loss in reptiles. Copeia 1980:425–439

The Evolution, Physiology and Ecology of the Australian Arid-Zone Frog Fauna

J. Dale Roberts and Danielle Edwards

Introduction

The Australian arid zone seems like an odd location for a discussion of a frog fauna. Aridity and frogs do not obviously mix, as irrespective of developmental mode, all anurans are dependent on water for egg and larval development. Even frogs with internal or underground egg development (e.g. now extinct *Rheobatrachus* (gastric-brooding frogs) and *Myobatrachus* (turtle frogs) – both from Australia – see Anstis 2013) require at the very least moist conditions, if not for reproduction, for adult survival. Despite this, the arid-zone frog fauna is diverse. To date, 52 species have been recorded in the "Deserts and Xeric Shrublands" Terrestrial Ecoregion (https://www.environment.gov.au/land/nrs/science/ibra/australias-ecoregions) – the region most Australians would consider as desert (Table 1, Appendix 1). That claim and the data in Table 1 are based on data records in the "Atlas of Living Australia" database. We recognise those data are incomplete compared with sampling in more mesic areas (cf. Slatyer et al. 2007), so the data in Table 1 represent a minimum estimate of species composition, but likely a fairly complete one given that (a) many species are widespread, e.g. *Neobatrachus sudelli* (Sudell's frog, Roberts 2010), *Dryopsophus occidentalis* (Western water-holding frog) and *D. platycephalus* (water-holding frog, Anstis et al. 2016), and (b) the restricted species are mostly confined to known sites of water availability, e.g. *Pseudophryne robinsoni* (Central Ranges toadlet) in north-western South Australia (Donnellan et al. 2012b).

J. D. Roberts (✉)
Centre of Excellence in Natural Resource Management, The University of Western Australia, Albany, WA, Australia

School of Biological Sciences, The University of Western Australia, Albany, WA, Australia
e-mail: dale.roberts@uwa.edu.au

D. Edwards
Life and Environmental Sciences, University of California, Merced, CA, USA
e-mail: dedwards5@ucmerced.edu

H. Lambers (ed.), *On the Ecology of Australia's Arid Zone*,
https://doi.org/10.1007/978-3-319-93943-8_7

Table 1 Arid zone frog diversity – Australia. Burrowing refers to species that are independently capable of burrowing outside the breeding season which excludes species in the genera *Pseudophryne* and *Uperoleia* (see text for details)

	Non-burrowing	Burrowing
Hylidae		
Litoria	8	0
Dryopsophus	3	11
Myobatrachidae		
Crinia	3	0
Limnodynastes	3	0
Neobatrachus	0	7
Notaden	0	3
Platyplectrum	0	2
Pseudophryne	5	0
Uperoleia	6	0

So why have frogs been so successful in a seemingly inhospitable environment? The arid zone is not always dry, and unlike common perceptions of what a desert is, in the Australian desert region, water is commonly or occasionally available for anuran breeding. Small, permanent water sources can occur in many inland range systems (e.g. the McDonnell, Everard and Flinders Ranges). In some regions of the arid zone, smaller rock outcrops (e.g. granite outcrops) may also focus drainage into quite small, persistent but not permanent, water bodies that support localised frog populations. Larger, more permanent river systems also occur within major drainage systems of the Pilbara Craton. There are several major western flowing river systems in Queensland and South Australia (e.g. Cooper's Creek) which derive water from rainfall as far east as the Great Dividing Range. These river systems may also gain sufficient water from local rainfall, as occurred in 2016, to flood normally dry, salt lake systems, like Lake Eyre. Sources of water also frequently come from locally intense rainfall. For example, during the summer months, cyclonic rains cross the Pilbara coast and move inland with ongoing major inland rainfall events. These cyclonic events may also move as far south as the Western Australian goldfields, and down to the south coast between Esperance and the Nullarbor Plain. In addition to cyclonic rain, significant local rainfall may come from local thunderstorm activity. These storms typically occur during summer and may generate sufficient rain to flood local drainage systems or depressions.

Water is not necessarily a limiting resource for arid-zone frogs in Australia, and this is reflected in the diversity of species found across the Australian arid zone. Australian frogs fall into two families: Myobatrachidae (ground frogs, with subfamilies Myobatrachinae, Australian froglets or toadlets, and Limnodynastinae, Australian ground frogs) and the Hylidae (tree frogs). Species in both families are found across the Australian arid zone in a diverse array of habitats. We use the "Deserts and Xeric Shrublands" ecoregion as outlined by the IBRA classification of Australian ecoregions (https://www.environment.gov.au/land/nrs/science/ibra/australias-ecoregions) as the definition and spatial extent of the arid zone for the purposes of this review (Appendix 1). We also use the list of frog species compiled within the Atlas of Living Australia database to determine which frog species occur within the arid zone. These records have been edited to remove obvious errors. For example, Global Biodiversity Information Facility records that place many Australian localities just north of the Northern Territory/South Australia border, or in Western Australia at close to Wiluna – "geographic centres" of the continent or state respectively; site descriptions close to the New South Wales coast – that include latitude and longitude data in the arid zone that are incompatible with the site description. One Interim Biogeographic Regionalisation for Australia (IBRA) region, the Flinders Lofty Block, extends into the Mount Lofty ranges near Adelaide, well outside arid regions. In this region we excluded records from subregions FLB01 and FLB02 and marginal records *for Limnodynastes dumerili* (Eastern banjo frog), *Crinia signifera* (Common eastern froglet) and *Litoria ewingi* (Brown tree frog) that fall just outside FLB01 and FLB02. These exclusions roughly mark the southern margin of the arid zone in South Australia as recognised early by Goyder's Line, demarcated in the early 1860s. North of the line, rainfall is low, unpredictable and generally unsuitable for agriculture, and most temperate-zone frog species (see http://www.southaustralianhistory.com.au/goyder.htm)!

None of the frog genera in the arid zone are endemic to the region, with all genera having related, often sister species, in adjacent temperate or tropical regions, but rarely both. While, representatives of the two major Australian frog families are represented within arid regions, no species from the families Microhylidae (narrow-mouthed frogs) or Ranidae (true frogs), both tropical lineages in Australia (Cogger 2014), have distributions, which extend into desert regions. In summary, Australia currently has 241 named frog species and roughly 20% of known frog species occur in the arid zone.

The suite of frogs whose distributions occur exclusively within, or extend into the Australian arid zone, includes several genera with species whose adults are able to persist, but not breed, independent of free water. Many species that live within the Australian arid zone have evolved unique adaptations to survive between sporadic rain events. Several genera form waterproof cocoons (*Neobatrachus*, *Dryopsophus* and *Platyplectrum*), while others rely solely on soil moisture for survival obtained by burrowing into moist soils (*Notaden*). Several other genera survive by using available moisture around breeding sites, with no described special adaptations or behaviours to reduce water loss (*Uperoleia*, *Pseudophryne*, *Dryopsophus*, *Litoria* and *Crinia*).

We discuss the Australian arid-zone frog fauna in six contexts. We detail (1) the biogeography of arid-zone taxa (what are they related to, how old are they and when did they evolve); (2) the physiology of anurans surviving in truly desert regions (which adaptations have evolved to reduce or eliminate water loss); (3) how anurans avoid water loss in arid regions without special structural adaptations; (4) the natural history and population biology of the arid-zone frog fauna (Why so many? Is it what they eat?); (5) the evolution of call structures and speciation of arid-zone frogs in the genera *Neobatrachus* and *Uperoleia* (What does an extra set of chromosomes do to a frog's call?); and (6) what are the conservation issues specific to arid Australian

Fig. 1 Arid zone frogs and frog breeding sites. (All photos by JD Roberts)
1. *Uperoleia glandulosa*, Port Hedland. 2. *Dryopsophus maini*, Port Hedland. 3. *Neobatrachus fulvus*, Exmouth. 4. Petermarer Creek, Port Hedland, 48 h after cyclonic rain. 5. Millstream, Pilbara – permanent, arid zone water. *Uperoleia saxatilis* was breeding in shallow drains and flooded, vegetated areas adjacent to this major spring and pool system. 6. Pool formed by run-off from Hospital Rocks – a granite outcrop, about 90 km west south west of Menzies. Silver circle is a lens cap just above water level – the zone where several *Pseudophryne occidentalis* were calling from breeding burrows. 7. *Notaden nichollsi*, Pt Hedland. 8. *Neobatrachus aquilonius*, Pt Hedland. 9. A “cocooned” specimen of *Neobatrachus kunapalari* from the wheatbelt, Western Australia

anurans – why have arid-zone frogs apparently evaded the current global anuran decline? Figure 1 gives an introduction to the arid-zone frog fauna and the sites they use for breeding.

Frog Fauna of the Australian Arid Zone

Evolution and Biogeography of the Arid-Zone Frog Fauna

Biogeographic and phylogenetic studies on the arid-zone frog fauna are limited for most groups but, in some genera, are extensive. The discussion that follows is based on mostly recent analyses of relationships using a variety of DNA sequence data.

Data for *Uperoleia* are comparatively robust using both nuclear and mitochondrial markers (e.g. Catullo and Keogh 2014). The data for *Litoria and Dryopsophus* species are based on a recent, very extensive data set using multiple markers, the most extensive data set accumulated to date, covering all Hylid frogs across the globe (Duellman et al. 2016). Some other data sets are based on a single gene, often a single mitochondrial DNA marker for a limited set of taxa (e.g. Donnellan et al. 2012b; Anstis et al. 2016), but we note the potential for "cross species" capture of mitochondria that may confound interpretation of this type of data (cf. Catullo and Keogh 2014).

Diversity and Biogeography of Arid-Zone Uperoleia *Species*

In the genus *Uperoleia*, the most species-rich myobatrachid genus with 25 species, several species occur in the Pilbara, Western Australia. *Uperoleia saxatilis* (Pilbara toadlet) and *U. glandulosa* (glandular toadlet) occur widely in the permanently wet drainages of the Pilbara Craton but extend onto the Pilbara coastal plain (Catullo et al. 2011; Catullo and Keogh 2014). *Uperoleia saxatilis* occurs on the Ashburton and De Grey River drainages, with its sister taxon, *U. russelli* (Russell's toadlet), on the Gascoyne coast on the Lyndon to Wooramel River drainages. Using molecular clocks, Catullo and Keogh (2014) estimated a divergence date of 1.55 million years before present (mybp) for this species pair placing it in the mid to early Pleistocene. The Pleistocene had multiple "glacial" phases, but the probable impact on the Pilbara coast was reduced rainfall, cooler climates and an exposed north-west shelf due to lower sea levels, further isolating drainage systems in areas of higher relief that were then further inland (Byrne et al. 2008; Pillans 2018). In turn, this species pair split from a five species clade that now occurs across northern Australia, with divergence amongst species distributed throughout the Kimberley to the Gulf of Carpentaria occurring around 5.65 mybp in the late Pliocene during a period of declining rainfall, cooling climates but also frequent rapid climate variation between wet and dry conditions (Byrne et al. 2008; Pillans 2018).

Uperoleia talpa (mole toadlet) occurs on the Pilbara coast, but its range extends, not east into the Pilbara or the Great Sandy Desert, but north along the coast into the west Kimberley (Catullo et al. 2011; Catullo and Keogh 2014). *Uperoleia talpa* is widespread in the Broome, Derby and Fitzroy Crossing region but apparently has a very narrow, coastal range further south, with records in the Port Hedland area and at Mandora further northeast. *Uperoleia micromeles* (Tanami toadlet) also occurs north of Port Hedland, but its range extends not north, but east, into the Great and Little Sandy Deserts and the Tanami Desert in central Australia (Catullo et al. 2011; Catullo and Keogh 2014; Morton et al. 1993).

The closest relatives of all arid-zone *Uperoleia* species and lineages in the western deserts and west coast are in the Kimberley with divergence dates ranging from ≈ 2.6 to 9 mybp (Catullo and Keogh 2014). The current extensions of species distributions across the 90 Mile Beach arid gap (between Port Hedland and Broome)

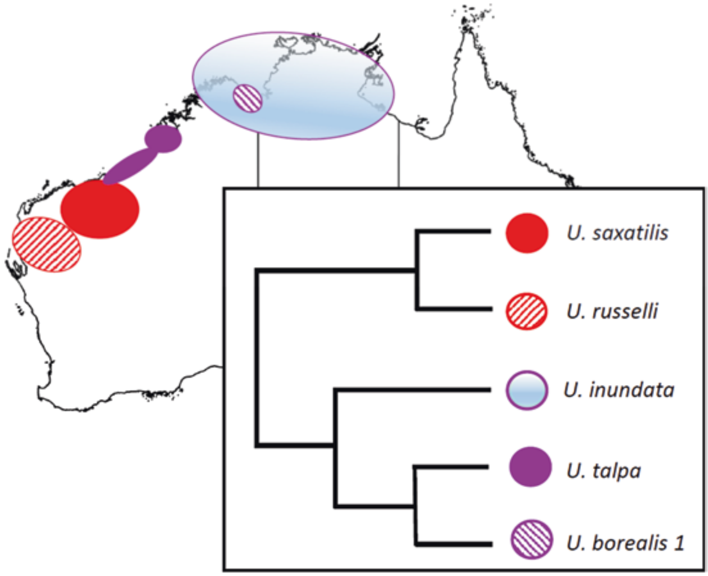


Fig. 2 Distribution and relationships of arid zone and tropical species of *Uperoleia*: *U. saxatilis* and *U. russelli* are sister taxa related to three Kimberley species, *U. inundata*, *U. talpa* and *U. borealis*. *Uperoleia talpa* illustrates the ongoing potential for dispersal from the west Kimberley to the Pilbara region. Text has further details. See Catullo et al. (2011) and Catullo and Keogh (2014) for supporting data

into the coastal Pilbara for some west Kimberley *Uperoleia* species (see above) suggest a simple model for derivation of older, Pilbara-specific species: range expansion into wetter drainages in the Pilbara followed by isolation during more arid periods leading to the formation of current *Uperoleia* Pilbara lineages. Desert *Uperoleia* species came out of the tropics. Tropical species are a major part of the diversity in this genus, which also has many species along the eastern coast of Australia as far south as Gippsland in eastern Victoria. Paradoxically, *Uperoleia* is the sister clade to the south-western Australian, monotypic genus, *Spicospina* (Sunset frog) with a divergence date estimated at 26 million years (Catullo and Keogh 2014) reflecting the long isolation of south-western Australia (Rix et al. 2015; Pillans 2018). Distribution and relationships of representative *Uperoleia* species occurring in the arid zone are given in Fig. 2.

Diversity and Biogeography of Arid-Zone Platyplectrum *Species*

Some arid-zone frog lineages are very old – dating back to the early Paleocene. *Platyplectrum spenceri* (Spencer's burrowing frog) was named in honour of Baldwyn Spencer, an early arid-zone naturalist and foundation Professor of Biology at the University of Melbourne. This species shares a most recent common ancestor with the lineage containing *Lechriodus fletcheri* (Fletcher's frog) and *Platyplectrum ornatum* (ornate burrowing frog), the former a rainforest species found on the Queensland/New South Wales border region, the latter found across tropical northern Australia and into northern New South Wales (Pyron and Wiens 2011; Cogger 2014). Pyron and Wiens (2011) showed that *L. fletcheri* and *P. ornatum* are sister species with the desert taxon, *P. spenceri* evolving earlier. Forget the confused taxonomy (they may well end up in one genus): this spatial pattern shares some clear elements with *Uperoleia*. In both cases the derived taxon has a broad distribution in the arid interior with a range from the west coast to central Australia, as for *U. micromeles*, but *P. spenceri* can also (a) burrow and (b) form waterproof cocoons when buried (Lee and Mercer 1967 – see below), and this may have been a critical step in surviving a drying continental interior – drying from the middle Miocene (Byrne et al. 2008; Pillans 2018) for frogs in a lineage derived in the early Tertiary close to 60 million years ago (age discussed as *Limnodynastes spenceri* by Roberts and Maxson 1986).

Diversity and Biogeography of Arid-Zone **Neobatrachus** *Species*

We know considerably less about the evolution of some arid-zone genera. *Neobatrachus* has a total of nine species: four occur outside the arid zone (*N. pictus* – painted frog): south and south-eastern Australia primarily in areas with a Mediterranean climate), or in south-western Australia, *N. pelobatoides* (humming frog), *N. kunapalari* (Kunapalari frog) and *N. albipes* (White-footed frog: distribution maps in Cogger 2014). Three species in this genus are tetraploid, *N. sudelli*, *N. aquilonius* (northern burrowing frog) and *N. kunapalari* (Roberts 1997a), but this is not associated with arid-zone success. Arid-zone species include three diploids, *N. sutor* (Shoemaker frog), *N. wilsmorei* (Goldfields bullfrog) and *N. fulvus* (Tawny frog), along with two of the tetraploids (*N. aquilonius* and *N. sudelli*, though the latter also extends into western Victoria and the south-east of South Australia – well outside the arid zone). The range of *N. kunapalari* is primarily the Western Australian wheatbelt – a region with reliable winter rainfall. There is some evidence *N. kunapalari* hybridises with *N. sudelli* where their ranges meet near Menzies (Roberts 1997b) and north of Wubin (M.J. Mahony, pers. comm.) in Western Australia.

The genus *Neobatrachus* has five species occurring exclusively in, or with the majority of their range in, the arid zone (*N. aquilonius*, *N. fulvus*, *N. sudelli*, *N. sutor*, *N. wilsmorei*) but only four largely confined to areas with a Mediterranean climate (*N. albipes*, *N. kunapalari* and *N. pelobatoides* in south-western Australia, with *N. pictus* in South Australia and western Victoria). The relationships of *Neobatrachus* species are not well resolved. *Neobatrachus sutor* and *N. wilsmorei* are sister taxa (Mable and Roberts 1997; Mahony et al. 1996) consistent with speciation within the arid zone, but unlike arid-zone speciation in *Pseudophryne* and *Crinia*, these two *Neobatrachus* species are broadly sympatric, and both co-occur with *N. fulvus*. *Neobatrachus fulvus* (a diploid species – Northwest Cape to about Carnarvon) and *N. aquilonius* (Pilbara to the Kimberley) are also sister taxa, but in this case the tetraploid occurs north of the range of the diploid. In some contacts between diploid and tetraploid species, there is evidence of complex patterns of gene exchange and hybridisation (Mahony et al. 1996; Roberts 1997b).

The impact of polyploidy on call structure evolution and as a contributor to speciation in this genus is discussed below.

Diversity and Biogeography of Arid-Zone **Pseudophryne** *Species*

Arid-zone species in this genus include *P. robinsoni* (Central Ranges toadlet), which occurs in the Everard and Musgrave Ranges, and *P. douglasi* (Douglas's toadlet) in the Pilbara and Cape range at Exmouth. These two species are sister taxa to *P. bibroni* (brown toadlet) from south and eastern Australia, but are not directly related to either of the *Pseudophryne* species found in south-western Australia (*P. guentheri*, Günther's toadlet, and *P. occidentalis*, Orange-crowned toadlet) (Donnellan et al. 2012b). The third arid-zone species, *P. occidentalis*, occurs from the eastern wheatbeIt in south-western Australia into the desert, almost extending to meet the range of *P. robinsoni*, in central Australia (Donnellan et al. 2012b). *Pseudophryne occidentalis* is most closely related to the broadly distributed, south-western species, *P. guentheri* (Donnellan et al. 2012b). This suggests an ancient, widely distributed lineage that occurred across Australia that left "relict" species in the Pilbara/Exmouth Cape Range region and in the Musgrave/Everard Ranges in central Australia. The separation of these taxa is likely associated with the aridification of central Australia that commenced in the early Miocene (20 mybp, Byrne et al. 2008; Pillans 2018), with subsequent extensive speciation along the eastern Australian coast (Donnellan et al. 2012b). The split between the central-eastern and south-western lineages is not seen in any other Australian frog lineage, where south-western species groups all have closest relatives in eastern Australia (Rix et al. 2015). The split between *P. guentheri* (confined to south-western Australia) and *P. occiden*talis – a species that ranges from the central wheatbelt in south-western Australia into the central deserts – is likely a comparatively recent event. Roberts and Maxson (1989) estimated divergence of these two species form south-western Australian at 5–6 mybp, with Donnellan et al. (2012b) supporting a later divergence date for this species pair than amongst other desert species of *Pseudophryne*.

Distribution and relationships of *Pseudophryne* species across Australia are illustrated in Fig. 3.

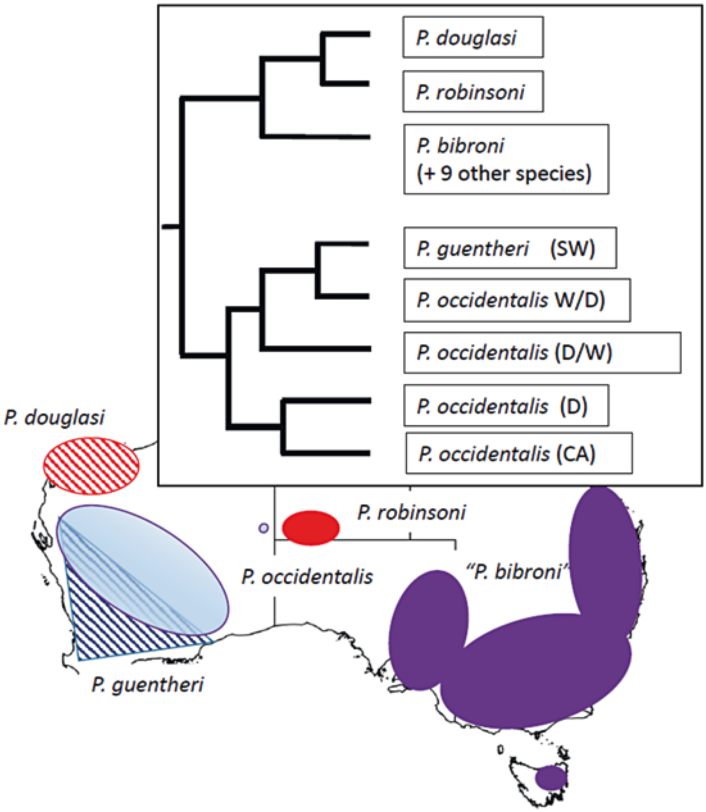


Fig. 3 Distribution and relationships between arid-zone species of *Pseudophryne* and their mesic relatives. *Pseudophryne occidentalis* is sympatric with *P. guentheri* in the central wheatbelt of south-western Australia but ranges well into the inland desert (W/D) with an outlier (D) near the South Australian border. *Pseudophryne douglasi* and *P. robinsoni* are sister taxa related to a nine species radiation of species in south-eastern and eastern Australia. "*P. bibroni*" covers the ranges of nine species: *P. bibroni*, *P. semimarmorata*, *P. dendyi*, *P. corroboree*, *P. pengilleyi*, *P coriacea*, *P. major*, *P. covacevichi* and *P. australis*. See Donnellan et al. (2012b) for supporting data

Diversity and Biogeography of Arid-Zone Notaden *Species*

Notaden nichollsi (desert spadefoot toad) occurs in Western and central Australia, but *N. bennettii* (crucifix toad) is found only in eastern Australia. *Notaden weigeli* (Weigel's toad) is restricted to acid sands in sandstone country in the west and north Kimberley, and *N. melanoscaphus* (northern spadefoot toad) is broadly distributed across tropical Australia, but does not occur in the arid zone. The relationships of these four species are not defined, but the pattern of an arid form likely derived from related "tropical" taxa is shared with several other frog genera.

Diversity and Biogeography of Arid-Zone Crinia *Species*

Three *Crinia* species occur in the arid zone: *C. riparia* (streambank froglet) and *C. flindersensis* (Northern Flinders' Ranges froglet), confined to the Flinders Ranges, occurring in permanently wet creek systems (Donnellan et al. 2012a). *Crinia deserticola* (desert froglet) occurs across northern, tropical Australia but also has an extensive distribution in the Channel Country in south-western Queensland into north-eastern South Australia. Cogger (2014) describes its habitats in those regions as being permanently moist. In phylogenetic analyses reported by Donnellan et al. (2012a), the two Flinders Ranges species are ancient, sister taxa estimated to have diverged 11.5 mybp (see also Symula et al. 2008)!

Diversity and Biogeography of Arid-Zone Limnodynastes *Species*

Two of the *Limnodynastes* species, *L. lignarius* (the woodworker frog) and *L. fletcheri*, are at their distributional limits in the arid zone. The single arid zone record of *L. fletcheri* from 1973 is on the far eastern edge of the Simpson Strezlecki dune field bioregion close to where one of us, JDR, also found this species in 1975, south of Tibooburra – on the western edge of the Murray-Darling basin: a river basin where this species is widespread. *Limnodynastes lignarius* has a primarily tropical range in the Kimberley and western Northern Territory. The only arid zone records of *L. lignarius* are recent, 2014, from a single locality, described as Oscar Range Quarry, in the Great Sandy Desert, south of the main Kimberley craton. This site presumably replicates some features of the normal rocky, wet systems where this species is found in northern, tropical Australia (cf. Tyler and Doughty 2009).

In contrast to the limited occurrence of *L. lignarius* and *L. fletcheri* in the arid zone, *L. tasmaniensis* (spotted grass frog) is widely distributed in the arid zone in permanent creek systems in the Flinders Ranges, in mound springs near the South Australian, Northern Territory border, and there are extensive records in western Queensland in the Channel Country and in river systems draining southwest towards lakes Eyre and Frome. No special adaptations to arid environments have ever been reported for this species; it appears to depend on available water that happens to persist in many of these systems. Range expansion during major flood events was reported by Roberts (1993), and flood events may have contributed to the arid-zone occurrences of this species or renewed populations that have gone extinct during extended periods of drought.

Diversity and Biogeography of Arid-Zone Litoria and Dryopsophus *Species*

Dryopsophus species that burrow have historically been placed in a separate genus, *Cyclorana*, because of a shared morphology of squat body shapes and short limbs, a morphology shared with burrowing myobatrachid frog species (cf. Vidal-García et al. 2014). Tyler (1971) showed that Australian tree frogs (then in the genus *Hyla*) and *Cyclorana* species shared a derived state of the submandibular musculature and synonymised them into a single genus *Litoria*. Various authors have rejected that split and maintained two generic names (e.g. Anstis 2013; Cogger 2014). Frost et al. (2006) and Pyron and Wiens (2011) maintained a single genus, *Litoria*, but that genus was split recently into *Litoria* and *Dryopsophus* with all burrowing species previously placed in *Cyclorana* forming a monophyletic block in *Dryopsophus* (Duellman et al. 2016).

Relationships have been repeatedly analysed in the burrowing *Dryopsophus* species (generally as *Cyclorana*, e.g. Maxson et al. 1985; Frost et al. 2006; Pyron and Wiens 2011; Anstis et al. 2016; Duellman et al. 2016). The derivation of arid-zone forms is much less clear than that in in some myobatrachid groups discussed above. For example, *Dryopsophus occidentalis* (western water-holding frog) found in western deserts is the apparent common ancestor of nine species, including a strictly desert species, *D. maini* (Main's frog), and a strictly tropical species, *D. manya* (small frog), found only on Cape York in northern Queensland (Anstis et al. 2016): the desert form may represent the ancestral state for this genus. Several species also range from near-coastal regions in eastern Australia well into the arid zone, e.g. *D. alboguttata* (striped burrowing frog) and *D. cryptotis* (Hidden-ear frog), or apparent sister taxa are broadly sympatric, e.g. *D. platycephala* and *D. verrucosa* (rough frog, Anstis et al. 2016). The resolution of phylogenetic trees backing some of these arguments may be poor, given they are based on a single mitochondrial gene sequence (ND4), but they raise the possibility of very different patterns for the origins of desert forms in the hylid fauna.

Other non-burrowing *tree frog* species, including *D. caeruleus* (green tree frog), *D. gilleni* (Centralian tree frog) and *L. rubella* (desert tree frog), all occur more or less widely in the arid zone. *Dryopsophus gilleni* is confined to permanently wet sites in central Australian range systems but is the sister taxon of *D. splendidus* (magnificent tree frog) from the Kimberley region (Young et al. 2005) or, based on a more comprehensive data set, part of a four species clade, *D. gilleni*, *D. splendidus* (both only found in the Kimberley) and a species pair of *D. cavernicolus* (cave-dwelling frog – also Kimberley only) and *D. caeruleus* (widespread across north and eastern Australia) with the divergences of these lines dated at 7.5 million years ago (Duellman et al. 2016).

Litoria rubella has a very broad range, the largest range of any Australian hylid species, across inland and northern Australia. *Litoria rubella* is related to *L. electrica* (Buzzing tree frog: Pyron and Wiens 2011; Duellman et al. 2016); the latter species occurs from the Gulf of Carpentaria to Windorah in far western Queensland in the

Channel Country (Anstis 2013). There have been several suggestions that *L. rubella* might be split into more than one species, e.g. Steinborner et al. (1994), S. Donnellan (pers. comm.), but based on male advertisement calls JD Roberts has heard or recorded in inland Western Australia, near Meekatharra, on the Pilbara coast, in both the east and west Kimberley and near Darwin in the Northern Territory, there is little evidence that call has differentiated significantly across the broad range of this species. Call in anurans is used to attract mates and recognise species, so is a useful clue to species differentiation and recognition (Gerhardt and Huber 2002). Determining what, if any, patterns of intraspecific differentiation occurred in this species needs additional work. By comparison, *N. sudelli* also has a low level of differentiation in call across a comparable, broad geographic range (summarised in Roberts 2010) with the bulk of that range in arid Australia.

Arid-Zone Frog Fauna: Overview

There is an extensive arid-zone frog fauna in Australia, and there are recurring patterns of derivation from tropical rather than southern, temperate lineages in several genera (*Uperoleia*, *Litoria*, *Dryosophus*, *Platyplectrum*, *Notaden*) but also speciation within the arid zone (*Pseudophryne*, *Crinia*, *Neobatrachus*, *Dryopsophus*). In cases where there is reliable dating from molecular clocks, these processes of initial lineage splitting and speciation are old, extending well back into the Miocene when the consensus view of Australian climates was of an aridifying central continent (Byrne et al. 2008; Pillans 2018), shifting from widespread rainforest and sclerophyll forest vegetation types at the Oligocene, Miocene boundary (Crisp and Cook 2013). That is best exemplified by the comprehensive data set on global relationships of hylid frogs and estimated ages of divergence reported in Duellman et al. (2016). Explicit geographical patterns have only been investigated comprehensively in one genus: *Uperoleia*. But even in this group, apart from isolation, the processes driving differentiation and shifts in structures of male call, a critical character in species recognition, and likely also subject to strong sexual selection, are unknown. However, the most widely distributed arid-zone species, *U. micromeles* (Tanami toadlet), is a recently derived taxon splitting from its Kimberley and Pilbara coast sister taxon, *U. talpa* (mole toadlet), only 1.22 million years ago (Catullo and Keogh 2014). Despite severe water deficits and seasonally extreme high temperatures, frogs have succeeded in the Australian arid zone.

Importantly, we also note that several genera in the arid zone, *Neobatrachus*, *Notaden* and *Dryopsophus*, have a diversity higher or about equal to that in wetter warmer and/or cooler regions of the continent. The arid zone may be a source of diversity that has spilled over into less arid regions, rather than being derivative or surviving as remnants from tropical or temperate lineages as the arid interior formed (cf. Byrne et al. 2008, 2011).

Coping with Aridity: Physiological, Morphological and Behavioural Adaptations

Arid environments present harsh conditions for the survival of anurans. Conditions are usually hot and dry, and rainfall is unpredictable. Anurans living in the arid zone have evolved some unique behavioural, morphological and physiological adaptations to coping with such inhospitable conditions including burrowing behaviours, cutaneous morphologies, as well as physiological adaptations, which all function to control water balance. We detail these specific adaptations in arid anuran genera below.

Coping with Water Loss in an Arid Environment Without Burrowing

How non-burrowing frogs persist in truly arid environments is largely unknown – this includes *Litoria* and *Dryopsophus* species, some *Uperoleia* and all *Pseudophryne* species.

Pseudophryne *P. robinsoni* and *P. douglasi* occur around permanently wet pools or streams in rocky systems (Donnellan et al. 2012b; Main 1964), with *P. douglasi* reported as depositing eggs in water (Main 1964) with many of the records of this species in permanently wet drainage systems in the Pilbara and Exmouth region. These habitats are comparable to those reported for *P. robinsoni* in the Everard and Musgrave ranges (Donnellan et al. 2012b). In other *Pseudophryne* species, eggs are deposited and develop in terrestrial burrows or nests that later flood. Eggs hatch when flooded resulting in a conventional, aquatic tadpole (Anstis 2013). One of us (JDR) has observed *P. occidentalis* breeding in terrestrial burrows around road verge ponds north of Leonora, Western Australia and in burrows in clay in run-off areas around granite outcrops at Hospital Rocks, west of Menzies, Western Australia. These areas may have more predictable rainfall or water availability allowing adoption of the more characteristic breeding biology for this genus. No unusual physiological capabilities have been described in *Pseudophryne*, but JDR has observed individual frogs in this genus under rocks above dry gorge systems in the southern Flinders Ranges in South Australia. Their occurrence in severely arid environments suggests a capacity to cope with dry conditions, but the mechanisms to cope with such dry environments are unknown.

For non-burrowing *Litoria* and *Dryopsophus* species, we similarly have little knowledge of how they persist in such hot and dry environments. Neither *D. gilleni* nor *L. rubella* have a heightened cutaneous resistance to water loss, but some other very small, arboreal, tropical hylid species (*L. bicolor*, *D. gracilentus*) do (Young et al. 2005; Withers et al. 1984). Young et al. (2005) summarised data on cutaneous resistance to water loss in Australian hylids, stating: “Many Australian species of hylids are 'atypical' in relation to water loss from the skin … there is a general consensus that resistance of *Litoria* species is intermediate (10–40 s cm^{-1}) between that of typical anuran amphibians (~1 s cm^{-1}) and the waterproof frogs from the genera *Chiromantis* and *Phyllomedusa* (1100 s cm^{-1})" (see Young et al. 2005 for references; Withers 1992, higher numbers mean greater resistance to water loss). However, resistance to water loss may also vary rapidly. Blaylock et al. (1976) reported lipid excretion onto the skin surface and subsequent wiping behaviours in *phyllomedusine* tree frogs from semiarid areas in Argentina. These behaviours covered the skin with a water-impermeable layer accounting for early reports of high skin resistance and very low evaporative water loss in these species, comparable with some desert reptiles (references in Blaylock et al. 1976).

Desert tree frogs must cope with extreme, high, diurnal air temperatures. Main (1968) reported tadpoles of *L. rubella* in water at 39.2°, and *L. rubella* was reported surviving for more than 8 h at 40 °C in low humidity, laboratory conditions by Warburg (1965). The only other species, out of 11 tested by Warburg, noted to survive in such conditions was *N. centralis* (or likely *N. sudelli*, cf. Roberts 2010), a burrowing species that can form waterproof cocoons (Lee and Mercer 1967). In laboratory studies, *L. rubella* can marginally reduce water loss by postural and colour changes (Withers 1995a), but not at sufficient levels to cope with extreme dry/hot conditions. How non-burrowing hylid frogs cope with the combined effects of high temperatures and low water availability is unknown, but these laboratory observations on *L. rubella* are matched by field performance of a south-western Australian, temperate-zone hylid, *D. moorei* (motorbike frog). *Dryopsophus moorei* has been observed voluntarily sitting in elevated air temperatures (averaging 34.4 °C from 08.30 to 19.30, shade temperatures peaked at 39.1 °C) with low relative humidity with a third of the upper body surface in direct sunlight for 6 h from 13.00 to 19.00. Based on theoretical models of water loss in frogs, this individual should have been dead (Roberts and Roberts 2012). Clearly, we do not know all there is to know about how non-burrowing, hylid frogs cope with extreme environments.

Burrowing Behaviour and Associated Morphologies as Adaptations to Aridity

Four genera: *Dryopsophus*, *Notaden*, *Neobatrachus* and *Pseudophryne* all have multiple species in the arid zone, with the first three all having species with adaptations to a burrowing habit. Burrowing frogs generally burrow backwards and consequently have relatively short limbs, and that is true for burrowing species of *Dryopsophus* and all *Neobatrachus* and *Notaden* species (e.g. Vidal-García et al. 2014). *Pseudophryne* species also form shallow breeding burrows (e.g. Anstis 2013), but are not normally characterised as a burrowing species outside the breeding season.

Burrowing frog species are also found in the Australian myobatrachid genera *Arenophryne* and *Myobatrachus* where frogs in both genera burrow forwards, with more conventional backwards burrowing in the genera *Heleioporus*, *Limnodynastes*, *Notaden*, *Neobatrachus* and *Platyplectrum*. Burrowing myobatrachid frog species are characteristically short-limbed, independent of whether environments are arid or more mesic or whether frogs burrow forwards (*Arenophryne*, *Myobatrachus*) or backwards (*Neobatrachus*, *Heleioporus*, burrowing *Limnodynastes* species), but forward burrowing species may have relatively longer arms (e.g. *Myobatrachus*; Vidal-García et al. 2014). The broad morphotype of squat bodies and relatively short limbs is shared with burrowing hylid species.

Waterproof Cocoons Within the range of burrowing frog species, two distinct approaches to dealing with maintaining water balance have been described. The first includes the formation of water-impermeable barriers generated by repeated sloughing of the skin, but, rather than losing or eating the skin as generally occurs in anurans, the sloughed skin is kept intact. This accumulation generates multiple layers of the skin, which harden to form cocoons that cover the whole body, including the cloaca and the mouth but not the nostrils. This pattern of cocoon formation was first described by Lee and Mercer (1967) and more extensively by Withers (1995b), who reported up to 95 "skin" layers forming a cocoon in *N. sutor*, but with 229 layers reported on field-excavated frogs, *N. aquilonius* (Cartledge et al. 2006). Studies by McMaster (2006) showed that the mouth, nostrils and cloaca were sealed by an invagination of the skin layers into the orifice. Extensive studies on cocooned frogs summarised by Withers 1995b, 1998) show that cocoon formation radically reduces water loss, and that the reduction in water loss occurs rapidly (< 20 days) and can be almost total. For example, *D. maini* individuals without a cocoon lose an average of 81.7 mg of water per gram of body mass per hour, but after 21 days in a cocoon, this drops to only 6.2 mg g^{-1} h^{-1}: a dramatic reduction. Water-loss reductions continue as cocoon layers are added and become close to zero after 60 days in this species. Although a feature of some arid-zone frog species, cocoon formation occurs in all *Neobatrachus* and burrowing *Dryopsophus* species, including species from more temperate areas in south-western Australia (Withers 1995b; Table 1).

Burrowing Species without Cocoons Some burrowing frog species maintain their position in moist soils to eliminate net water loss without forming or with no capacity to form waterproof cocoons. Such maintenance of position with respect to soil moisture may also be accompanied by frequent or occasional use of available moisture at the soil surface, even though that availability may be fleeting after very small rain events (Predavec and Dickman 1993; Thompson et al. 2005). *Notaden* species do not form cocoons and are much more likely to be detected active on dune systems than *Neobatrachus* species that occur in the same areas with activity occurring even after very small amounts of rain (< 10 mm; Predavec and Dickman 1993; Thompson et al. 2005). *Notaden nichollsi* has been excavated from sandy soils in the Gibson Desert in the same area where *N. sudelli* was excavated from clay soils between dune ridges (Thompson et al. 2005). *Uperoleia micromeles* has also been found in the same burrows as *N. nichollsi*. With no reported evidence that *Uperoleia* species form cocoons or are able to burrow (cf. Vidal-García et al. 2014), it is likely this species also maintains its water balance by a combination of surface activity in conditions where moisture is available, and by going deep enough in loose soils formed by *Notaden* burrowing, to be in contact with moist soils. This pattern of nocturnal activity of a burrowing frog species, water loss during the active phase and water uptake from moist soil when back underground during the following day, is also known in *Heleioporus eyrei*, which is commonly active on hot, dry summer nights in south-western Australia, but actively rehydrates from moist soils during the day (Lee 1968). It is not a unique property of desert anurans and likely occurs in other burrowing myobatrachid species, e.g. members of the *L. dorsalis* group that primarily occur in eastern temperate and tropical Australia (Martin 1972).

Uperoleia micromeles, widely distributed from the central deserts to the west coast (Cogger 2014), has been excavated from deep underground in burrows formed by *N. nichollsi* (Thompson et al. 2005). Frogs in the genus *Uperoleia* do not have any of the general morphological characteristics of other burrowing frog species (Vidal-García et al. 2014) and likely go underground as *Notaden* burrows downwards – in a commensal relationship.

Cocoon or No Cocoon? Although these two strategies involve very different ways of coping with water loss, cocooning species, particularly *Neobatrachus*, may use both strategies: only forming extensive cocoons when in very dry soils. McMaster (2006) reported *Neobatrachus sudelli* excavated from sand dune soils that had cocoons with only two skin layers despite the last significant rainfall at the collection site being 6 months earlier. Cartledge et al. (2006) reported excavating *N. aquilonius* without cocoons from sand dunes where *Notaden nichollsi* was also found. This suggests a common use of moist soils for rehydration and maintenance of water balance for all burrowing frog species if water is available, but this is an obligate mechanism in species that cannot form waterproof cocoons, e.g. desert species of *Notaden* and *Uperoleia*.

Energetics of Dormancy While Waiting for Rain

Water loss may be avoided by burrowing, but extended periods underground generate another cost, energy depletion, as cocooned or buried frogs cannot feed. Associated with cocoon formation in burrowing species is a radical reduction in metabolic rate. Aestivating frogs depress metabolic rate by up to 85% of standard metabolic rate (Withers 1993; Table 2; see also McMaster (2006) for data showing similar metabolic depression in *N. nichollsi*). This reduction may make a marginal contribution to reduced water loss, but its critical role is in allowing cocooned/buried frogs to survive inactive, underground, without feeding, relying on fat bodies and other energy reserves. Van Beurden (1980) measured metabolic rates of

Table 2 Water loss in arid and southwest temperate zone frogs from Australia

	Water loss (mg g^{-1} h^{-1})			
	Standard	Cocooned	% reduction	Days cocooned
Arid zone				
Neobatrachus sutor	60.3	3.9	94	70
Neobatrachus sudelli	44.2	6.8	85	57
Neobatrachus fulvus	13.9	3.3	76	44
Neobatrachus wilsmorei	21.2	5.4	75	61
Litoria maini	81.7	6.2	92	21
Litoria platycephala	16.9	2	88	–
South-western Australia				
Neobatrachus pelobatoides	56.7	7	88	63
Neobatrachus kunapalari	34.2	2.6	92	61

Data from Withers (1998)

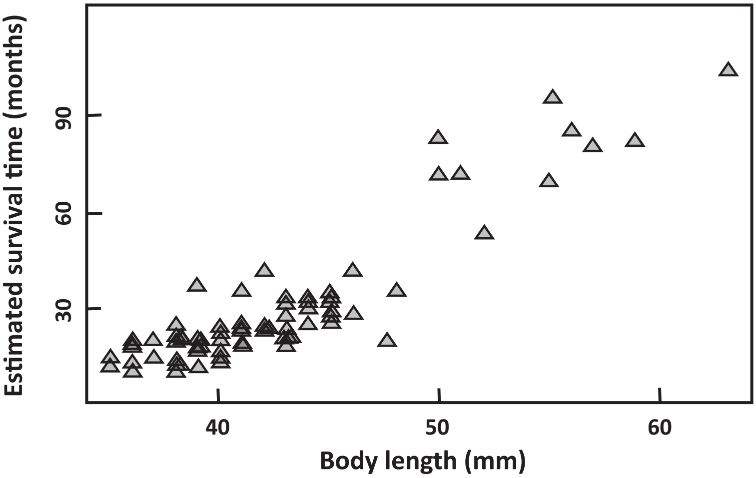


Fig. 4 Estimated survival time and body length in *Dryopsophus platycephalus*. Redrawn from Van Beurden (1980). Darker triangles result from overlapping data points

cocooned specimens of *D. platycephalus*, measured fat bodies and other energy reserves of cocooned frogs and predicted survival rates, assuming no limiting effects of water loss. Figure 4 is redrawn from his paper and shows minimal survival times at just under 3 years, but maximum survival times at nearly 8 years, without feeding. This result is “almost” matched by data for *N. aquilonius* reported by McMaster (2006), where the number of layers in the cocoon from frogs excavated in the field was used to back-estimate a duration of time underground based on rates of cocoon formation in lab studies. The estimates varied from 83 to 1145 days, based on minimum and maximum rates of cocoon formation, a potential maximum of just over 3 years without feeding.

Diets of Frogs in the Arid Zone

How can frogs generate energy reserves that might allow a frog to last 8 years or more underground? North American frog species in the genus *Scaphiopus* have very strong similarities to the Australian genus *Neobatrachus*, both contain exclusively burrowing species and both have species in arid, desert systems and in more temperate areas. *Scaphiopus* also spend extended periods underground. *Scaphiopus* eat termites, beetles and an array of other invertebrates but have very fast assimilation rates for termites (Dimmit and Ruibal 1980). Based on data on measured metabolic rates of dormant *Scaphiopus*, assimilation rates and known food intake in this species (primarily termites), Dimmit and Ruibal (1980) very conservatively estimated that an individual *S. couchii* could ingest enough termites in two nights of feeding to form a fat body that would last a dormant frog 15 months. A more realistic estimate by Dimmit and Ruibal (1980) demonstrated only *one night of feeding on termites* could generate a fat body that would last a frog 15 months without feeding.

What do arid-zone frogs in Australia eat? Studies on diets of arid-zone frogs in Australia are limited, but they do show that termites can be a significant food item. Main and Calaby (1957) reported stomach contents from *Platyplectrum* (then *Limnodynastes*) *spenceri* and *C. cultripes* (likely *D. maini*) as primarily termites and ants. Lindgren (1960) reported termites as the primary component of the diets of frogs (*P. spenceri* and *N. nichollsi*) collected at Jigalong (east of Newman, Western Australia), and Calaby (1960) reported two species of termites from *D. maini* and *P. spenceri*, but also ants, weevils, cockroaches and bugs, and large numbers of termites from *N. nichollsi* with some ant species. *Notaden nichollsi* from the Simpson Desert in southwest Queensland also consumed primarily termites (≈2/3 of gut contents, Predavec and Dickman 1993) with ants being the only other diet item. In comparison with the availability of different food items, both termites and ants are heavily over-represented in the diet of *N. nichollsi* (Predavec and Dickman 1993). In the same habitat, *N. sudelli* (reported as *N. centralis*) preferred ants, termites and beetles, and *Dryopsophus australis* ate beetles, and lepidopteran larvae, again, with both over-consuming preferred items relative to availability. Calaby (1960) noted, rather than being selective feeders, desert frogs may simply be consuming what is available during periods of peak surface activity, e.g. termites that swarm after major rainfall events. Consistent with that suggestion, one of us (JD Roberts) has watched *N. nichollsi* gorging on termites falling from a lit headlight at night at Port Hedland – the frog stopped *en route* to a breeding pond 15–20 m away across a road, 36 h after cyclonic rains fell in the region. However, patterns of surface activity are not always associated with major rainfall events, particularly in *N. nichollsi*, with both Predavec and Dickman (1993) and Thompson et al. (2005) reporting *Notaden* active after either no rain or very small rain events (≈3 mm, Thompson et al. 2005). The strong diet selectivity shown in the study by Predavec and Dickman (1993 – see above) also contradicts Calaby's claim.

Population Density

Anyone who has observed frogs active after cyclonic rains in desert environments has seen or heard very, very large numbers of frogs. Despite that experience, there are comparatively few but some very impressive reports of frog densities in arid environments. The most extreme is by Read (1992), who reported a pit-trapping study of terrestrial vertebrates (reptiles, mammals and frogs) at Olympic Dam in northern South Australia. In that study, total captures of a single frog species, *Neobatrachus sudelli* (reported as *N. centralis*), exceeded the combined number of all other vertebrates caught in a 5-year study. Read (1992) reported 358 captures of 6 mammal species, 1257 captures of 37 reptile species but 6243 captures of *N. sudelli*. Those data are matched in the Tanami Desert where Morton et al. (1993) reported 422 captures of *Neobatrachus* spp. (spp. uncertain, either *N. aquilonius* or *N. sudelli*) over 8 trapping sites and estimated frog densities at 34 to 68 per ha. Other frog species were captured but in considerably lower numbers (*Cyclorana maini*, 15; *Notaden nichollsi*, 12; *Uperoleia micromeles*, 9). Morton et al. (1993) speculated that termites were a critical food source, because of the synchronous emergence of frogs and winged termites. However, *Neobatrachus* can also emerge in extremely large numbers after rain events in temperate, non-arid habitats, where termites certainly occur but are much less obvious. Davis and Roberts (2004) reported 21 females and 35 males of *Neobatrachus kunapalari* in a 5 m by 30 m pond near Narembeen in south-western Australia, an area with reliable winter rainfall. On April 1, 2008, after a major rainfall on March 30, 2008, in the central wheatbelt of Western Australia, JDR observed extremely high densities of *N. kunapalari* over whole landscapes, east of Beverley. *Neobatrachus* can be very abundant at both local and landscape scales outside the arid zone; termites may not be the only determinant of abundance of frogs in this genus.

JD Robert's experience working after and during cyclonic rains in the coastal arid zone near Port Hedland, Karratha and Exmouth is that all frog species in those areas that breed in temporary water bodies are abundant after major rain events: *Uperoleia*, *Neobatrachus, Platyplectron* and *Dryopsophus* species. That abundance has not been quantified, but that is also true of most frog species anywhere in Australia!

How Do Frogs in the Arid Zone Speciate?

Call Structure and Evolution by Polyploidy in Arid-Zone Frogs: The Genus Neobatrachus

In most anuran species, only males call, and call is a critical element in both species recognition and mate choice by females (Wells 2007). Roberts (1997b) discussed the evolution of polyploid frogs in the genus *Neobatrachus* and speculated about their origins based on call structure given that data on mtDNA sequence data (Mable and Roberts 1997), karyotype structure (Mahony and Robinson 1986) and allozyme data had not clarified their evolution (Mahony et al. 1996). Arguments by Roberts (1997) were partly derived from the observation that in tetraploid anuran species with known diploid ancestors, the derived tetraploid commonly had calls with a lower pulse rate than the ancestral diploid (examples in Keller and Gerhardt 2001). Given that pulse rate is commonly used as a metric for species recognition by female frogs (Gerhardt and Huber 2002), call structure shifts likely promote speciation because tetraploid females are unlikely to mate with the diploid ancestor (and vice versa), because of the pulse rate shift. In North America *Hyla versicolor* is a tetraploid species that has been repeatedly derived from its diploid ancestor, *Hyla chrysoscelis* (Ptacek et al. 1994), with a complex pattern of interbreeding of independently derived tetraploid lineages generating a single species (Holloway et al. 2006). Calls of *H. versicolor* have lower pulse rates than the diploid ancestor, and this is a broad pattern in several other diploid/tetraploid species pairs (Keller and Gerhardt 2001). Generally, tetraploids have a greater nuclear volume than ancestral diploids, and experimental studies of artificially generated polyploid frogs generally follow that maxim; calls of polyploids (both triploids and tetraploids) have lower pulse rates than the diploid parental species (e.g. Keller and Gerhardt 2001). Keller and Gerhardt (2001) showed that call structure mirrors ploidy level; calls of diploids have higher pulse rates than triploids, and triploids higher than tetraploids – in most cases. This effect was assumed to be a specific consequence of ploidy level or some combination of ploidy level and nuclear or cell volume as both cell and nuclear volume normally increase with ploidy level. However, Keller and Gerhardt (2001) generated some triploid embryos by cold shock that had the nuclear and cell volumes characteristic of diploids, but not the expected values of triploid forms. The "diploid" nuclear/cell volume triploid frogs had calls with pulse rates characteristic of the diploid species, *H. chrysoscelis*, implying cell or nuclear size properties are more important than ploidy level. The mechanism is unknown.

Roberts (1997a) could not find any obvious diploid/tetraploid species pairs in the genus *Neobatrachus*, but the calls of all species were generally distinct in either broad structure (single pulse calls: *N. sutor* and *N. wilsmorei*) versus multiple pulse calls (all other species) or in pulse number, call duration, pulse rate, dominant frequency or some combination of those features. In multivariate space, the calls of *N. fulvus* (diploid), recorded on the Exmouth Peninsula; *N. aquilonius* (tetraploid), recorded near Port Hedland; and *N. sudelli* (tetraploid), recorded from south-western Australia to Queensland, were most similar. The origins of tetraploid species of *Neobatrachus* are poorly resolved (Mable and Roberts 1997; Mahony et al. 1996), and the origins of differences in call structure are equally uncertain (Roberts 1997a).

Hybridisation and Gene Exchange Roberts (1997b) recorded calls intermediate between the calls of *N. kunapalari* (tetraploid) and *N. sudelli* (also tetraploid) near Menzies in Western Australia. These frogs have a variety of morphological abnormalities including malformed feet, bones growing from the chest and reduced testis volumes, suggesting strong developmental barriers to gene exchange between arid- (*N. sudelli*) and temperate-zone (*N. kunapalari*) tetraploid species. In contrast, on northern Eyre Peninsula in South Australia, Mahony et al. (1996) showed evidence of gene exchange between the temperate diploid *N. pictus* and the arid-distributed, tetraploid *N. sudelli* based on extensive allozyme data.

Tetraploid Origins: Some Speculation The origins of tetraploid forms in this genus are very unclear, but properties of arid-zone breeding sites may contribute to this process. Both cold shock and high-temperature shock during egg development can induce polyploidy in anurans (Schmid et al. 2015). Breeding sites for *Neobatrachus* may be exposed to both temperature extremes. For example, Hyden in the eastern wheatbelt of Western Australia has a record high temperature maximum of 48.6 °C and a record low of −5.6 °C (http://www.bom.gov.au/climate/data/ data from location no. 010568). Breeding by diploid species after summer thunder storms, or, on clear nights that typically follow the passage of cold fronts producing winter rainfall (Main 1968) may expose developing eggs to either heat or cold shock. Understanding tetraploid origins is a difficult process (cf. Holloway et al. 2006 for a well-studied anuran example; Schmid et al. 2015 for Amphibia more broadly).

Call Evolution in Non-polyploid, Arid-Zone Frogs Three factors likely impose selection on call structure in anurans: (a) the local acoustic environment where calls may adapt to peculiarities of interfering acoustic signals, e.g. calls of other frog species and environmental noise (e.g. rainfall, thunder, wind, anthropogenic noise sources); (b) interactions between closely related species, e.g. driven by selection against hybridisation where hybrids may be infertile or have reduced viability, reinforcement or reproductive character displacement; or (c) local patterns of sexual selection that drive differences in male call due to shifts in female preference or male-male interaction patterns (e.g. Andersson 1997; Gerhardt and Huber 2002; Wells 2007).

Studies on acoustic behaviour of *Uperoleia laevigata* by Robertson (1984, 1986a, 1986b, 1990) demonstrate a complex set of acoustic behaviours related to defence of calling territories, male-male interactions and female attraction. Most interestingly, females prefer to mate with males that weigh 70% of the female's body mass (Robertson 1990), and this maximises fertilisation success. In the *Uperoleia* species reported by Robertson, amplexed pairs make repeated movements to the bottom of breeding ponds to deposit eggs, and mass matching optimises egg fertilisation success. Patterns of sexual selection, both intersexual selection – female choice of mates with a specific body mass – and intrasexual selection, male-male interactions that may make certain males distinctive or available as mates (Andersson 1997; Gerhardt and Huber 2002), may have driven local adaptation in call structure in arid-zone *Uperoleia* species.

There is considerable variation in body and limb length between *Uperoleia* species using multivariate descriptors of morphology (Catullo et al. 2011, 2014; Vidal-García et al. 2014) and in male call (e.g. Catullo et al. 2014). Some call variation in anurans is related to morphology, e.g. larger species generally have lower dominant frequencies in male advertisement calls (Hoskin et al. 2009). Contrarily, in eastern and western forms of *U. trachyderma* well-differentiated acoustically and clearly defined by differences in nuclear and mitochondrial DNA sequence data, there is little differentiation in morphology (Catullo et al. 2014).

Arid-zone frogs breed in high-density, multispecies choruses. Sexual selection, male-male interactions and female choice, the complex acoustic environments generated by multiple species breeding simultaneously and polyandrous mating systems where more than one male mates with a female may all impose novel, strong selection pressures on male call (Andersson 1997; Gerhardt and Huber 2002; Roberts and Byrne 2011).

Conservation Status and Challenges for Arid Australian Anurans

In the current listing of threatened Australian frog species under the criteria set out by the Environment Protection and Biodiversity Conservation Act 1999 (listed at http://www.environment.gov.au/cgi-bin/sprat/public/publicthreatenedlist.pl), no frog species found in the arid zone are listed.

Are there threats to arid-zone frogs?

Climate change may pose a threat for arid Australian anurans. Historical rainfall and climate reconstructions in both south-western and eastern Australia demonstrate major rainfall variation over the past ≈ 500–1000 years (Cullen and Grierson 2009; Palmer et al. 2015; Tozer et al. 2016) with droughts and rainfall highs, similar to more recent events in the last 100 years of instrumental record commonly used as a baseline in Australia. These reflect El Niño and La Niña events in the Pacific and shifts in the Indian Ocean Dipole, with a negative Indian Ocean Dipole, as what occurred in 2016, generating high rainfall in inland and eastern Australia. There is no published modelling that we are aware of for future climate impacts specifically focused on arid-zone frogs. Hotter and drier conditions may impact on some: particularly species with small ranges, reliant on small, permanent water bodies (e.g. *Pseudophryne robinsoni*, which is confined to the Everard and Musgrave ranges; Donnellan et al. 2012b).

Table 3 Metabolic rates in arid and southwest temperate zone frogs from Australia

	Metabolic rate (μL O_2 g^{-1} h^{-1})			
	Standard	Aestivating	% reduction	Days cocooned
Arid zone				
Neobatrachus sutor	63	14.1	78	50
Neobatrachus sudelli	90	20.8	77	68
Neobatrachus fulvus	97	33.2	66	44
Neobatrachus wilsmorei	81	12.1	85	68
Litoria maini	67	25.2	62	36
Litoria platycephala	46	8.7	81	50
South-western Australia				
Neobatrachus pelobatoides	130	18.6	86	60
Neobatrachus kunapalari	72	15.9	78	68

Data from Withers (1993)

Extensive grazing throughout the arid regions may pose challenges for arid-zone frogs. In some regions of the Northern Territory, cattle grazing may be reducing the distribution and abundance of *Uperoleia* species (R. Catullo, pers. comm. 2014). There are documented, negative impacts of stock grazing on vegetation and fauna in relation to water points (e.g. James et al. 1999; Davies et al. 2010) but, paradoxically, including suggestions that termites may increase in abundance due to higher nutrient levels in the soil (James et al. 1999). Higher termite abundance may favour arid-zone frog species that often consume them (see diet data discussed above).

Despite being linked to global amphibian declines, the chytrid fungus, *Batrachochytrium dendrobatidis*, is not considered a threat in arid environments – temperatures may be too high for the fungus to survive (e.g. Liu et al. 2013) (Table 3).

Conclusions

Arid-zone anurans in Australia are diverse but have a long, complex history whose details are only now being unravelled. The combination of an ability to form waterproof cocoons and reduce metabolic rates or exploit water in moist soils at depth may give frogs an unmatched ability to persist at high densities in arid environments (Read 1992). The incredible abundance of *Neobatrachus sudelli* at Olympic Dam in South Australia reported by Read (1992) can probably be matched by many other desert frog species if researchers were in the right place at the right time – during major rain events when the desert is least accessible and, if the rain is cyclonic, most dangerous.

There is a lot to learn about the role of anurans in arid zone ecosystems.

Appendix 1: Frog Species in the Deserts and Xeric Shrublands Ecoregion Subdivided by IBRA Regions. See Text for Further Detail and Sources

Broken Hill Complex	*Litoria rubella*
Broken Hill Complex	*Neobatrachus pictus*
Broken Hill Complex	*Neobatrachus sudelli*
Broken Hill Complex	*Limnodynastes tasmaniensis*
Broken Hill Complex	*Litoria cultripes*
Burt Plain	*Litoria alboguttata*
Burt Plain	*Litoria australis*
Burt Plain	*Litoria gilleni*
Burt Plain	*Litoria maini*
Burt Plain	*Litoria rubella*
Burt Plain	*Neobatrachus aquilonius*
Burt Plain	*Neobatrachus sudelli*
Burt Plain	*Notaden nichollsi*
Burt Plain	*Platyplectrum spenceri*
Carnarvon	*Litoria maini*
Carnarvon	*Litoria occidentalis*
Carnarvon	*Litoria rubella*
Carnarvon	*Neobatrachus fulvus*
Carnarvon	*Neobatrachus pelobatoides*
Carnarvon	*Neobatrachus sudelli*
Carnarvon	*Neobatrachus sutor*
Carnarvon	*Neobatrachus wilsmorei*
Carnarvon	*Notaden nichollsi*
Carnarvon	*Platyplectrum spenceri*
Carnarvon	*Pseudophryne douglasi*
Carnarvon	*Pseudophryne occidentalis*
Carnarvon	*Pseudophryne guentheri*
Central Ranges	*Litoria maini*
Central Ranges	*Litoria occidentalis*
Central Ranges	*Litoria rubella*
Central Ranges	*Neobatrachus sudelli*
Central Ranges	*Platyplectrum spenceri*
Central Ranges	*Pseudophryne occidentalis*
Central Ranges	*Pseudophryne robinsoni*
Channel Country	*Crinia deserticola*
Channel Country	*Litoria alboguttata*
Channel Country	*Litoria brevipes*
Channel Country	*Litoria caerulea*
Channel Country	*Litoria cultripes*
Channel Country	*Litoria electrica*

(continued)

Channel Country	*Litoria inermis*
Channel Country	*Litoria latopalmata*
Channel Country	*Litoria novaehollandiae*
Channel Country	*Litoria pallida*
Channel Country	*Litoria platycephala*
Channel Country	*Litoria rubella*
Channel Country	*Litoria verrucosa*
Channel Country	*Neobatrachus sudelli*
Channel Country	*Platyplectrum ornatum*
Channel Country	*Platyplectrum spenceri*
Channel Country	*Uperoleia rugosa*
Davenport Murchison Ranges	*Crinia deserticola*
Davenport Murchison Ranges	*Litoria alboguttata*
Davenport Murchison Ranges	*Litoria australis*
Davenport Murchison Ranges	*Litoria caerulea*
Davenport Murchison Ranges	*Litoria cultripes*
Davenport Murchison Ranges	*Litoria longipes*
Davenport Murchison Ranges	*Litoria maculosa*
Davenport Murchison Ranges	*Litoria maini*
Davenport Murchison Ranges	*Litoria platycephala*
Davenport Murchison Ranges	*Litoria rubella*
Davenport Murchison Ranges	*Neobatrachus aquilonius*
Davenport Murchison Ranges	*Notaden melanoscaphus*
Davenport Murchison Ranges	*Notaden nichollsi*
Davenport Murchison Ranges	*Platyplectrum ornatum*
Davenport Murchison Ranges	*Platyplectrum spenceri*
Finke	*Litoria maini*
Finke	*Litoria platycephala*
Finke	*Litoria gilleni*
Finke	*Litoria rubella*
Finke	*Neobatrachus sudelli*
Finke	*Neobatrachus aquilonius*
Finke	*Platyplectrum spenceri*
Finke	*Platyplectrum ornatum*
Finke	*Platyplectrum spenceri*
Flinders Lofty Block	*Litoria rubella*
Flinders Lofty Block	*Crinia flindersensis*
Flinders Lofty Block	*Crinia riparia*
Flinders Lofty Block	*Crinia signifera*
Flinders Lofty Block	*Limnodynastes dumerilii*
Flinders Lofty Block	*Limnodynastes tasmaniensis*
Flinders Lofty Block	*Neobatrachus pictus*
Flinders Lofty Block	*Neobatrachus sudelli*
Flinders Lofty Block	*Pseudophryne bibronii*
Flinders Lofty Block	*Litoria platycephala*

(continued)

Gascoyne	*Uperoleia russelli*
Gascoyne	*Litoria maini*
Gascoyne	*Litoria occidentalis*
Gascoyne	*Litoria rubella*
Gascoyne	*Neobatrachus aquilonius*
Gascoyne	*Neobatrachus fulvus*
Gascoyne	*Neobatrachus sutor*
Gascoyne	*Neobatrachus wilsmorei*
Gascoyne	*Notaden nichollsi*
Gascoyne	*Platyplectrum spenceri*
Gascoyne	*Pseudophryne douglasi*
Gascoyne	*Uperoleia russelli*
Gascoyne	*Uperoleia saxatilis*
Gawler	*Crinia signifera*
Gawler	*Limnodynastes tasmaniensis*
Gawler	*Litoria ewingii*
Gawler	*Litoria platycephala*
Gawler	*Neobatrachus pictus*
Gawler	*Neobatrachus sudelli*
Gibson Desert	*Litoria maini*
Gibson Desert	*Neobatrachus sutor*
Gibson Desert	*Neobatrachus sudelli*
Gibson Desert	*Notaden nichollsi*
Great Sandy Desert	*Limnodynastes lignarius*
Great Sandy Desert	*Litoria australis*
Great Sandy Desert	*Litoria caerulea*
Great Sandy Desert	*Litoria cultripes*
Great Sandy Desert	*Litoria longipes*
Great Sandy Desert	*Litoria maini*
Great Sandy Desert	*Litoria nasuta*
Great Sandy Desert	*Litoria occidentalis*
Great Sandy Desert	*Litoria pallida*
Great Sandy Desert	*Litoria rubella*
Great Sandy Desert	*Neobatrachus aquilonius*
Great Sandy Desert	*Neobatrachus sudelli*
Great Sandy Desert	*Neobatrachus sutor*
Great Sandy Desert	*Notaden nichollsi*
Great Sandy Desert	*Platyplectrum ornatum*
Great Sandy Desert	*Platyplectrum spenceri*
Great Sandy Desert	*Uperoleia glandulosa*
Great Sandy Desert	*Uperoleia micromeles*
Great Sandy Desert	*Uperoleia saxatilis*
Great Sandy Desert	*Uperoleia talpa*

(continued)

Great Victoria Desert	*Neobatrachus aquilonius*
Great Victoria Desert	*Neobatrachus kunapalari*
Great Victoria Desert	*Neobatrachus pictus*
Great Victoria Desert	*Neobatrachus sudelli*
Great Victoria Desert	*Neobatrachus sutor*
Great Victoria Desert	*Notaden nichollsi*
Great Victoria Desert	*Pseudophryne occidentalis*
Great Victoria Desert	*Litoria maini*
Great Victoria Desert	*Litoria occidentalis*
Little Sandy Desert	*Uperoleia micromeles*
Little Sandy Desert	*Litoria maini*
Little Sandy Desert	*Litoria longipes*
Little Sandy Desert	*Neobatrachus aquilonius*
Little Sandy Desert	*Neobatrachus sudelli*
Little Sandy Desert	*Neobatrachus sutor*
Little Sandy Desert	*Notaden nichollsi*
Little Sandy Desert	*Litoria rubella*
Little Sandy Desert	*Platyplectrum spenceri*
Little Sandy Desert	*Litoria cultripes*
MacDonnell Ranges	*Litoria cultripes*
MacDonnell Ranges	*Litoria maini*
MacDonnell Ranges	*Litoria platycephala*
MacDonnell Ranges	*Litoria gilleni*
MacDonnell Ranges	*Litoria rubella*
MacDonnell Ranges	*Neobatrachus sudelli*
MacDonnell Ranges	*Neobatrachus sutor*
MacDonnell Ranges	*Notaden nichollsi*
MacDonnell Ranges	*Uperoleia micromeles*
Murchison	*Litoria maini*
Murchison	*Litoria occidentalis*
Murchison	*Litoria rubella*
Murchison	*Neobatrachus aquilonius*
Murchison	*Neobatrachus kunapalari*
Murchison	*Neobatrachus sudelli*
Murchison	*Neobatrachus sutor*
Murchison	*Neobatrachus wilsmorei*
Murchison	*Notaden nichollsi*
Murchison	*Platyplectrum spenceri*
Murchison	*Pseudophryne guentheri*
Murchison	*Pseudophryne occidentalis*
Nullarbor	*Litoria rubella*
Nullarbor	*Neobatrachus aquilonius*
Nullarbor	*Neobatrachus kunapalari*
Nullarbor	*Neobatrachus sudelli*
Nullarbor	*Pseudophryne occidentalis*

(continued)

Nullarbor	*Pseudophryne guentheri*
Nullarbor	*Litoria cyclorhyncha*
Nullarbor	*Neobatrachus sutor*
Pilbara	*Litoria australis*
Pilbara	*Litoria maini*
Pilbara	*Litoria occidentalis*
Pilbara	*Litoria rubella*
Pilbara	*Neobatrachus aquilonius*
Pilbara	*Neobatrachus sutor*
Pilbara	*Notaden nichollsi*
Pilbara	*Platyplectrum spenceri*
Pilbara	*Pseudophryne douglasi*
Pilbara	*Uperoleia glandulosa*
Pilbara	*Uperoleia saxatilis*
Pilbara	*Uperoleia talpa*
Simpson Strezlecki Dunefields	*Crinia deserticola*
Simpson Strezlecki Dunefields	*Limnodynastes fletcheri*
Simpson Strezlecki Dunefields	*Limnodynastes tasmaniensis*
Simpson Strezlecki Dunefields	*Litoria brevipes*
Simpson Strezlecki Dunefields	*Litoria caerulea*
Simpson Strezlecki Dunefields	*Litoria cultripes*
Simpson Strezlecki Dunefields	*Litoria latopalmata*
Simpson Strezlecki Dunefields	*Litoria longipes*
Simpson Strezlecki Dunefields	*Litoria maini*
Simpson Strezlecki Dunefields	*Litoria platycephala*
Simpson Strezlecki Dunefields	*Litoria rubella*
Simpson Strezlecki Dunefields	*Neobatrachus pictus*
Simpson Strezlecki Dunefields	*Neobatrachus sudelli*
Simpson Strezlecki Dunefields	*Notaden nichollsi*
Simpson Strezlecki Dunefields	*Platyplectrum spenceri*
Stony Plains	*Limnodynastes tasmaniensis*
Stony Plains	*Litoria platycephala*
Stony Plains	*Litoria maini*
Stony Plains	*Litoria platycephala*
Stony Plains	*Litoria rubella*
Stony Plains	*Neobatrachus sudelli*
Stony Plains	*Platyplectrum spenceri*
Tanami	*Litoria australis*
Tanami	*Litoria caerulea*
Tanami	*Litoria coplandi*
Tanami	*Litoria cultripes*
Tanami	*Litoria inermis*
Tanami	*Litoria longipes*
Tanami	*Litoria maini*
Tanami	*Litoria pallida*

(continued)

Tanami	*Litoria rubella*
Tanami	*Litoria watjulumensis*
Tanami	*Neobatrachus aquilonius*
Tanami	*Neobatrachus sudelli*
Tanami	*Notaden nichollsi*
Tanami	*Platyplectrum ornatum*
Tanami	*Platyplectrum spenceri*
Tanami	*Uperoleia borealis*
Tanami	*Uperoleia micromeles*

References

Andersson M (1997) Sexual selection. Princeton University Press, Princeton

Anstis M (2013) Tadpoles and frog of Australia. New Holland, London

Anstis M, Price LC, Roberts JD, Catalano SR, Hines HB, Doughty P Donnellan SC (2016) Revision of the water-holding frogs, *Cyclorana platycephala* (Anura: Hylidae), from arid Australia, including description of a new species. Zootaxa 4126:451–479

Blaylock LA, Ruibal R, Platt-Alola K (1976) Skin structure and wiping behaviour of Phyllomedusine frogs. Copeia 1976:283–295

Byrne M, Yeates DK, Joseph L, Kearney M, Bowle J, Williams MAJ, Cooper S, Donnellan SC, Keogh JS, Leys R, Melville J, Murphy DJ, Porch N, Wyrwoll K-H (2008) Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. Mol Ecol 17:4398–4417

Byrne M, Steane DA, Joseph L, Yeates DK, Jordan GJ, Crayn D, Aplin K, Cantrill DJ, Cook LG, Crisp MD, Keogh JS, Melville J, Moritz C, Porch N, Sniderman JMK, Sunnucks P, Weston PH (2011) Decline of a biome: evolution, contraction, fragmentation, extinction and invasion of the Australian mesic zone biota. J Biogeogr 38:1635–1656

Calaby JH (1960) A note on the food of Australian desert frogs. West Aust Nat 7:79–80

Cartledge VA, Withers PC, McMaster KA, Thompson GG Bradshaw SD (2006) Water balance of field-excavated aestivating Australian desert frogs, the cocoon forming *Neobatrachus aquilonius* and the non-cocooning *Notaden nichollsi* (Amphibia: Myobatrachidae). J Exp Biol 209:3309–3321

Catullo RA, Keogh JS (2014) Aridification drove repeated episodes of diversification between Australian biomes: evidence from a multi-locus phylogeny of Australian toadlets (*Uperoleia*: Myobatrachidae). Mol Phylogenet Evol 79:106–117

Catullo RA, Doughty P, Roberts JD, Keogh JS (2011) Multi-locus phylogeny and taxonomic revision of *Uperoleia* toadlets (Anura: Myobatrachidae) from the western arid zone of Australia, with a description of a new species. Zootaxa 2902:1–43

Catullo RA, Lanfear R, Doughty P, Keogh JS (2014) The biogeographical boundaries of Northern Australia: evidence from ecological niche models and a multi-locus phylogeny of *Uperoleia* toadlets (Anura: Myobatrachidae). J Biogeogr 41:659–672

Cogger HG (2014) Reptiles & amphibians of Australia, 7th edn. CSIRO Publishing, Collingwood

Crisp MD, Cook LG (2013) How was the Australian flora assembled over the last 65 million years? A molecular perspective. Annu Rev Ecol Evol Syst 44:303–324

Cullen LE, Grierson PF (2009) Multi-decadal scale variability in autumn-winter rainfall in South-Western Australia since 1655 AD as reconstructed from tree rings of *Callitris columellaris*. Clim Dyn 33:433–444

Davies KF, Melbourne BA, James CD, Cunningham RB (2010) Using traits of species to understand responses to land use change: birds and livestock grazing in the Australian arid zone. Biol Conserv 143:78–85

Davis RA, Roberts JD (2004) Operational sex ratio and mating behaviour of the myobatrachid frog *Neobatrachus kunapalari*. J R Soc West Aust 87:97–99

Dimmit MA, Ruibal R (1980) Exploitation of food resources by spadefoot toads (*Scaphiopus*). Copeia 1980:854–862

Donnellan S, Anstis M, Price L, Wheaton L (2012a) A new species of *Crinia* (Anura: Myobatrachidae) from the Flinders Ranges, South Australia. Zootaxa 3499:1–26

Donnellan SC, Mahony MJ, Bertozzi T (2012b) A new species of *Pseudophryne* (Anura: Myobatrachidae) from the central Australian ranges. Zootaxa 3476:69–85

Duellman WE, Marion AB, Hedges SB (2016) Phylogenetics, classification, and biogeography of the treefrogs (Amphibia: Anura: Arboranae). Zootaxa 4104:1–109

Frost DR, Grant T, Faivovich J, Bain RH, Haas A, Haddad CFB, De Sá RO, Channing A, Wilkinson M, Donnellan SC, Raxworthy CJ, Campbell JA, Blotto BL, Moler P, Drewes RC, Nussbaum RA, Lynch JD, Green DM, Wheeler WC (2006) The amphibian tree of life. Bull Am Mus Nat Hist 297:370

Gerhardt HC, Huber F (2002) Acoustic communication in insects and anurans. The University of Chicago Press, Chicago

Holloway AK, Cannatella DC, Gerhardt HC, Hillis DM (2006) Polyploids with different origins and ancestors form a single sexual polyploid species. Am Nat 167:E88–E101

Hoskin CJ, James S, Grigg GC (2009) Ecology and taxonomy-driven deviations in the frog call–body size relationship across the diverse Australian frog fauna. J Zool 278:36–41

James CD, Landsberg J, Morton SR (1999) Provision of watering points in the Australian arid zone: a review of effects on biota. J Arid Environ 41:87–121

Keller MJ, Gerhardt HC (2001) Polyploidy alters advertisement call structure in gray treefrogs. Proc R Soc Lond B 268:341–345

Lee AK (1968) Water economy of the burrowing frog, *Heleioporus eyrei* (Gray). Copeia 1968:741–745

Lee AK, Mercer EH (1967) Cocoon surrounding desert-dwelling frogs. Science 157:87–88

Lindgren E (1960) Frogs at Jigalong. West Aust Nat 7:78–79

Liu X, Rohr JR, Li Y (2013) Climate, vegetation, introduced hosts and trade shape a global wildlife pandemic. Proc R Soc Lond B 280:2012–2506

Mable BK, Roberts JD (1997) Mitochondrial DNA evolution of tetraploids in the genus *Neobatrachus* (Anura: Myobatrachidae). Copeia 1997:680–689

Mahony MJ, Robinson ES (1986) Nucleolar organiser region (NOR) location in karyotypes of Australian ground frogs (Family Myobatrachidae). Genetica 68:119–127

Mahony MJ, Donnellan SC, Roberts JD (1996) An electrophoretic investigation of relationships of diploid and tetraploid species of Australian desert frogs *Neobatrachus* (Anura: Myobatrachidae). Aust J Zool 44:639–650

Main AR (1964) A new species of *Pseudophryne* (Anura: Leptodactylidae) from North-Western Australia. West Aust Nat 9:66–72

Main AR (1968) Ecology, systematics and evolution of Australian frogs. Adv Ecol Res 5:37–85

Main AR, Calaby JH (1957) New records and notes on the biology of frogs from North-Western Australia. West Aust Nat 5:216–228

Martin AA (1972) Studies in Australian amphibia III. The *Limnodynastes dorsalis* complex (Anura: Leptodactylidae). Aust J Zool 20:165–211

Maxson LR, Ondrula DP, Tyler MJ (1985) An immunological perspective on evolutionary relationships in Australian frogs of the Hylid genus *Cyclorana*. Aust J Zool 33:17–22

McMaster KA (2006) Ecophysiology of Australian cocooning and non-cocooning, burrowing, desert frogs. PhD thesis, School of Animal Biology, University of Western Australia

Morton SR, Masters P, Hobbs TJ (1993) Estimates of abundance of burrowing frogs in spinifex grasslands of the Tanami desert, Northern Territory. The Beagle Rec North Territory Mus Arts Sci 10:67–70

Palmer JG, Cook ER, Turney CSM, Allen K, Fenwick P, Cook BI, O'Donnell A, Lough J, Grierson P, Baker P (2015) Drought variability in the Eastern Australia and New Zealand summer drought atlas (ANZDA, CE 1500-2012) modulated by the Interdecadal Pacific oscillation. Environ Res Lett 10:124002

Pillans B (2018) Seeing red: some aspects of the geological and climatic history of the Australian arid zone. In: Lambers H (ed) On the ecology of Australia's arid zone. CSIRO Publishing, Melbourne, pp 5–43

Predavec M, Dickman CR (1993) Ecology of desert frogs: a study from Southwestern Queensland. In: Lunney D, Ayres D (eds) Herpetology in Australia a diverse discipline, Transactions of the Royal Zoological Society of New South Wales. Royal Zoological Society of New South Wales, Mosman, pp 159–169

Ptacek MB, Gerhardt HC, Sage RD (1994) Speciation by polyploidy in treefrogs: multiple origins of the tetraploid, *Hyla versicolor*. Evolution 48:898–908

Pyron RA, Wiens JJ (2011) Large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. Mol Phylogenet Evol 61:543–583

Read JL (1992) Influence of habitats, climate, grazing and mining on terrestrial vertebrates at Olympic dam, South Australia. Rangel J 14:143–156

Rix MG, Edwards DL, Byrne M, Harvey MS, Joseph L, Roberts JD (2015) Biogeography and speciation of terrestrial fauna in the South-Western Australian biodiversity hotspot. Biol Rev 90:762–793

Roberts JD (1993) Hybridisation between the western and northern call races of the *Limnodynastes tasmaniensis* complex (Anura: Myobatrachidae) on the Murray River in South Australia. Aust J Zool 41:101–122

Roberts JD (1997a) Call evolution in *Neobatrachus* (Anura: Myobatrachidae): speculations on tetraploid origins. Copeia 1997:791–801

Roberts JD (1997b) Geographic variation in calls of males and determination of species boundaries in tetraploid frogs of the Australian genus *Neobatrachus* (Myobatrachidae). Aust J Zool 45:95–112

Roberts JD (2010) Taxonomic status of the Australian burrowing frogs *Neobatrachus sudelli*, *N. centralis* and *Neoruinosus* and clarification of the type specimen of *N. albipes*. Rec West Aust Mus 25:455–458

Roberts JD, Byrne PG (2011) Polyandry, sperm competition and the evolution of anuran amphibians. Adv Study Behav 43:1–53

Roberts JD, Maxson LR (1986) Phylogenetic relationships in the genus *Limnodynastes* (Anura: Myobatrachidae): a molecular perspective. Aust J Zool 34:561–573

Roberts JD, Maxson LR (1989) A molecular perspective on relationships of Australian *Pseudophryne* (Anura: Myobatrachidae). Syst Zool 38:154–165

Roberts BP, Roberts JD (2012) *Litoria moorei* (Motorbike Frog) temperature. Herpetolog Rev 43:466–467

Robertson JGM (1984) Acoustic spacing by breeding males of *Uperoleia rugosa*(Anura: Leptodactylidae). Zeitschrift für Tierpsychologie 64:283–297

Robertson JGM (1986a) Male territoriality, fighting and assessment of fighting ability in the Australian frog *Uperoleia rugosa*. Anim Behav 34:763–772

Robertson JGM (1986b) Female choice, male strategies and the role of vocalizations in the Australian frog *Uperoleia rugosa*. Anim Behav 34:773–784

Robertson JGM (1990) Female choice increases fertilization success in the Australian frog, *Uperoleia laevigata*. Anim Behav 39:639–645

Schmid M, Evans BJ, Bogart JP (2015) Polyploidy in Amphibia. Cytogenet Genome Res 145:315–330

Slatyer C, Rosauer D, Lemckert F (2007) An assessment of endemism and species richness patterns in the Australian Anura. J Biogeogr 34:583–596

Steinborner ST, Gao CW, Raftery MJ, Waugh RJ, Blumenthal T, Bowie JH, Wallace JC, Tyler MJ (1994) The structures of four tryptophyllin and three rubellidin peptides from the Australian red tree frog *Litoria rubella*. Aust J Chem 47:2099–2108

Symula R, Keogh JS, Cannatella DC (2008) Ancient phylogeographic divergence in southeastern Australia among populations of the widespread common froglet, *Crinia signifera*. Mol Phylogenet Evol 47:569–580

Thompson GG, Withers PC, McMaster KA, Cartledge VA (2005) Burrows of desert-adapted frogs, *Neobatrachus aquilonius* and *Notaden nichollsi*. J R Soc West Aust 88:17–23

Tozer CR, Vance TR, Roberts JL, Kiem AS, Curran MAJ, Moy AD (2016) An ice core derived 1013-year catchment-scale annual rainfall reconstruction in subtropical eastern Australia. Hydrol Earth Syst Sci 20:1703–1717

Tyler MJ (1971) The phylogenetic significance of vocal sac structure in hylid frogs. Uni Kansas Publ Mus Nat Hist 19:319–360

Tyler MJ, Doughty P (2009) Field guide to frogs of Western Australia, 4th edn. Western Australian Museum, Perth

Van Beurden E (1980) Energy metabolism of dormant Australian water-holding frogs (*Cyclorana platycephalus*). Copeia 1980:787–799

Vidal-García MV, Byrne PG, Roberts JD, Keogh JS (2014) The role of phylogeny and ecology in shaping morphology in 21 genera and 127 species of Australo-Papuan myobatrachid frogs. J Evol Biol 27:181–192

Warburg M (1965) Studies on the water economy of some Australian frogs. Aust J Zool 13:317–330

Wells KD (2007) The ecology and behaviour of anurans. University of Chicago Press Ltd, London

Withers PC (1992) Comparative animal physiology. Saunders College Publishing, Fort Worth

Withers PC (1993) Metabolic depression during aestivation in the Australian frogs, *Neobatrachus* and *Cyclorana*. Aust J Zool 41:467–473

Withers PC (1995a) Evaporative water loss and colour change in the Australian desert tree frog *Litoria rubella* (Amphibia: Hylidae). Rec West Aust Mus 17:277–281

Withers PC (1995b) Cocoon formation and structure in the aestivating Australian desert frogs, *Neobatrachus* and *Cyclorana*. Aust J Zool 43:429–441

Withers PC (1998) Evaporative water loss and the role of cocoon formation in Australian frogs. Aust J Zool 46:405–418

Withers PC, Hillman SC, Drewes RC (1984) Evaporative water loss and skin lipids of anuran amphibians. J Exp Zool 232:11–17

Young JE, Christian KA, Donnellan S, Tracy CR, Parry D (2005) Comparative analysis of cutaneous evaporative water loss in frogs demonstrates correlation with ecological habits. Physiol Biochem Zool: Ecol Evol Approaches 78:847–856

Terrestrial and Inland-water Invertebrates of the Australian Arid Zone

Jonathan D. Majer, Mark S. Harvey, W. F. Humphreys, Jenny A. Davis, and Alan L. Yen

Introduction

Life on earth consists of a wondrous array of organisms, from bacteria and viruses, to redwoods and whales. But it's the invertebrates – those animals without a backbone – that have diversified most notably. Wilson (1987) called them the 'little things that run the world' and made a call to arms to bring invertebrate conservation to the forefront of our minds.

The Australian terrestrial invertebrate fauna – which we here define as occurring in terrestrial and inland-water environments – is highly diverse, with many immense radiations as well as archaeic, relictual elements. While the fauna of the Australian mesic and tropical zones has been well studied, even if all taxa are not yet named, the arid zone fauna has arguably received considerably less attention.

J. D. Majer (✉)
School of Biological Sciences, The University of Western Australia,
Crawley (Perth), WA, Australia

School of Molecular and Life Sciences, Curtin University, Bentley, WA, Australia
e-mail: jonathan.majer@uwa.edu.au

M. S. Harvey · W. F. Humphreys
Department of Terrestrial Zoology, Western Australian Museum,
Welshpool DC, WA, Australia

School of Biological Sciences, The University of Western Australia, Crawley, WA, Australia

J. A. Davis
College of Engineering, IT and Environment, Charles Darwin University,
Darwin, NT, Australia

A. L. Yen (deceased)
Department of Economic Development, Jobs, Transport and Resources, La Trobe University,
Bundoora, VIC, Australia

School of Applied Systems Biology, AgriBio, La Trobe University, Bundoora, VIC, Australia

H. Lambers (ed.), *On the Ecology of Australia's Arid Zone*,
https://doi.org/10.1007/978-3-319-93943-8_8

Fig. 1 Representative invertebrates of the Australian arid zone: A, land snail (Camaenidae, *Granulomelon grandituberculatum*); B, scorpion (Buthidae, *Lychas* sp.); C, scorpion (Urodacidae, *Urodacus butleri*); D, pseudoscorpions (Garypidae, *Synsphyronus* sp.); E, harvestman (Assamiidae, *Dampetrus* sp.); F, schizomid (Hubbardiidae, *Draculoides* sp.); G, tarantula spider (Theraphosidae, *Selenocosmia* sp.); H, wolf spider (Lycosidae, *Hoggicosa bicolor*); I, centipede (Scolopendridae, *Scolopendra morsitans*); J, centipede (Scutigeridae, *Allothereua* sp.); K, millipede (Trigoniulidae, *Austrostrophus* sp.); L, keeled millipede (Paradoxosomatidae, *Antichiropus* sp.); M, slater (Armadillidae, *Buddelundia* sp.); N, freshwater isopod (Amphisopodidae, *Phreatomerus latipes*); O, bathynelloid (Parabathynellidae, *Brevisomabathynella uramurdahensis*); P, thermosbaenacean (Halosbaenidae, *Halosbaena* sp.). Images by V. Kessner (A), M. Harvey (B–M), J. Davis (N), K. Abrams (O), D. Elford (P)

In this chapter we outline the current state of knowledge about terrestrial invertebrates of the arid zone, their origins, how they cope with the conditions in the arid zone, their value as food for humans, and their conservation status. Although this chapter deals with terrestrial invertebrates, we also consider how the fauna can be enriched by surface water manifestations at soaks and mound springs. Some representatives of the major invertebrate lineages are depicted in Figs. 1 and 2.

An earlier book entitled *Evolution of the Flora and Fauna of Arid Australia* (Barker and Greenslade 1982) stated that, in contrast to plants and vertebrates, 'our knowledge of the terrestrial invertebrates of the arid zone (and) their representation in collections' is very poor. Although the situation has greatly improved, the relative scarcity of available information on terrestrial invertebrates, when compared with plants and vertebrates, still remains. This is probably due to the fact that the majority of our population and our research and teaching institutions are situated close to the coast, creating cost and time impediments to research and surveys in the arid zone. Furthermore, the work that has been performed in the arid zone tends to be confined to brief surveys, rather than long-term studies, which is also an inevitable consequence of distance.

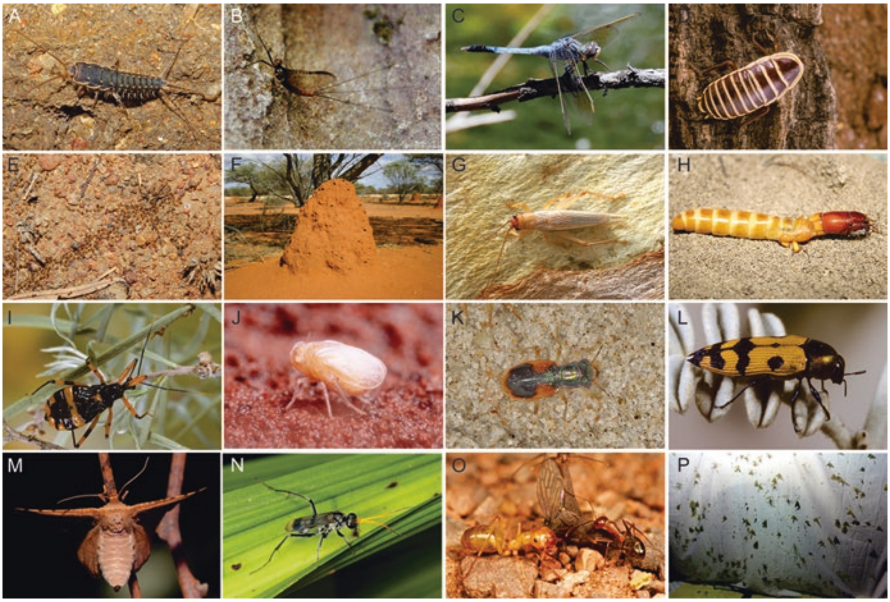


Fig. 2 Representative invertebrates of the Australian arid zone: A, silverfish (Lepismatidae); B, unidentified mayfly; C, dragonfly (Libellulidae, *Orthetrum caledonicum*); D, cockroach (Blattidae, *Desmozosteria cincta*); E, termites (Termitidae); F, termite mound (Termitidae); G, cricket (Gryllidae, *Raitina* sp.); H, sand groper (Cylindrachetidae, *Cylindraustralia* sp.); I, assassin bug (Reduviidae, possibly, *Poecilosphodrus* sp.); J, plant hopper (Meenoplidae, *Phaconeura* sp.); K, tiger beetle (Carabidae, *Megacephala* sp.); L, jewel beetle (Buprestidae, *Castiarina* sp.); M, picture-winged moth (Thyrididae, *Misalina innotata*); N, wasp (Pompilidae, possibly *Fabriogenia* sp.); O, ants (Formicidae, *Melophorus* sp.); P, insects attracted to a light sheet in arid Australia. Images by D. Rentz (A, E, K–N); J. Davis (B, C); Museum Victoria (D, I); M. Harvey (F–H); D. Elford (J); A. Narendra (O); A. Austin (P)

History and Scope of Knowledge

The arid zone has been the subject of various forays by generalist and specialist scientists since the early days of exploration through to the present time. Historical information on invertebrates of the arid regions of Australia is very limited. Although most of the Australian continent is semiarid or arid, the invertebrate fauna is hardly mentioned in any of the earlier entomology books (e.g. Froggatt 1907; Tillyard 1926). It does get a brief coverage in Froggatt (1901), and Matthews (1976) provides a broader ecological discussion.

Information on arid zone invertebrates has accumulated from five different sources: (1) explorers; (2) scientific expeditions; (3) plant and vertebrate surveys in which some invertebrates were collected; (4) in more recent years, invertebrate biodiversity and environmental assessments; and (5) ad hoc collectors. Arid zone invertebrates are both species-rich and abundant, yet the early collections made were relatively small. This was primarily influenced by the technical aspects of the early expeditions (transport by horses and camels), the reliance on a small number of collecting techniques (mainly direct hand collecting or netting), a greater interest in the vertebrates, and a lack of realisation of the true diversity of the invertebrate fauna and species turnover associated with distance. One significant change in surveying invertebrates has been the introduction of pitfall trapping, which, along with light trapping and also baiting, results in much more extensive catches.

Explorers

Invertebrates, in particular, were not the main concern of the early explorers. Most considered the ants and flies a hindrance (e.g. Sturt 1849; Warburton 1875; Giles 1889). Sturt (1849) but Tietkens (1891) did, however, relate an occasional observation on moths and termites, and, along with Giles (1889), they collected a few specimens of butterflies, ants and a scorpion. The fate of these specimens is not known, a situation that has happened with many of the expeditions. Sturt (1849) provided a bird list that included many insectivorous species (based on observations during that expedition). An earlier explorer, John Eyre, actually collected some specimens, and descriptions of new species are found in Appendix 1 of Eyre (1845). These include Orthoptera, Neuroptera and Hemiptera species described by Adam White and moths by Edward Doubleday.

Scientific Expeditions

The arid zone has been the subject of several early scientific expeditions. These expeditions had different aims and emphases, and the amount of invertebrate material resulting from each expedition varied considerably. One of the better-known expeditions was the disastrous Burke and Wills expedition that started from Melbourne to the north coast and passed through some semiarid regions of New South Wales and Queensland (1860–1861). Ludwig Becker was the zoologist who died during the expedition; he made notes on invertebrates and painted a small number of species (Yen 2011). Becker stated that he collected flies for scientific study, but the fate of that collection is not known. Hermann Beckler, who was more interested in plants and geology, also made notes on invertebrates. Beckler also collected specimens that he sent back to Germany (Yen 2011). The collection of specimens that were sent to Europe was a relatively common phenomenon in the nineteenth century, but the location of much of this material is in many cases unknown.

David Lindsay led the 12-month Elder Scientific Expedition (1891–1892) through South and Western Australia. More than 150 new species of invertebrates were collected by the naturalist Richard Helms, and these were listed as follows:

molluscs (Bednall 1892, 1894), beetles (Blackburn 1892, 1893; Sloane 1893a, b), Lepidoptera (Lower 1892) and Hymenoptera (Froggatt 1893).

Incidental insect material was also collected by people while working on other disciplines. For example, the South Australian Museum has material collected by the palaeontologist Amandus Zietz at Lake Callabonna in 1893, from which Tepper (1893, 1895) described Orthoptera and Blattodea, Sloane (1895) identified Carabidae and Blackburn included other species of beetles into several papers (e.g. Blackburn 1895). Tate (1894) diagnosed some molluscs from Central Australia but did not state how the specimens were procured.

In 1894, the Horn Expedition collected material in Central Australia from Oodnadatta through to the Alice Springs region and southwest to the Uluru region (Spencer 1896a). The expedition members worked on plants, animals, fossils, geology and anthropology. With regard to invertebrates, 415 species were collected, including 124 new species (Yen 1996). The invertebrates were Mollusca (Tate 1896), Oligochaeta (Spencer 1896b), Araneae (Hogg 1896), Blattodea, Mantodea, Dermaptera, Orthoptera, Phasmatodea (Tepper 1896), Coleoptera (Blackburn 1896; Sloane 1896), Lepidoptera (Lower 1896), ants (Froggatt 1896; Kirby 1896), other Hymenoptera (Kirby 1896), Isoptera (Froggatt 1898) and Hemiptera (Bergoth 1916).

White (1910) conducted an ornithological expedition to the Eyre Peninsula that resulted in a few minor observations on insects and many comments on insect diet of birds, although no insects were apparently collected. Later expeditions included the 1913 expedition from Oodnadatta to the Alice Springs region (White 1914); the invertebrates collected were Mollusca (Matthews 1914), Crustacea (Baker 1914), Arachnida (Pulleine 1914), beetles (Lea 1914b), butterflies (Waterhouse 1914), moths (Turner 1914) and Hymenoptera (Froggatt 1914), while Lea (1914a) listed the stomach content of birds. The South Australian Museum organised an expedition to Strzelecki and Coopers Creek in 1916 (Waite 1917), and the invertebrates collected were Crustacea (Chilton 1917), insects (Lea 1917b), arachnids (Rainbow 1917) and stomach contents of birds (Lea 1917a). The Royal Society of South Australia organised a 1939 Simpson Desert Expedition to study the flora and fauna. The only resulting publications were on spiders and scorpions (Hickman 1944) and Hemiptera (Musgrave 1945).

The earlier expeditions were primarily conducted in South Australia, Western Australia and the southern part of the Northern Territory. Wells (1993) outlines a history of entomologists collecting in the Northern Territory, and it was all conducted in the wetter northern parts of the Territory.

Plant and Vertebrate Surveys (Invertebrates Secondary)

The expeditions up to the end of World War I relied on animal transportation (camels or horses). The introduction of motorised transport resulted in surveys that could include repeat visits to selected locations (thus allowing for seasonal differences to be determined), using different collecting techniques, and as there was development in the arid zone, the establishment of field research stations (such as CSIRO in Alice Springs and the University of New South Wales at Fowler's Gap in western New South Wales) and experimental locations (e.g. Kunoth Paddock near Alice Springs). Research on flora and fauna was transformed from a pure species inventory survey approach to more functional and applied approaches. However, the emphasis was primarily on plants and vertebrates, land-use issues (often about how land could be used for commercial activities such as cropping or grazing) and eventually for land management with conservation outcomes. For instance, in Western Australia the 12 *Biological Survey of the Eastern Goldfields of Western Australia* reports (Biological Surveys Committee 1984–1995) all contained chapters on plants and vertebrates, but none on invertebrates. A similar situation arose with the *Biological Survey of the Nullarbor Region, South and Western Australia in 1984*, which contained no chapters on invertebrates (McKenzie and Robinson 1987). Invertebrates were not considered in much of this work, until there was some recognition that many of the ecological functions essential in the arid zone involved invertebrates. These include seed dispersal (Morton 1982) and the food requirements of insectivorous vertebrates (Morton and James 1988). The survey situation had improved by the last decade, when the *Biodiversity of the Carnarvon Basin* survey (Burbidge et al. 2000) included chapters on aquatic invertebrates, scorpions, mygalomorph spiders, araneomorph spiders and myriapodous groups, as well as a subsequent paper on ants (Gunawardene and Majer 2004). Shortly afterwards, the *Biodiversity Survey of the Pilbara Region of Western Australia, 2002–2007* (George et al. 2010), encompassed surveys and papers on aquatic invertebrates, scorpions, spiders, beetles and ants. Finally, although not part of a government survey, the Chevron-sponsored surveillance programme on Barrow Island resulted in a book entitled *The Terrestrial Invertebrate Fauna of Barrow Island, Western Australia* (Gunawardene et al. 2013), which covered all sampled groups of terrestrial invertebrates.

The vastness of arid Australia, the inaccessible nature of parts of it and the species turnover associated with the invertebrates make it difficult to systematically conduct a comprehensive species inventory for the region. Early records were biased towards larger-bodied and easy to collect and identify insects, but the recognition of the ecological roles of different invertebrate groups revealed the importance of social insects such as ants and termites. The use of pitfall traps to collect ground-active invertebrates significantly increased the number of species collected during surveys. Parts of the arid zone are subjected to unpredictable weather and climate (droughts and floods) that can result in massive temporal changes in the fauna, as we discuss later. To complicate matters further, fire is an important ecological factor, and as we discuss later, how it affects invertebrates is still unclear. There have been some preliminary attempts to understand the roles of invertebrates without full taxonomic identities in semiarid and arid Australia (Greenslade 1978a, b, 1982, 1985a, b; Greenslade and Greenslade 1984, 1989; Matthews 1976; Yen 1989).

One recent initiative has increased knowledge of the invertebrate species in parts of Australia considerably. The Bush Blitz programme, started in 2010, was implemented to survey newly established reserves across Australia for flora and fauna. Several of the surveys have been conducted in arid Australia, such as Henbury Station (NT) (ABRS 2015a), Hiltaba Station (ABRS 2015b), Bon Bon Reserve (ABRS 2013a), Witchelina Station (SA) (ABRS 2013b), Credo Station (ABRS 2015c), Cane River (ABRS 2014a) (WA) and Ned's Corner (ABRS 2014b) (Vic).

The Uluru fauna surveys initially only collected vertebrates (Reid et al. 1993) but included invertebrates in 1995, 1997, 2000 and 2004 (Yen et al. 1996; Yen and Wainer 2003). Further south from Uluru, the Anangu Pitjantjatjara lands in South Australia were surveyed for both vertebrates and invertebrates (Robinson et al. 2003), and further east in the semiarid northwest of Victoria, both vertebrates and invertebrates were surveyed in a pitfall trapping programme from 1984 to 1985 (Robertson et al. 1989; Yen 1987).

The material from expeditions and surveys that was deposited in institutions such as the state museums and the Australian National Insect Collection in Canberra was used, in conjunction with smaller ad hoc collections for taxonomic research of some invertebrate groups. In South Australia, the collections provided material to prepare identification guides to ants (Greenslade 1979) and to several families of beetles (Matthews 1980, 1982, 1984, 1985, 1987, 1992, 1997; Matthews and Reid 2002).

In summary, invertebrates have been collected from various parts of arid Australia. The collections have accumulated over the last 150 years and resulted from ad hoc collections of invertebrates of interest, to flora and fauna surveys, and, in more recent years, environmental assessments.

Invertebrates in the Arid Zone: Origins and Diversity

Taxonomic Composition and Phylogenetic Patterns

The vast majority of terrestrial invertebrate orders that occur in Australia (Harvey and Yen 1989) also occur in the arid zone. Notable absentees include velvet worms (Onychophora), leeches (Hirudinidea), whip spiders (Amblypygi), craterostigmatid centipedes (Craterostigmatida), pill millipedes (Sphaerotheriida), sucking millipedes (Siphonophorida), craspedosomatid millipedes (Craspedosomatida) and alder flies (Megaloptera), which are all confined to the mesic zones of southern and/or eastern Australia. Members of a few other orders are extremely rare or highly localised.

While the origins of many taxa are unclear, others show either clear southern or northern origins or are at least most closely related to such groups. For example, the arachnid order Schizomida (Fig. 1) occurs in the tropics of northern Australia with various taxa occurring in subterranean ecosystems in the arid zone (Harvey 1992; Harvey et al. 2008). Conversely, the trapdoor spider family Idiopidae is abundant in mesic and semiarid zones in southern and eastern Australia, with multiple incursions into the arid zone, particularly of the genus *Aganippe* (Main 1957). Such contrasting patterns are not unexpected, of course, and fit similar patterns of non-invertebrate groups.

The Australian arid zone includes many relictual taxa, some with naturally small distributions that are sometimes known as short-range endemic species (see Harvey 2002; Harvey et al. 2011; Majer 2009). Most of these relictual taxa are remnants of a more widespread mesic zone fauna that was gradually extirpated or displaced by aridification processes that commenced in the Miocene-Pliocene (Byrne et al. 2008; Rix et al. 2015), and they tend to occupy habitat refugia such as mound springs, mountain ranges or subterranean ecosystems (see below), where climatic extremes are mollified.

One of the better-studied groups, land snails, is particularly subject to desiccation, and their beta diversity is greatest in mesic environments where constant high moisture levels allow for population persistence. Nevertheless, numerous land snails occur in the arid zone, particularly where sufficient habitat heterogeneity provides feeding and aestivation sites. Their activity is usually restricted to rainfall events, either during or after monsoonal events or winter rainfall. The three species of the camaenid genus *Granulomelon* occupy upland habitats in Central Australia (Fig. 1) and are hypothesised to have diverged during the intensely arid mid-Pleistocene (Criscione and Köhler 2016). Another camaenid genus, *Rhagada*, exhibits complex patterns of diversification and shell morphology that are only becoming apparent through the use of molecular sequence data (e.g. Johnson et al. 2004, 2012; Hamilton and Johnson, 2015; Stankowski 2015). Such detailed studies are largely lacking for other invertebrate taxa.

Other invertebrate groups, including beetles, ants and other Hymenoptera, plant bugs, termites (Fig. 2) and spiders (Fig. 1), show extremely high diversification levels in the Australian arid zone. The prevailing hypothesis of progressive diversification since the onset of aridity in the Miocene is supported by molecular phylogenies of various plant and animal groups that exhibit post-Miocene radiation patterns (e.g. see reviews by Byrne et al. 2008, 2011; Rix et al. 2015). Unfortunately, many taxonomic treatments of hyper-diverse arid zone invertebrate taxa are currently lacking complementary molecular treatments which are hampering our understanding of the evolutionary origins of the modern Australian arid invertebrate fauna. However, notable exceptions include genetic studies of subterranean fauna (see below).

Diversity

The world's invertebrate fauna is the least known of all multicelled biota, with a recent estimate of the Australian fauna comprising ca. 340,000 species, of which only ca. 98,000 have been described (Chapman 2009). The largest terrestrial group, the insects, comprises ca. 205,000 species, with only ca. 62,000 named. The second most diverse group, the Arachnida, has only 6615 named species with an estimated total of ca. 31,000 species. In contrast, the Australian flora comprises 26,845 species of which 24,716 are named, and the terrestrial vertebrate fauna (excluding fishes) comprises 2470 species of which 2358 are named (Chapman 2009). This lack of basic knowledge of the Australian invertebrate fauna, the taxonomic impediment (Taylor 1983), is intensified in the arid zone due to large distances from the major population centres, although the past 30 years has certainly seen an increase in survey effort. The lack of taxonomic knowledge is even exemplified at the generic level as new genera are being described every year. The lack of formal taxonomic names also hampers ecological studies and, most importantly, conservation efforts (Harvey et al. 2011).

Coping with Life in the Arid Zone

Aridity and Unpredictability of Rainfall

By its very nature, the arid zone is characterised by its low rainfall (Wyrwoll this book), which restricts plant productivity and presents a generally harsh environment, posing restrictions for invertebrates living in this region. In addition to this, rainfall is highly unpredictable in its occurrence, both in terms of the months in which it falls and by the amount of rain, which can vary from almost none in a given year through to levels sufficient to cause flooding. Despite this, the diversity of many invertebrate groups is remarkably high in the arid zone, with the fauna exhibiting various responses, both at the individual species and community level.

With few long-term studies being available for the arid zone, community responses are not well known. The invertebrate surveys carried out on Barrow Island (see Gunawardene et al. 2013), 56 km off the mainland of northwest Australia, provide a rare opportunity to examine this. As an example, one set of 12 ‘gas plant’ (GP) sites was sampled by an array of procedures in the March 2006 wet period and resampled by identical methods during the September 2006 dry period (Callan et al. 2011). A non-parametric multidimensional scaling (NMDS) ordination of the 12 GP sites is shown in Fig. 3a. The distances in ordination space between the wet season samples were less than those for the dry season samples, indicating that site variability in terms of invertebrate composition was less after rain than during dry conditions. The two seasons of sampling are clearly separated, with the two clusters being significantly different (global R = 0.979; $P = 0.001$). The ordering of the sites along the second axis is similar for both seasons and appears to be associated with other factors such as distance from the coast (global R = 0.166; $P = 0.03$) and soil type (global R = 0.159; $P = 0.057$) but only weakly and not significantly so with vegetation type (global R = 0.078; $P = 0.174$; n.s.). This ordination, therefore, indicates that rainfall has a more profound influence on the composition of the fauna than do site factors.

A further set of 13 ‘nonindigenous species’ (NIS) sites was sampled in May 2006 and resampled by identical methods in May 2007, ostensibly during the same season (Callan et al. 2011). Figure 3b shows the NMDS ordination. The 2 years of

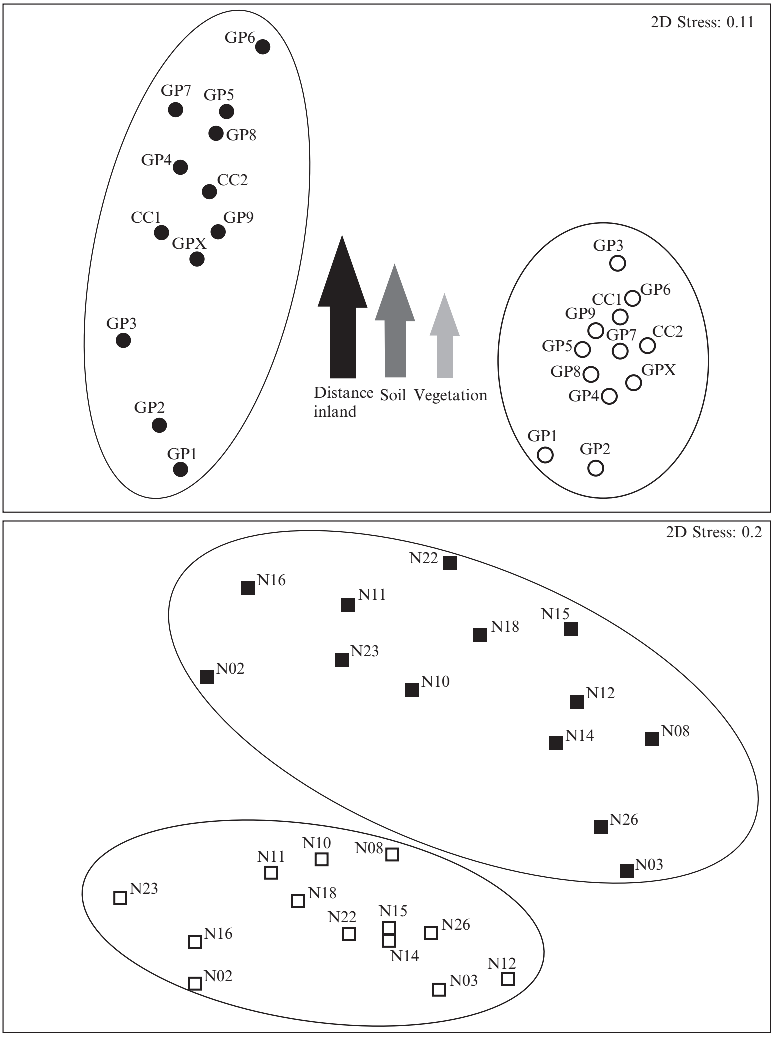


Fig. 3 Non-parametric multidimensional scaling (NMDS) ordination of the Barrow Island gas plant (GP) sites (top) and the nonindigenous species survey (NIS) sites (bottom), both of which were sampled twice. The left-hand cluster of the GP ordination delimits the March 2006 wet season, and the right-hand cluster delimits the September 2006 dry season samples; the left- and right-hand clusters of the NIS ordination delimit the May 2006 and May 2007 samples, respectively (Source: Diagram from Majer et al. 2013)

sampling are separated on the first axis, and the 2 years are significantly different (ANOSIM global R = 0.687; $P = 0.001$). This highlights the fact that, with the unpredictable rainfall patterns in this climatic zone, the same periods in different years cannot be assumed to be equivalent in terms of seasonal phases on the biota. Although the two ordinations are not entirely equivalent in terms of number of taxa and sites, the size of the global R statistics indicates that inter-year variation in the biota can be almost as great as the variation between wet and dry seasons within a given year.

These two surveys highlight the massive turnover of species, with over half the species sampled during one survey being absent in the next. So, how do such organisms survive during the intervening periods? Some groups, such as Collembola, may have desiccation-resistant anhydric stages or may retreat into moist microsites such as under bark (Greenslade 1981) where they are not readily sampled. Many other groups may survive arid periods through quiescent egg or pupal stages, only emerging when conditions are favourable. Other taxa may use migration as a means to avoid arid periods and capitalise on conditions when water becomes available. This is exemplified by conditions on Barrow Island, where there are no permanent waterbodies and hence no habitat for species that have an aquatic stage in their life cycle. Long-term sampling on Barrow Island revealed the presence of dragonflies following rain, which presumably arrived from the mainland when water became available.

Subterranean Life: The Ultimate Solution to Aridity

Representatives of many invertebrate groups have avoided aridity by colonising the subterranean realm, usually evolving morphological traits such as loss of eyes, elongate appendages and reduction of pigmentation (Figs. 1O, P and 2J). The onset of arid conditions across Australia during the Miocene was probably responsible for at least the initial phases of this colonisation, with impressive radiations, notably in the Pilbara and Yilgarn regions of Western Australia and on the Nullarbor Plain.

Notable invertebrate groups with subterranean representatives in the arid zone include aquatic worms (e.g. Brown et al. 2015), spiders (e.g. Baehr et al. 2012), pseudoscorpions (e.g. Harvey and Edward 2007; Harrison et al. 2014), schizomids (Fig. 1; e.g. Harvey et al. 2008), crustaceans such as amphipod and isopods (Fig. 1; e.g. King 2009; King et al. 2012; Page et al. 2008; Abrams et al. 2012; Javidkar et al. 2015) and hexapods including silverfish, cockroaches and beetles (e.g. Cooper et al. 2002; Leijs et al. 2012; Smith et al. 2012).

In a pioneer study titled *The Biogeography of Cape Range*, Humphreys (1993) focused on the cave fauna of this tertiary orogenic karst in north-western Australia, and the report includes papers on non-marine molluscs, cavernicolous arachnids and myriapods, crustaceans and subterranean biology. It was the prelude to a wave of discoveries across Australia of possibly the most diverse subterranean fauna globally which, surprisingly, is concentrated in the arid zone. Troglobionts occur in all types of subterranean voids including novel systems such as groundwater calcretes and pisolites, i.e. sedimentary rocks made of pisoids, which are concretionary grains, often of calcium carbonate. This fauna comprises obligate subterranean lineages with both terrestrial and aquatic habits, respectively, comprising troglobionts and stygobionts. Stygobionts predominantly comprise crustaceans belonging to the bathynellaceans, copepods, ostracods, amphipods and isopods. Troglobionts are predominantly slaters, arachnids, myriapods and a rather restricted set of hexapods (diplurans, springtails, silverfish, crickets, cockroaches, bugs and beetles; Figs. 1 and 2). The species richness at any one site (the α-diversity; 54 species in a single borehole) is unexceptional to a surface biologist, but in the context of subterranean biology, it greatly exceeds subterranean species densities recorded globally. Subterranean species have very small distributions, and so β-diversity (between site diversity) is also very high, as also is γ-diversity (a measure of differences between regions) with an almost complete turnover of genera of stygofauna between the contiguous Pilbara and Yilgarn regions (Humphreys 2008).

Initially the arid zone subterranean fauna was studied in caves in typical carbonate karst (Nullarbor, Cape Range, Barrow Island) and in alluvial aquifers (Humphreys 1999). Increasingly, the subterranean fauna in the arid zone is typically accessed down boreholes (wells) in areas completely lacking in caves. These include groundwater calcretes in the Yilgarn (Leijs et al. 2012) and Northern Territory (Cho et al. 2006) and lacustrine and groundwater calcretes in the Pilbara (Poore and Humphreys 1998; Finston et al. 2009) and in the fractured rock and goethite pisolite formations derived from Precambrian banded iron formations and their derivatives. In the arid zone, the overwhelmingly greater part of the subterranean fauna is in areas lacking caves.

The subterranean fauna is poorly described but is best known from the Western Shield, and our understanding of it is changing rapidly. Guzik et al. (2010) considered that 960 species of non-crustacean terrestrial troglobionts awaited discovery, mainly in the Western Shield, but this is likely a considerable underestimate, as 566 troglobiont species were recorded by sampling just ~1% of the area of the Pilbara and another 92 species from the Yilgarn (Halse and Pearson 2014). In addition 350 species of stygobiont were recorded by Halse et al. (2014) from the Pilbara, despite only one sample site per 460 km^2.

The best-studied subterranean aquatic systems are the calcretes that form from groundwater as it approaches the base level at salt lakes, becoming gradually more saline owing to evaporation. They have been described as groundwater estuaries and likened to anchialine habitats at the coast that also support stygobionts, but largely with marine affinities (Humphreys et al. 2009). In the Yilgarn, calcrete aquifers are typically salinity-stratified, becoming markedly hypersaline with depth, but with water conditions highly variable with both depth and spatially over short distances (Watts and Humphreys 2003, 2006). Some stygobionts such as parabathynellids (Fig. 1) that are considered freshwater animals occur in situations where the surface water is already at typical marine salinity (Humphreys 2006). Conversely, groundwater in the Pilbara is typically fresh throughout its depth and supports a remarkable diversity of ancient lineages. These include two of the four species of Spelaeogriphacea (others in South Africa and Brazil), Thermosbaenacea (Fig. 1; considered a Tethyan lineage) and Candonini ostracods that occur in groundwater of Australia, Africa and South America, indicating a Gondwanan heritage (Humphreys 2008). The three tribes comprise 13 genera, and all but one of the genera are endemic to the Pilbara, with the genus *Candanopsis* occurring in the Yilgarn and the other two continents.

The onset of aridity in Australia has long been proposed as the major driver of subterranean colonisation, subsequent isolation and speciation. Hypotheses about the ecological processes that led to the diversity of subterranean fauna in the Australian arid zone have been derived from our sparse knowledge. The development of aridity was proposed at a landscape scale to account for the formation in Cape Range of genetic 'provinces' within humid forest lineages of terrestrial troglobionts, entirely dependent on high humidity and allochthonous organic carbon (Humphreys 1991), for which no close relatives of the cave fauna have persisted on the surface in this now arid area (Humphreys 1993; Humphreys and Adams 2001). The diving beetles are considered to have had preadaptations, often referred to as exaptations — such as preference for temporary, but seasonally reliable, water and preference to live amongst gravel and sand along running water — that would have favoured transitions from surface to subterranean life, but the much smaller body size of stygiobiont species due to larger body size limiting the likelihood of successful transitions (Leys and Watts 2008). Populations of stygobiont amphipods have become isolated in headwater tributaries in the Pilbara (Finston et al. 2007) consistent with the pattern expected from the changes in flow conditions and water quality from the progressive development of aridity (Humphreys 2001), the headwater isolation model. Conversely, the diving beetle faunas of the isolated calcretes distributed along the length of in the Yilgarn palaeovalleys do not map the drainage pattern. Rather, the molecular phylogeny supports a model of multiple independent invasions of calcretes across a wide region (Leys et al. 2003), a model applicable also to the parabathynellids, amphipods and isopods inhabiting the calcrete aquifers (Cooper et al. 2007, 2008; Abrams et al. 2012; Guzik et al. 2008, 2009; Watts and Humphreys 2009). This 'groundwater island model', whereby each isolated calcrete contains an endemic troglobiont fauna, originally established for stygobionts (Cooper et al. 2002) is being extended to terrestrial troglobionts (Javidkar 2014). The ecological and geographical context of this fauna is more fully described elsewhere (Humphreys 2008, 2012).

Arid Zone Aquatic Invertebrates and the Importance of Refugia

Since arid landscapes are highly water-limited environments, no permanently flowing rivers or deep freshwater lakes are present in the ancient and topographically subdued landscapes of arid Australia. The ongoing aridification of inland Australia which started in the Miocene has resulted in contraction of once widespread mesic habitats and the associated fragmentation and isolation of aquatic habitats (Byrne et al. 2008). However, although large volumes of perennial surface waters are not present, the arid and semiarid regions of inland Australia contain a diverse array of aquatic habitats. These include perennial or near-perennial waterholes in temporary river networks, permanent groundwater-fed springs and a range of temporary and ephemeral waterbodies fed by infrequent and unpredictable episodic rain events. The latter include small rock holes and large shallow freshwater lakes and wetlands,

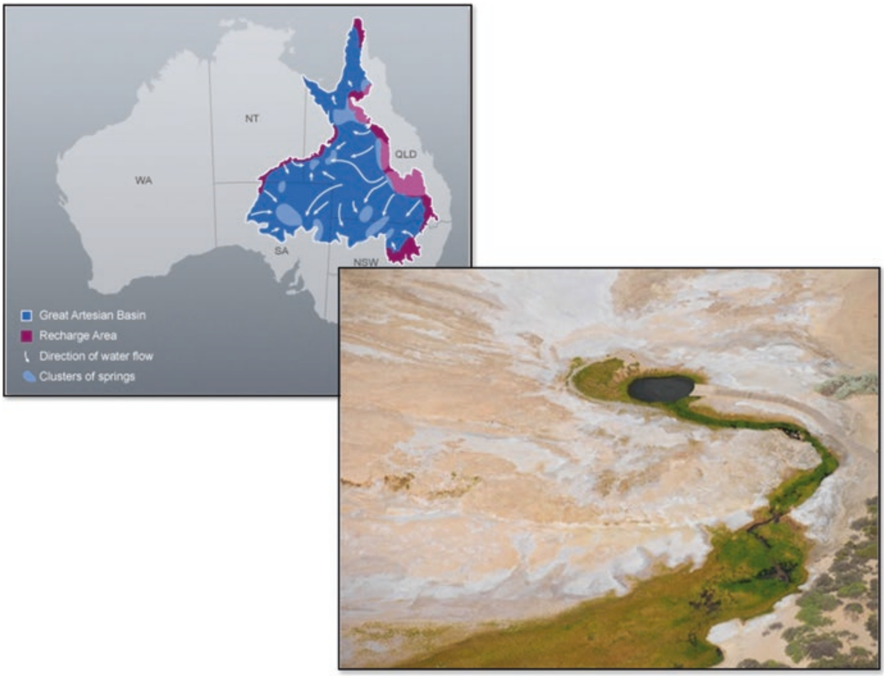


Fig. 4 Location of Great Artesian Basin mound springs (**a**) and (**b**) aerial photograph of The Bubbler, northern South Australia. Sources: (**a**) adapted from http://www.abc.net.au/science/articles/2012/04/04/3470245.htm; (**b**) J. Davis

claypans and salt lakes (Davis et al. 2013a). All of these systems support aquatic invertebrates with a range of life history strategies, behaviours and ecological attributes that enable them to persist in these often harsh and sometimes extreme environments (Boulton et al. 2014).

Relatively diverse communities of aquatic invertebrates have been recorded from the waterholes of the riverine networks of the Pilbara-Hammersley region (in north-western Australia) (Pinder et al. 2010), the eastern Lake Eyre basin (Sheldon and Puckridge 1998; Sheldon et al. 2002) and the Finke River in Central Australia (Davis 1997; Brim Box et al. 2008, 2014). Complexes of groundwater springs fed by the Great Artesian Basin (Fig. 4) represent highly fragmented freshwater ecosystems, 'aquatic islands of biodiversity in a sea of sand' and contain a suite of relictual and endemic aquatic invertebrates, mainly species of Crustacea (Fig. 1) and Mollusca (Murphy et al. 2010). Springs fed by local fractured rock aquifers in the Central Australian ranges also support relictual and endemic aquatic invertebrates, which are dominated by Insecta (Davis et al. 2013a). The aquatic invertebrate faunas of temporary freshwater pools, claypans and salt lakes, which are largely dominated by Crustacea, are relatively well known through the studies of Timms (2001, 2006, 2007) and Williams (1998).

Despite a recent increase in studies of aquatic invertebrates (see Brim Box et al. 2014; Davis et al. 2013b; Murphy et al. 2015a, b; Pinder et al. 2010), understanding of the biodiversity and biogeography of Australian arid zone freshwater invertebrates is hindered by a lack of taxonomic knowledge for many groups. For example, although 83% of the invertebrates collected (95 taxa) from the George Gill Range in Central Australia were identified to the level of genus, only 45% were identified to species (Davis et al. 1993). Some groups such as the Odonata (Fig. 2) and Dytiscidae are relatively well known; however, keys do not exist or are incomplete, for many species and distributional records may be misleading, because of lack of sampling across entire species ranges. This problem may be rectified as molecular approaches, e.g. metabarcoding, become both cheaper and easier to apply.

The origins of many of groups of aquatic organisms are unknown, but most are likely to have ancient origins and have ultimately been derived from ancestors inhabiting mesic environments. This is especially true of taxa such as the chironomid midge genus *Archaeochlus* whose closest living relatives nowadays exist in southern Africa and are most likely Gondwanan in origin (Withers and Edward 1998).

One major order of aquatic insects, the Plecoptera (stoneflies), is notable in its absence from Australian arid zone waterbodies. Although stoneflies have been recorded from intermittent stream habitats in North America, they are confined to the temperate regions of southern Australia and the Queensland highlands (Williams 1980). It seems likely that their thermal tolerance is exceeded in many inland Australian regions (Davis et al. 1993).

Groundwater-fed, perennial spring habitats have long been recognised as important refugia for aquatic invertebrates and desert fishes (Myers and Resh 1999; Shepard 1993; Ponder 2002; Kodric-Brown and Brown 2007). The global importance of springs and spring-fed aquatic habitats (groundwater-dependent ecosystems) as biodiversity hotspots was described by Bogan et al. (2014). Many arid zone waterbodies have the potential to act as climate refugia. Keppel and Wardell-Johnson (2012) defined refugia as habitats that biota retreat to, persist in and potentially expand from under changing environmental conditions. Gollan et al. (2014) suggested that the presence of microrefugia sites, particularly stable ones, with cooler maximum temperatures that are decoupled from the regional climate, has been imperative for the persistence of species over many millennia and multiple climate change events. These climatically decoupled sites serve as a source for recolonisation when the regional climate becomes favourable again (see also Dobrowski 2011).

In an investigation of key arid zone climate refugia, Davis et al. (2013a) extended the work of Fensham et al. (2011) to consider the importance of perennial, temporary and ephemeral waterbodies as either evolutionary or ecological refugia, or both, for freshwater biota. Based on an understanding of phylogenetic relationships, life histories and ecologies of arid zone aquatic invertebrates and fishes, they defined evolutionary refugia as perennial waterbodies (groundwater-dependent ecosystems) that support short-range endemics or vicariant relicts (species with ancestral characteristics that have become geographically isolated over time). Although these species often have very small geographical ranges, their populations are relatively stable and high levels of genetic diversity are present. Groundwater dominance means that not only are these aquatic habitats hydrologically decoupled from regional precipitation, they may also provide some thermal buffering from the regional climate. In contrast, ecological refugia vary hydrologically in both space and time, depending on unpredictable, episodic rainfall events. They are important for ‘boom and bust’ species and support aquatic taxa with a range of dispersal traits. They range from perennial groundwater-dependent ecosystems and large, deep, rainfall-fed riverine waterholes to temporary and ephemeral aquatic systems supported by local rainfall events. Gnamma holes and rock holes which occur in hard rock, particularly granite outcrops in arid Western Australia, not only represent important ecological refuges; they were also critical sources of drinking water for Aboriginal people moving across the landscape (Bayly 2002).

Clearly, evolutionary refugia play an important role, at the local scale, in protecting arid zone aquatic invertebrates that are unable to disperse widely or adapt to environmental change. In contrast, ecological refugia are important habitats at larger spatial scales (regional to continental) for organisms with a variety of dispersal mechanisms and life history attributes. Recently, Murphy et al. (2015a, b) found that despite major life history differences amongst endemic invertebrate taxa that inhabit Australian desert spring refugia, they demonstrate remarkable similarities in their evolutionary histories. All groups have multiple lineages that extend back to a time before the formation of present-day deserts and exhibit significant geographic-based diversification since adapting to a refugial habitat. They concluded that their results provide further evidence that refugia act as ‘museums of biodiversity’, preserving lineages that would have otherwise gone extinct. However, they also suggested that fragmented refugia provide ideal conditions for the generation of ‘future biodiversity hotspots’ based on their findings that isolation in refugia corresponds with significant diversification, leading to a recently evolved, novel endemic invertebrate fauna.

There is much that we still need to learn about Australian arid zone aquatic invertebrates, in general, and the role of refugia under global climate change. However, we also have a new suite of tools at our disposal, including molecular approaches to understanding connectivity and dispersal, remote sensing, geographic information systems (GIS) and smart data that can be collected using the *Internet of Things*. The following decades likely provide an unprecedented increase in our knowledge and understanding of the diversity, biogeography and ecology of arid zone aquatic invertebrates. This information should ultimately result in better management and conservation of species, communities, habitats and ecosystems.

Fire

One consequence of aridity is the vulnerability of the vegetation to fire. Lightning-caused fires have always been a natural occurrence, although this pattern was modified with the arrival of the original native inhabitants of Australia, who practiced frequent, low-intensity mosaic burning. This new regime of burning continued for at least 40,000 years until the time when Europeans arrived, which led to depopulation of some areas and replacing the mosaic burns with less frequent, but large-scale hot fires associated as a result of some of their activities. Whichever the scenario, fire has been an evolutionary force to which the biota would be expected to show a range of adaptations.

Three invertebrate taxa have been the focus of fire studies in the arid zone: spiders (Langlands et al. 2006, 2011, 2012), scorpions (Smith and Morton 1990) and ants (Andersen and Yen 1985; Andersen et al. 2012, 2014 and references therein; Gunawardene and Majer 2005). This is a fortuitous combination of taxa, as the former are largely present above the ground surface, although burrowing species such as trapdoor spiders are an exception, whereas many scorpions and ants of the arid zone are soil or dead wood nesters, thus allowing comparison of the impact of fire on exposed versus more protected organisms.

The first spider study compared the influence of seasonality, inter-year rainfall and fire on spider assemblages in the Great Victoria Desert of Western Australia (Langlands et al. 2006). Spiders were trapped over a 14-year period from plots with a range of fire histories that were part of a before-after-control-impact (BACI) experimental fire study including multiple taxa. They found that there was indeed an effect of fire, with initial reductions in spider abundance following a fire, but rainfall appeared to have the dominant influence, both seasonally and between years. Langlands et al. (2011, 2012) followed this study up at Lorna Glen Conservation Park, near Wiluna in Western Australia. This time, they used a chronosequence approach, with replicated sites representing areas burnt experimentally (0 and 0.5 years) and areas burnt by wildfires (3, 5, 8 and 20+ years since the last fire). The changes in species richness, evenness and composition immediately after the fire were equivocal, possibly due to issues associated with the small-scale experimental burns in these younger plots (0 and 0.5 years), but large reductions in richness and evenness and changes in species composition were evident by 3 years after the fire (Fig. 5).There were clear trends in recovery of richness and evenness and species composition thereafter, with convergence towards the prefire situation. Both papers concerning this study revealed particular spider species that were characteristic of certain stages after the fire, indicating the value of having a diversity of fire histories to support a greater biodiversity of spiders.

The scorpion study followed scorpion abundance 1, 2, 5 and 8 years after fire in the Tanami Desert of the Northern Territory (Smith and Morton 1990). Five species were present, but only one species, *Lychas alexandrines*, was sufficiently abundant to allow statistical analysis. Captures were moderate in all postfire stages but were significantly greater 2 years after the fire than in the other stages. Scorpions exhibited a better index of body condition 5 years after burning. It was concluded that populations reacted to changes in the vegetation and that mid-stages in the postfire succession supported more active and relatively larger scorpions.

One of the earliest studies on the effect of fire on ants in the arid zone is that of Andersen and Yen (1985), who followed the impact of an intense wildfire in the

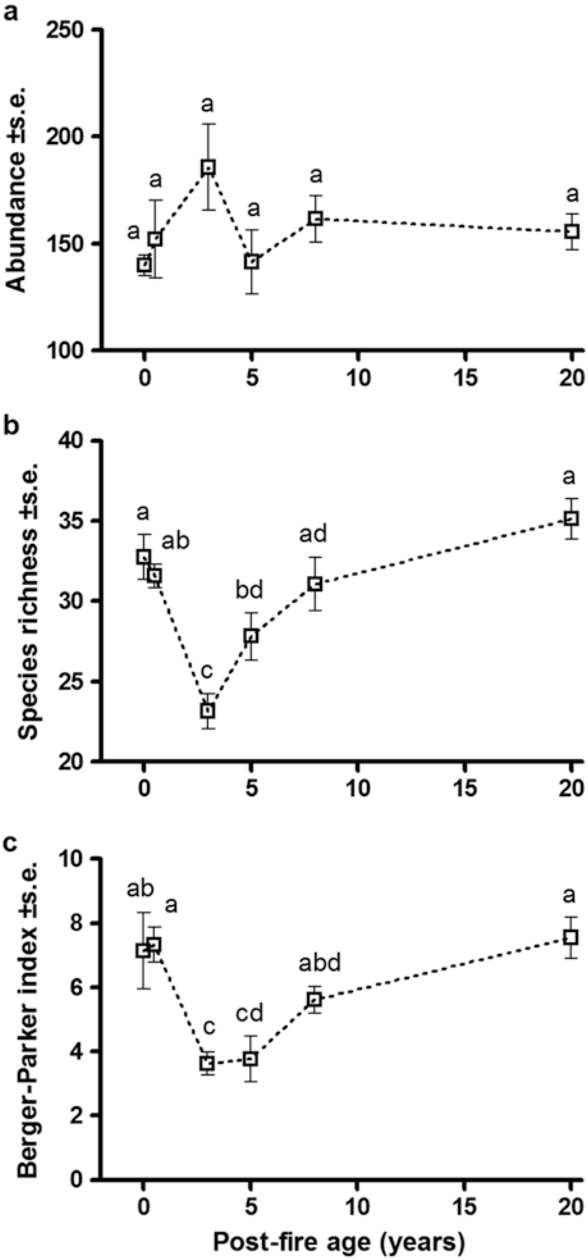


Fig. 5 Mean (**a**) spider abundance, (**b**) species richness and (**c**) Berger-Parker evenness index plotted against postfire age. Unlike letters indicate significant differences ($P < 0.05$) from PERMANOVA pairwise tests (Diagram reproduced with publishers permission [John Wiley & Sons Ltd] from Langlands et al. 2012)

semiarid Mallee region of Victoria. As with spiders, there was an initial reduction in the abundance of ants, but this was largely due to reductions of those species that previously foraged in high numbers above ground, most notably the dominant dolichoderine *Iridomyrmex* spp., and to a lesser extent certain *Monomorium* and *Melophorus* ants. A seeming paradox was that the number of species falling into the pitfall traps doubled after the fire. Although this result could partly be explained by sampling biases, as ants are more likely to encounter and fall into pitfall traps in the now simplified environment, the authors postulated that much of the increase could be due to a relaxation of competition from previously dominant ants, most notably the *Iridomyrmex* species.

A more recent study is that of Gunawardene and Majer (2005), who studied the impact of a wildfire in two types of spinifex grassland and a mulga community. As with the previous study, there was an apparent increase in number of ant species in two of the three vegetation associations. An ordination analysis of species composition indicated a changed profile in the burnt sites for all three vegetation associations, with the ant fauna of the three burnt sites becoming slightly more homogenous than they were before the fire. Notwithstanding, the authors concluded that the impact of fire on ants was not profound and that it was difficult to generalise about the effect of fire in different vegetation associations.

The effects of fires in the tropical savannas of northern Australia have been well studied. Although this area does not classify as arid Australia in the strict sense, the issues are similar and the findings relevant. The group's findings are collated in two recent publications (Andersen et al. 2012, 2014), with the earlier paper also considering impacts on vertebrates. The motivation for these studies is the notion that pyrodiversity has generally been regarded as a means to enhance biodiversity, which in turn has led to an interest in patch mosaic burning to create a heterogeneous landscape of different fire histories (Parr and Brockett 1999).

To evaluate the notion of fire being used to enhance biodiversity, Andersen et al. (2014) evaluated ant abundance, species richness and composition in six experimental fire regimes with varying fire frequency and seasonality. Ants were sampled prior to the burns and then annually for 5 years. The authors found no significant difference in any of the ant response variables when individual fire treatments were compared with each other. It was only when treatments were bulked into two contrasting fire frequencies (low – once every 5 years; high every 1 or 2 years) that differences could be detected and then only after 3 years of fire treatment. Frequent burning seemed to encourage dominant dolichoderine *Iridomyrmex* spp. and hot-climate specialists. By contrast, the increased shade associated with dense plant growth in long unburnt areas increased shade-tolerant genera such as *Nylanderia*, *Tetramorium*, *Pheidole* and *Odontomachus*. These results highlight the high degree of resilience that ants have to fire and suggest that for ants at least, it is only necessary to create a landscape of two widely contrasting fire regimes, rather than one of areas with multiple fire histories.

The results on ants, and perhaps those for scorpions, contrast with those for spiders, which, as mentioned, are much less resilient to fire and exhibit preferences for particular phases in the postfire succession. They also align to a much lesser extent to impacts on vertebrate fauna that, it is suggested, require less frequent and finer-scale fires plus the provision of large, infrequently burnt source areas (Andersen et al. 2012). There is also a need for studies on other invertebrate groups, particularly of those that have a greater dependence on the vegetation such as the hemipteran orders or butterflies and moths.

Resilience to Other Disturbances in the Arid Zone

In addition to the influence of fire, the arid zone is under the impact of a range of human-related activities, such as agriculture, feral animals, tourism pressure and mining. It is important to understand how resilient the arid zone is in comparison with habitats in more mesic areas. In order to provide the context for this, it is desirable to have comparable data from a range of climatic zones. The rate of return of insects in rehabilitated minesites provides one example where comparable data are available. Using mean number of ant species that have colonised at 3 years as a measure of resilience, Majer (1990) found that in areas outside of the arid zone, the rate of return of species tends to drop in a linear relationship as rainfall, and favourable distribution of rainfall throughout the year, decreased. Although this finding is for ants, the richness and composition of ant faunas tend to be a good surrogate for other invertebrate taxa (Majer et al. 2007) which suggests that it is not just ants, but the invertebrate fauna as a whole, that is less resilient to disturbance in areas of lower rainfall.

A series of studies on rehabilitated minesites situated deeper into the arid zone has produced some unexpected results, however. For instance, in Pilbara iron ore mines, Dunlop et al. (1985) found twice as many ant species in 3-year-old areas than would be expected from the linear rainfall-ant resilience relationship described in Majer (1990). What is the reason for this apparent anomaly? To understand this it is useful to consider the arid zone in terms of Southwood's (1977) habitat template. The template condenses the variety of habitats onto two axes equivalent to their favourableness (particularly for breeding) and predictability (Fig. 6). Within each of these zones of the template, there is selection for organisms with particular ecological strategies. For instance, highly fecund pioneer or opportunistic species, more correctly termed r-strategists, are favoured in less predictable environments such as temporary pools, transient decomposition habitats and arable land. On the other hand, more numerically constant species, whose numbers remain near their carrying capacity, are selected for in more predictable and generally favourable environments such as oligotrophic lakes, rainforest leaf litter and climax forest communities. These are known as K-strategists. Biological diversity is usually high in these habitats, as selection is for specialisation, and mechanisms to ensure individual and progeny survival. An adversity, or A-selection strategy, is selected for in habitats that are predictable but very unfavourable, in other words, many areas in the arid

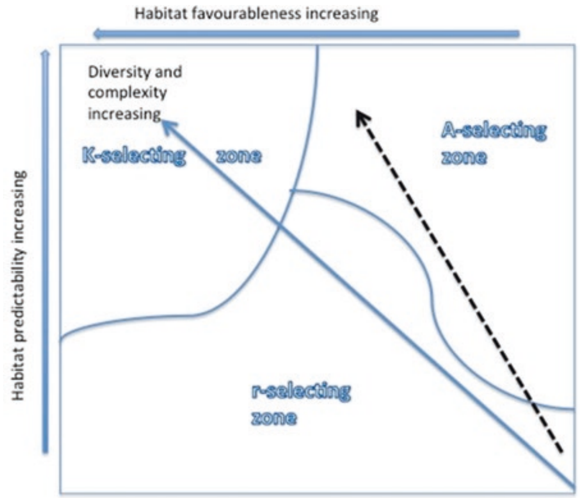


Fig. 6 The habitat template (after Southwood 1977), depicting the relationship between habitat predictability, habitat favourableness, biological diversity and complexity and selection processes. The K-, r-, and A-selecting regions are areas in which each type of selection tends to predominate. The dashed line represents the theoretical strategy of a rehabilitated arid zone minesite. (Diagram modified from Greenslade and Greenslade 1983)

zone. The harshness of these environments leads to low species diversity, so there may be little interaction between species. In consequence, selection is for adaptation to the physical environment, for low energy cost resting stages, and for mechanisms to ensure synchrony of activity when favourable conditions resume. It should be stressed that the three types of selection intergrade with each other and that there are no clear boundaries between them.

So, where does an area of a recently disturbed minesite fall on the habitat template? Prior to rehabilitation being carried out, the degraded land is usually characterised by a low spatial complexity, an absence of biological diversity, a harsh microclimate and, in biological terms, an extremely unpredictable future. These conditions place the degraded area within the r-selecting region of the habitat template or, in the case of the arid zone, within or close to the adversity region of the template (Fig. 6). The pool of organisms available to colonise the rehabilitated area is therefore moulded by the type of surrounding environment in which the disturbed land is located. Disturbed land that occurs within an r and/or A selecting environments should have a large pool of suitably adapted species that can colonise the area which is not necessarily the case for more predictable and mesic environments. This may explain why resilience of rehabilitated minesites in certain arid zones may be much greater than expected from rainfall alone.

The findings from these minesite studies relate to a type of disturbance where the succession has been deliberately enhanced by the introduction of seeds and plant propagules. The degree to which areas that have been left to recover naturally, such as areas where grazing has been removed, remains to be compared with more mesic areas in terms of their resilience.

Edible Insects

A less obvious type of invertebrate information from the arid parts of Australia involved Aboriginal use of invertebrates as food, as medicine, or as part of their cultural beliefs. This information was generally collected by nonbiologists, explorers, anthropologists and missionaries. Consequently, while information is available in publications by these nonbiologists, these claims were rarely backed up by specimens, so the identities of many of them cannot be considered accurate. More accurate information was obtained by a few biologists such as Spencer (1896a) and Tindale (1953), who retained specimens.

Insects were a significant component of Aboriginal diet in Australia (Yen 2005), possibly of greater importance in the arid regions (Tindale 1981). Eyre (1845) discusses use of grubs from *Xanthorrhoea*, some unidentified grubs and white ants used as food by the Aborigines as well as honey from native bees. There were observations on insect foods during the Horn Expedition (Spencer 1896a) and early reviews by Froggatt (1903), Campbell (1926), McKeown (1936, 1945) and Tindale (1966). In arid Australia, much emphasis is placed on two types of edible insects: wood-feeding grubs (commonly called witchetty grubs or bardi grubs) and honey ants. There is only one species of honey ant commonly used as food, *Camponotus inflatus* (Devitt 1986), from which the gaster and contained liquid are eaten, but the identity of the various edible grubs that are consumed is still to be resolved. Tindale (1953) made observations on the witchetty (witjuti) grub *Endoxyla leucomorpha*, but there are many different species of edible grubs from amongst the moths (Cossidae, Hepialidae and possibly Sphingidae) and beetles (Cerambycidae). This diversity is reflected by the Aboriginal ethnospecies names found across the many different Aboriginal languages (Latz 1995; Yen et al. 1997; Turpin (2013). In September 2015, the Bush Blitz programme included Aboriginal edible insects in the survey conducted in the Kiwirrkurra Indigenous Protected Area in the Gibson Desert, Western Australia (ALYen, unpublished data).

Aboriginal traditional knowledge on edible insects has ecologically important information about the host plant identities of the plant-feeding species and the biology of the insects including phenology and behaviour. Sustainable utilisation of these insects was controlled by cultural practices such as totemism, increase ceremonies (ceremonies to increase numbers of plants and animals) and appropriate firing of the country if required (Yen 2014). There are important dreaming locations for insects, both edible and nonedible species. One of the better-known stories is about the Yeperenye caterpillar, one of the insect species responsible for the formation of the ranges around Alice Springs (Brooks 2003).

Status of Biodiversity in the Arid Zone

Since the human population is sparse in the arid zone, decreasing still further towards the interior of the country, its impact on biodiversity should be less than elsewhere in the country. To quantify this, Majer and Beeston (1996) devised a biodiversity integrity index to portray the status of the composition and richness of biodiversity in different geographic zones of Western Australia. It first quantified the percentage of land covered by each of the major land uses in each geographic zone, namely, urbanisation, transport corridors, mining, agricultural clearing and rangeland grazing. It then incorporated the degree to which each of these land uses altered biodiversity of focus taxa. The biodiversity integrity index was then calculated for each zone as a product of the area occupied by each land use and the degree to which each land use altered biodiversity, with 100 being the pristine state of each geographic zone.

The biodiversity integrity index used ant assemblages as the response group on which to base calculations which is fortuitous as ants tend to be good surrogates (sensu McGeoch 1998) for the diversity and species composition of other taxa (Majer et al. 2007). The geographic zones used were Beard's (1990) phytogeographic regions. Figure 7 shows the outcome of this exercise, with darker areas indicating progressively more intact biodiversity. It is evident from this that biodiversity is more intact in the extreme-arid interior of Western Australia, although it declines as we move westwards and northwards with the influence of rangeland grazing, mining and a general increase in human activity.

Of course, this only provides a coarse snapshot of the status of biodiversity, as there are other degrading influences acting upon invertebrate biodiversity throughout the arid regions. Influences such as feral animals, altered fire regimes, mine exploration and tourist pressure all impact on soil and vegetation, which undoubtedly have flow-on effects to invertebrates (Naeem et al. 1995). In addition, although Western Australia has clearing bans in place for much of the arid zone, other more populous States, such as Queensland, still clear large areas of plant communities such as brigalow, so the arid interior there may not necessarily be in the same condition as in Western Australia. However, as a generalisation, invertebrate biodiversity does seem to be in a better state in the less populated arid zones than in the areas closer to the coast where the influence of humans is greater.

Concluding Comment

This review of invertebrates in the arid zone has only grazed the surface of our knowledge on their diversity and biology. A more comprehensive account would merit an entire volume or set of volumes, even though there is still much to be learned about the fauna of the arid zone. Nevertheless, we hope that the presentation of this information will encourage others to initiate detailed and long-term investigations into this important component of the biota Australia's arid zone.

Fig. 7 Biodiversity integrity index values in the 24 phytogeographic regions of Western Australia. Lighter colours signify greater losses of biodiversity integrity, with the greatest loss being in the Western Australian Wheatbelt. (Source: Based on data in Majer and Beeston 1996)

References

Abrams KM, Guzik MT, Cooper SJ, Humphreys WF, King RA, Cho JL, Austin AD (2012) What lies beneath: molecular phylogenetics and ancestral state reconstruction of the ancient subterranean Australian Parabathynellidae (Syncarida, Crustacea). Mol Phylogenet Evol 64:130–144

ABRS (2013a) 'Bon Bon Station Reserve SA 24–30 October 2010'. A Bush Blitz survey report, ABRS, Commonwealth of Australia

ABRS (2013b) 'Witchelina Reserve SA 10–23 October 2010'. A Bush Blitz survey report, ABRS, Commonwealth of Australia

ABRS (2014a) 'Cane River Conservation Park WA 20 June–1 July 2011'. A Bush Blitz survey report, Commonwealth of Australia

ABRS (2014b) 'Neds Corner Station Victoria 2011'. A Bush Blitz survey report, Commonwealth of Australia

ABRS (2015a) 'Henbury Station Northern Territory, 12–24 May 2013'. A Bush Blitz survey report, Commonwealth of Australia

ABRS (2015b) 'Hiltaba Nature Reserve Gawler Ranges National Park SA 12–23 November 2012'. A Bush Blitz survey report, ABRS, Commonwealth of Australia

ABRS (2015c) 'Credo Station Reserve WA 29 August–9 September 2011'. A Bush Blitz survey report, ABRS, Commonwealth of Australia

Andersen AN, Yen AL (1985) Immediate effects of fire on ants in the semi-arid mallee region of North-Western Victoria. Aust J Ecol 10:25–30

Andersen AN, Woinarski JCZ, Parr CL (2012) Savanna burning for biodiversity: fire management for faunal composition in Australian tropical savannas. Austral Ecol 37:658–667

Andersen AN, Ribbons RR, Pettit M, Parr CL (2014) Burning for biodiversity: highly resilient ant communities respond only to strongly contrasting fire regimes in Australia's seasonal tropics. J Appl Ecol 51:1406–1413

Baehr BC, Harvey MS, Burger M, Thoma M (2012) The new Australasian goblin spider genus *Prethopalpus* (Araneae, Oonopidae). Bull Am Mus Nat Hist 763:1–113

Baker WH (1914) Crustacea. Trans R Soc S Aust 38:446–447

Barker WR, Greenslade PJM (1982) Evolution of the flora and fauna of arid Western Australia. Peacock Publications, Frewville

Bayly, IAE (2002) The life of temporary waters in Australian gnammas (rockholes) Verh. Internat Verein Limnol 28:41–48

Beard JS (1990) Plant life of Western Australia. Kangaroo Press, Perth

Bednall WF (1892) Land and fresh water Mollusca. Trans R Soc S Aust 16:62–67

Bednall WF (1894) On a new land shell from Central Australia. Trans R Soc S Aust 18:190

Bergoth E (1916) Heteropterous Hemiptera collected by Professor W. Baldwin Spencer during the Horn expedition in Central Australia. Proc R Soc Victoria 29:19–39

Biological Surveys Committee (1984–1995) The biological survey of the Eastern Goldfields of Western Australia, parts 1–12. Records of the Western Australian Museum. Supplement(s) 18, 30,31,40,41,42,47,49

Blackburn T (1892) Coleoptera. Trans R Soc S Aust 16:16–61

Blackburn T (1893) Coleoptera (continued). Trans R Soc S Aust 16:177–202

Blackburn T (1895) Further notes on Australian Coleoptera, with descriptions of new genera and species. Trans R Soc S Aust 19:27–60

Blackburn T (1896) Coleoptera. In: Spencer B (ed) Report on the work of the Horn scientific expedition to Central Australia, part 2. Melville, Mullen and Slade, Melbourne, pp 254–308

Bogan MT, Noriega-Felix N, Vidal-Aguilar SL, Findley LT, Lytle DA, Gutierrez-Ruacho OG, Alvarado-Castro JA, Varela-Romero A (2014) Biogeography and conservation of aquatic fauna in spring-fed tropical canyons of the southern Sonoran Desert, Mexico. Biodivers Conserv 23:2705–2748

Boulton AJ, Brock MA, Robson BJ, Chambers JM, Ryder DS, Davis JA (2014) Australian freshwater ecology. Wiley-Blackwell, Chichester

Brim Box J, Duguid A, Read RE, Kimber RG, Knapton A, Davis J, Bowland AE (2008) Central Australian waterbodies: the importance of permanence in a desert land- scape. J Arid Environ 72:1395–1413

Brim-Box J, Davis J, Strehlow K, McBurnie G, Duguid A, Brock C, McConnell K, Day C, Palmer C (2014) Persistence of central Australian aquatic invertebrate communities. Mar Freshw Res 65:562–572

Brooks D (2003) A town like Mparntwe. IAD Press, Alice Springs

Brown L, Finston T, Humphreys G, Eberhard S, Pinder A (2015) Groundwater oligochaetes show complex genetic patterns of distribution in the Pilbara region of Western Australia. Invertebr Syst 29:405–420

Burbidge AH, Harvey MS, McKenzie NL (2000) Biodiversity survey of the southern Carnarvon Basin. Rec West Aust Mus Suppl 61:1–595

Byrne M, Yeates DK, Joseph L, Kearney M, Bowler J, Williams MAJ, Cooper S, Donnellan SC, Keogh JS, Leys R, Melville J, Murphy DJ, Porch N, Wyrwoll K-H (2008) Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. Mol Ecol 17:4398–4417

Byrne M, Steane DA, Joseph L, Yeates DK, Jordan GJ, Crayn D, Aplin K, Cantrill DJ, Cook LG, Crisp MJ, Keogh JS, Melville J, Moritz C, Porch N, Sniderman JMK, Sunnucks P, Weston PH (2011) Decline of a biome: evolution, contraction, fragmentation, extinction and invasion of the Australian mesic zone biota. J Biogeogr 38:1635–1656

Callan SK, Majer JD, Edwards K, Moro D (2011) Documenting the terrestrial invertebrate fauna of Barrow Island, Western Australia. Aust J Entomol 50:323–343

Campbell TG (1926) Insect foods of the Aborigines. Aust Mus Mag 1:407–410

Chapman AD (2009) Numbers of living species in Australia and the world. Australian Biological Resources Study, Canberra

Chilton C (1917) Crustacea. Trans R Soc S Aust 41:475–482

Cho J-L, Humphreys WF, Lee S-D (2006) Phylogenetic relationships within the genus *Atopobathynella* Schminke, 1973 (Bathynellacea, Parabathynellidae): with the description of six new species from Western Australia. Invertebr Syst 20:9–41

Cooper SJB, Hinze S, Leys R, Watts CHS, Humphreys WF (2002) Islands under the desert: molecular systematics and evolutionary origins of stygobitic water beetles (Coleoptera: Dytiscidae) from Central Western Australia. Invertebr Syst 16:589–598

Cooper SJB, Bradbury JH, Saint KM, Leys R, Austin AD, Humphreys WF (2007) Subterranean archipelago in the Australian arid zone: mitochondrial DNA phylogeography of amphipods from Central Western Australia. Mol Ecol 16:1533–1544

Cooper SJ, Saint KM, Taiti S, Austin AD, Humphreys WF (2008) Subterranean archipelago II: mitochondrial DNA phylogeography of stygobitic isopods (Oniscidea: *Haloniscus*) from the Yilgarn region of Western Australia. Invertebr Syst 22:195–206

Criscione F, Köhler F (2016) Snails in the desert: assessing the mitochondrial and morphological diversity and the influence of aestivation behavior on lineage differentiation in the Australian endemic *Granulomelon* Iredale, 1933 (Stylommatophora: Camaenidae). Mol Phylogenet Evol 94:101–112

Davis JA (1997) Conservation of aquatic invertebrate communities in Central Australia. Mem Mus Victoria 56:491–503

Davis JA, Harrington SA, Friend JA (1993) Invertebrate communities of relict streams in the arid zone: the George Gill Range, Central Australia. Aust J Mar Freshwat Res 44:483–505

Davis JA, Pavlova A, Thompson R, Sunnucks P (2013a) Evolutionary refugia and ecological refuges: key concepts for conserving Australian arid zone freshwater biodiversity under climate change. Glob Chang Biol 19:1970–1984

Davis J, Sunnucks P, Thompson R, Sim L, Pavlova A, Morán-Ordóñez A, Brim Box J, McBurnie, G, Pinder A, Choy S, McNeil D, Hughes J, Sheldon F, Timms B (2013b) Building the climate resilience of arid zone freshwater biota, National Climate Change Adaptation Research Facility, Gold Coast. NCCARF Publication 111/13

Devitt J (1986) A taste for honey: Aborigines and the collection of ants associated with Mulga in Central Australia. In: Sattler PS (ed) The Mulga lands. Royal Society of Queensland, Brisbane, pp 40–44

Dobrowski SZ (2011) A climatic basis for microrefugia: the influence of terrain on climate. Glob Chang Biol 17:1022–1035

Dunlop JN, Majer JD, Morris CJ, Walker KJ (1985) A preliminary assessment of minesite rehabilitation in the Pilbara iron ore province using ant communities as ecological indicators. Mulga Res Cent J 8:25–31

Eyre EJ (1845) Journals of expeditions o discovery into Central Australia and overland from Adelaide to King George's Sound in the years 1840–1, vol 1 and 2. T. and W. Boone, London

Fensham R, Silcock JL, Kerezsy A, Ponder W (2011) Four desert waters: setting arid zone wetland conservation priorities through understanding patterns of endemism. Biol Conserv 144:2459–2467

Finston TL, Johnson M, Humphreys WF, Eberhard S, Halse S (2007) Cryptic speciation in two widespread subterranean amphipod genera reflects historical drainage patterns in an ancient landscape. Mol Ecol 16:355–365

Finston T, Francis CJ, Johnson MS (2009) Biogeography of the stygobitic isopod *Pygolabis* (Malacostraca: Tainisopidae) in the Pilbara, Western Australia: evidence for multiple colonisations of the groundwater. Mol Phylogenet Evol 52:448–460

Froggatt WW (1893) Hymenoptera. Trans R Soc S Aust 16:69–73

Froggatt WW (1896) Honey ants. In: Spencer B (ed) Report on the work of the Horn scientific expedition to Central Australia, Part 2. Melville. Mullen and Slade, Melbourne, pp 385–392

Froggatt W (1898) Australian Termitidae. Part III. Proc Linnean Soc NSW 22:721–758

Froggatt WW (1901) Typical insects of Central Australia. Agric Gaz NSW 12:1203–1212

Froggatt WW (1903) Insects used as food by the Australian natives. Sci Man 6:11–13

Froggatt WW (1907) Australian insects. William Books and Co. Ltd., Sydney

Froggatt WW (1914) Insecta: Hymenoptera. Trans R Soc S Aust 38:459

George AS, McKenzie NL, Doughty P (2010) A biodiversity survey of the Pilbara region of Western Australia. Rec West Aust Mus Suppl 78:1–311

Giles E (1889) Australia twice traversed. Sampson Low, Marston, Searle and Rivington, London

Gollan JR, Ramp D, Ashcroft MB (2014) Assessing the distribution and protection status of types of cool environment to facilitate their conservation under climate change. Conserv Biol 28:456–466

Greenslade P (1978a) Collembola. In: Low WA, Milllington RW, Winkworth RE, Sullivan ME, Johnson D, Wright MJ, Lendon C, Ross MA, Watson JAL, Barrett RA, Greenslade PJM, Low BS (eds) The physical and biological features of Kunoth Paddock in Central Australia. CSIRO division of land management technical paper 4, pp 114–123

Greenslade PJM (1978b) Ants. In: Low WA, Milllington RW, Winkworth RE, Sullivan ME, Johnson D, Wright MJ, Lendon C, Ross MA, Watson JAL, Barrett RA, Greenslade PJM, Low BS (eds) The physical and biological features of Kunoth Paddock in Central Australia. CSIRO Australia, division land management technical paper 4 4, pp 109–113

Greenslade PJM (1979) A guide to ants of South Australia. South Australian Museum, Adelaide

Greenslade P (1981) Survival of Collembola in arid environments, observations in South Australia and the Sudan. J Arid Environ 4:219–228

Greenslade P (1982) Origins of the collembolan fauna of arid Australia. In: Barker WR, Greenslade PJM (eds) Evolution of the flora and fauna of arid Australia. Peacock Publications, Adelaide, pp 267–272

Greenslade P (1985a) Terrestrial invertebrates of the mound spring bores, creek beds and other habitats. In: Greenslade PJM, Joseph L, Reeves A (eds) South Australia's mound springs. Nature Conservation Society of South Australia Inc, Adelaide, pp 64–77

Greenslade PJM (1985b) First report on ants and post-fire succession in the Tanami Desert, N. T. CSIRO Division of Soils, Technical Memorandum 21/1985, pp 1–21

Greenslade PJM, Greenslade P (1983) Ecology of soil invertebrates. In: Lee K (ed) Soils: an Australian viewpoint. CSIRO Publishing, Melbourne, pp 645–649

Greenslade PJM, Greenslade P (1984) Soil surface insects of the Australian arid zone In: Cogger H, Cameron EE (ed) Arid Australia. Proceedings of the Museum sesquicentennial symposium on Australian Deserts, September 1976, Sydney, pp 153–176

Greenslade PJM, Greenslade P (1989) Ground layer invertebrate fauna. In: Noble JC, Bradstock RA (eds) Mediterranean landscapes in Australia: mallee ecosystems and their management. CSIRO Publishing, East Melbourne, pp 266–284

Gunawardene NR, Majer JD (2004) Ants of the southern Carnarvon Basin, Western Australia: an investigation into patterns of association. Rec West Aust Mus 22:219–239

Gunawardene NR, Majer JD (2005) The effect of fire on ant assemblages in the Gibson Desert Nature Reserve, Western Australia. J Arid Environ 63:725–739

Gunawardene NR, Majer JD, Taylor CK, Harvey MS (eds) (2013) The terrestrial invertebrate fauna of Barrow Island, Western Australia. Rec West Aust Mus Suppl 83:1–406

Guzik MT, Abrams K, Cooper SJB, Humphreys WF, Cho J-L, Austin A (2008) Phylogeography of the ancient Parabathynellidae (Crustacea: Bathynellacea) from the Yilgarn region of Western Australia. Subterranean connections. *Invertebr Syst* 22:205–216

Guzik MT, Cooper SJB, Humphreys WF, Austin AD (2009) Fine-scale comparative phylogeography of a sympatric sister species triplet of subterranean diving beetles from a single calcrete aquifer in Western Australia. Mol Ecol 18:3683–3698

Guzik M, Austin AD, Cooper SJB, Harvey MS, Humphreys WF, Bradford T, Eberhard SM, King RA, Leijs R, Muirhead KA, Tomlinson M (2010) Is the Australian subterranean fauna uniquely diverse? Invertebr Syst 24:407–418

Halse SA, Pearson GB (2014) Troglofauna in the vadose zone: comparison of scraping and trapping results and sampling adequacy. Subterranean Biol 13:17–34

Halse SA, Scanlon M, Cocking JS, Barron HJ, Richardson JB, Eberhard SM (2014) Pilbara stygofauna: deep groundwater of an arid landscape contains globally significant radiation of biodiversity. Rec West Aust Mus Suppl 78:443–483

Hamilton Z, Johnson MS (2015) Hybridization between genetically and morphologically divergent forms of *Rhagada* (Gastropoda: Camaenidae) snails at a zone of secondary contact. Biol J Linn Soc 114:348–362

Harrison SE, Guzik M, Harvey MS, Austin AD (2014) Molecular phylogenetic analysis of Western Australian troglobitic chthoniid pseudoscorpions (Pseudoscorpiones : Chthoniidae) points to multiple independent subterranean clades. Invertebr Syst 28:386–400

Harvey MS (1992) The Schizomida (Chelicerata) of Australia. Invertebr Taxon 6:77–129

Harvey MS (2002) Short-range endemism in the Australian fauna: some examples from non-marine environments. Invertebr Syst 16:555–570

Harvey MS, Edward KL (2007) A review of the pseudoscorpion genus *Ideoblothrus* (Pseudoscorpiones, Syarinidae) from western and northern Australia. J Nat Hist 41:445–472

Harvey MS, Yen AL (1989) Worms to wasps: an illustrated guide to Australia's terrestrial invertebrates. Oxford University Press, Melbourne

Harvey M, Berry O, Edward KL, Humphreys G (2008) Molecular and morphological systematics of hypogean schizomids (Schizomida: Hubbardiidae) in semi-arid Australia. Invertebr Syst 22:167–194

Harvey MS, Rix MG, Framenau VW, Hamilton ZR, Johnson MS, Teale RJ, Humphreys G, Humphreys WF (2011) Protecting the innocent: studying short-range endemic taxa enhances conservation outcomes. Invertebr Syst 25(1):10

Hickman VV (1944) The Simpson Desert expedition, 1939 – scientific reports. no. 1, biology: scorpions and spiders. Trans R Soc S Aust 68:18–48

Hogg HR (1896) Araneidae. In: Spencer (ed) Report on the work of the Horn scientific expedition to Central Australia, part 2. Melville, Mullen and Slade, Melbourne, pp 309–356

Humphreys WF (1991) Experimental re-establishment of pulse-driven populations in a terrestrial troglobite community. J Anim Ecol 60:609–623

Humphreys WF (ed) (1993) The biogeography of cape range, Western Australia. Rec West Aust Mus Suppl 45:1–248

Humphreys WF (1999) Relict stygofaunas living in sea salt, karst and calcrete habitats in arid northwestern Australia contain many ancient lineages. In: Ponder W, Lunney D (eds) The Other 99%. The Conservation and Biodiversity of Invertebrates. Transactions of the Royal Zoological Society of New South Wales, Mosman, pp 219–227

Humphreys WF (2001) Groundwater calcrete aquifers in the Australian arid zone: the context to an unfolding plethora of stygal biodiversity. In: Humphreys WF, Harvey M (eds) Subterranean biology in Australia 2000. Rec West Aust Mus Suppl 64:63–83

Humphreys WF (2006) Aquifers: the ultimate groundwater dependent ecosystems. In: Eamus D (ed) Special edition on groundwater dependent ecosystems. Aust J Bot 54:115–132

Humphreys WF (2008) Rising from down under: developments in subterranean biodiversity in Australia from a groundwater fauna perspective. Invertebr Syst 22:85–101

Humphreys WF (2012) Diversity patterns in Australia. In: White WB, Culver DC (eds) Encyclopedia of caves, 2nd edn. Academic, San Diego, pp 203–219

Humphreys WF, Adams M (2001) Allozyme variation in the troglobitic millipede Stygiochiropus communis (Diplopoda: Paradoxosomatidae) from arid tropical cape range, northwestern Australia: population structure and implications for the management of the region. In: Humphreys WF, Harvey MS (eds) Subterranean biology in Australia 2000. Rec West Aust Mus Supple 64:15–36

Humphreys WF, Watts CHS, Cooper SJB, Leijs R. (2009) Groundwater estuaries of salt lakes: buried pools of endemic biodiversity on the western plateau, Australia. *Hydrobiologia* 626:79–95. Erratum: Hydrobiologia 632:377

Javidkar M (2014) Molecular systematics and biogeographic history of oniscidean isopod troglofauna in groundwater calcretes of Central Western Australia. PhD dissertation. Australian Centre for Evolutionary Biology and Biodiversity, University of Adelaide, South Australia

Javidkar M, Steven JB, Cooper RA, King HWF, Austin AD (2015) Molecular phylogenetic analyses reveal a new southern hemisphere oniscidean family (Crustacea: Isopoda) with a unique water transport system. Invertebr Syst 29:554–577

Johnson MS, Hamilton Z, Murphy CE, MacLeay CA, Roberts B, Kendrick PG (2004) Evolutionary genetics of island and mainland species of *Rhagada* (Gastropoda: Pulmonata) in the Pilbara region, Western Australia. Aust J Zool 52:341–355

Johnson M, Hamilton Z, Teale RJ, Kendrick PG (2012) Endemic evolutionary radiation of *Rhagada* land snails (Pulmonata: Camaenidae) in a continental archipelago in northern Western Australia. Biol J Linn Soc 106:316–327

Keppel G, Wardell-Johnson G (2012) Refugia: keys to climate change management. Glob Chang Biol 18:2389–2391

King RA (2009) Two new genera and species of chiltoniid amphipods (Crustacea: Amphipoda: Talitroidea) from freshwater mound springs in South Australia. Zootaxa 2293:35–52

King R, Bradford T, Austin AD, Humphreys WF, Cooper SJB (2012) Divergent molecular lineages and not-so-cryptic species: the first descriptions of stygobitic chiltoniid amphipods (Talitroidea: Chiltoniidae) from Western Australia. J Crustac Biol 32:465–488

Kirby WF (1896) Hymenoptera. In: Spencer B (ed) Report on the work of the Horn scientific expedition to Central Australia, part 2. Melville, Mullen and Slade, Melbourne, pp 203–209

Kodric-Brown A, Brown JH (2007) Native fishes, exotic mammals, and the conservation of desert springs. Front Ecol Environ 5:549–553

Langlands PR, Brennan KEC, Pearson DJ (2006) Spiders, spinifex rainfall and fire: long-term changes in an arid spider assemblage. J Arid Environ 67:36–59

Langlands PR, Brennan KEC, Framenau VW, Main BY (2011) Predicting the post-fire responses of animal assemblages: testing a trait-based approach using spiders. J Anim Ecol 80:558–568

Langlands PR, Brennan KEC, Ward B (2012) Is the reassembly of an arid spider assemblage following fire deterministic? Austral Ecol 37:429–434

Latz P (1995) Bushfires and bushtucker. IAD Press, Alice Springs

Lea AM (1914a) Stomach contents of birds. Trans R Soc S Aust 38:439–440

Lea AM (1914b) Insecta: Coleoptera. Trans R Soc S Aust 38:448–454

Lea AM (1917a) Stomach contents of birds. Trans R Soc S Aust 41:466–468

Lea AM (1917b) Insecta. Trans R Soc S Aust 41:489–630

Leijs R, van Nes EH, Watts CH, Cooper SJB, Humphreys WF, Hogendoorn K (2012) Evolution of blind beetles in isolated aquifers: a test of alternative modes of speciation. PLoS One 7:e34260

Leys R, Watts CH (2008) Systematics and evolution of the Australian subterranean hydroporine diving beetles (Dytiscidae), with notes on *Carabhydrus*. Invertebr Syst 22:217–225

Leys R, Watts CHS, Cooper SJB, Humphreys WF (2003) Evolution of subterranean diving beetles (Coleoptera: Dytiscidae: Hydroporini, Bidessini) in the arid zone of Australia. Evolution 57:2819–2834

Lower O (1892) Lepidoptera. Trans R Soc S Aust 16:10–15

Lower O (1896) Lepidoptera. In: Spencer B (ed) Report on the work of the Horn scientific expedition to Central Australia, part 2. Melville. Mullen and Slade, Melbourne, pp 249–253

Main BY (1957) Biology of aganippine trapdoor spiders (Mygalomorphae: Ctenizidae). Aust J Zool 5:402–473

Majer JD (1990) Rehabilitation of disturbed land: long-term prospects for the recolonisation of fauna. Proc Ecol Soc Aust 16:509–517

Majer JD (2009) Saga of the short-range endemic. Aust J Entomol 48:265–268

Majer JD, Beeston G (1996) Biodiversity integrity index: an illustration using ants in Western Australia. Conserv Biol 10:65–73

Majer JD, Orabi G, Bisevac L (2007) Ants (Hymenoptera: Formicidae) pass the bioindicator scorecard. Myrmecol News 10:69–76

Majer JD, Callan SK, Edwards K, Gunawardene NR, Taylor CK (2013) Baseline survey of the terrestrial invertebrate fauna of Barrow Island. Rec West Aust Mus Suppl 83:13–112

Matthews EH (1914) Mollusca. Trans R Soc S Aust 3:446

Matthews EG (1976) Insect ecology. University of Queensland Press, St. Lucia

Matthews EG (1980) *A guide to the genera of beetles of South Australia. Part 1*. South Australian Museum, Adelaide

Matthews EG (1982) *A guide to the genera of beetles of South Australia. Part 2*. South Australian Museum, Adelaide

Matthews EG (1984) *A guide to the genera of beetles of South Australia. Part 3*. South Australian Museum, Adelaide

Matthews EG (1985) *A guide to the genera of beetles of South Australia. Part 4*. South Australian Museum, Adelaide

Matthews EG (1987) *A guide to the genera of beetles of South Australia. Part 5*. South Australian Museum, Adelaide

Matthews EG (1992) A guide to the genera of beetles of South Australia. Part 6. South Australian Museum, Adelaide

Matthews EG (1997) A guide to the genera of beetles of South Australia part 7. South Australian Museum, Adelaide

Matthews EG, Reid CAM (2002) A guide to the genera of beetles of South Australia part 8. South Australian Museum, Adelaide

McGeoch MA (1998) The selection, testing and application of terrestrial insects as bioindicators. Biol Rev 73:181–201

McKenzie NL, Robinson AC (1987) A biological survey of the Nullarbor Region South and Western Australia in 1984. South Australian Department of Environment and Planning, Adelaide, Department of Conservation and Land management, Perth and Australian National Parks and Wildlife Service, Canberra

McKeown KC (1936) Insect wonders of Australia. Angus and Robertson, Sydney

McKeown KC (1945) Australian insects, 2nd rev. edn. Royal Zoological Society of New South Wales, Sydney

Morton SR (1982) Granivory in the Australian arid zone: diversity of harvester ants and structure of their communities. In: Barker WR, Greenslade PJM (eds) Evolution of the flora and fauna of arid Australia. Peacock Publications, Adelaide, pp 257–262

Morton SR, James CD (1988) The diversity and abundance of lizards in arid Australia: a new hypothesis. Am Nat 132:237–256

Murphy NP, Guzik MT, Worthington Wilmer J (2010) Understanding the influence of landscape and dispersal on species distributions in fragmented groundwater dependent springs. Freshw Biol 55:2499–2509

Murphy NP, Guzik MT, Cooper JB, Austin A (2015a) Desert spring refugia: museums of diversity or evolutionary cradles? Zool Scr 44:693–701

Murphy NP, King RA, Delean S (2015b) Species, ESUs or populations? Delimiting and describing truly morphologically cryptic diversity in Australian desert springs. Invertebr Syst 29:457–467

Musgrave A (1945) The Simpson Desert expedition, 1939 – scientific reports. no. 4, biology: hemiptera. Trans R Soc S Aust 69:14–15

Myers MJ, Resh V (1999) Spring-formed wetlands of the arid west: islands of aquatic invertebrate biodiversity. In: Batzer D, Rader RB, Wissinger SA (eds) Invertebrates in freshwater wetlands of North America: ecology and management. Wiley, New York, pp 811–828

Naeem S, Thompson LJ, Lawler SP, Lawton JH, Woodfin RM (1995) Empirical evidence that declining species diversity may alter the performance of terrestrial ecosystems. Philos Trans R Soc London B Biol Sci 347:249–262

Page TJ, Humphreys WF, Hughes JM (2008) Shrimps down under: evolutionary relationships of subterranean crustaceans from Western Australia (Decapoda: Atyidae: *Stygiocaris*). PLoS One 3:e1618

Parr CL, Brockett BH (1999) Patch-mosaic burning: a new paradigm for savanna fire management in protected areas? Koedoe 42:117–130

Pinder AM, Halse S, Shiel RJ, McRae JM (2010) An arid zone awash with diversity: patterns in the distribution of aquatic invertebrates in the Pilbara region of Western Australia. Rec West Aust Mus 78:205–246

Ponder W (2002) Desert springs of the Australian Great Artesian Basin. In: Sada DW, Sharpe SE (eds) Proceedings of the meeting on Spring-fed wetlands: important scientific and cultural resources of the intermountain region 7–9 May, Las Vegas, Nevada, USA, pp 1–13. Available at: http://wetlands.dri.edu

Poore GCB, Humphreys WF (1998) First record of Spelaeogriphacea from Australasia: a new genus and species from an aquifer in the arid Pilbara of Western Australia. Crustaceana 71:721–742

Pulleine RH (1914) Arachnida. Trans R Soc S Aust 38:447–448

Rainbow WJ (1917) Araneidae. Trans R Soc S Aust 41:482–489

Reid JRE, Kerle JA, Morton SR (1993) Uluru fauna. Australian National Parks and Wildlife Service, Canberra

Rix MG, Edwards DL, Byrne M, Harvey MS, Joseph L, Roberts JD (2015) Biogeography and speciation of terrestrial fauna in the south-western Australian biodiversity hotspot. Biol Rev 90:762–793

Robertson P, Bennett AF, Lumsden LF, Silveira CE, Johnson PG, Yen AL, Milledge GA, Lillywhite PK, Pribble HJ (1989) Fauna of the Mallee study area, north- western Victoria. Arthur Rylah Institute for Environmental Research, Technical report series no. 87. 91 pp

Robinson A, Copley PB, Canty PD, Baker LM, Nesbitt BJ (eds) (2003) A biological survey of the Anangu Pitjantjatjara lands, South Australia, 1991–2001. Department for Environment and Heritage, Adelaide

Sheldon F, Puckridge JT (1998) Macroinvertebrate assemblages of Goyder Lagoon, Diamantina River, South Australia. Trans R Soc S Aust 122:17–31

Sheldon F, Boulton J, Puckridge JT (2002) Conservation value of variable connectivity: aquatic invertebrate assemblages of channel and floodplain habitats of a Central Australian arid-zone river, Cooper Creek. Biol Conserv 103:13–31

Shepard WD (1993) Desert springs-both rare and endangered. Aquat Conserv Mar Freshwat Ecosyst 3:351–359

Sloane TG (1893a) Broscides. Trans R Soc S Aust 16:203–213

Sloane TG (1893b) Amycterini. Trans R Soc S Aust 16:213–236

Sloane TG (1895) Notes on Carabidae from Lake Callabonna, Central Australia. Trans R Soc S Aust 19:124–137

Sloane TG (1896) Carabidae. In: Spencer B (ed) Report on the work of the Horn scientific expedition to Central Australia, part 2. Melville, Mullen and Slade, Melbourne, pp 380–384

Smith GT, Morton SR (1990) Responses by scorpions to fire-initiated succession in arid Australian spinifex grasslands. J Arachnol 18:241–244

Smith GB, Eberhard SM, Perina G, Finston T (2012) New species of short range endemic troglobitic silverfish (Zygentoma: Nicoletiidae) from subterranean habitats in Western Australia's semi-arid Pilbara region. Rec West Aust Mus 27:101–116

Southwood TRE (1977) Habitat, the templet for ecological strategies. J Anim Ecol 46:337–365

Spencer W (1896a) Report on the work of the Horn scientific expedition to Central Australia, parts I-IV. Melville, Mullen and Slade, London/Melbourne

Spencer B (1896b) *Acanthodrilus eremius*, a new species of earthworm. In: Spencer B (ed) Report on the work of the Horn scientific expedition to Central Australia, part 2. Melville, Mullen and Slade, Melbourne, pp 416–420

Stankowski S (2015) Layers of contingency shroud pervasive ecological divergence in a local radiation of land snails. Biol J Linn Soc 116:267–276

Sturt C (1849) Narrative of an expedition into Central Australia. T. and W. Boone, London

Tate R (1894) Brief diagnoses of Mollusca from Central Australia. Trans R Soc S Aust 18:191–194

Tate R (1896) Mollusca. In: Spencer B (ed) Report on the work of the Horn scientific expedition to central Australia, part 2. Melville, Mullen and Slade, Melbourne, pp 227–248

Taylor RW (1983) Descriptive taxonomy: past, present, and future. In: Highley E, Taylor RW (eds) Australian systematic entomology: a bicentenary perspective. CSIRO Publishing, Canberra, pp 93–134

Tepper JGO (1893) Orthoptera. Trans R Soc S Aust 16:151–153

Tepper JGO (1895) Descriptions of little-known species of Blattariae, Gryllacridae, and Stenopelmatidae, collected at Lake Callabonna, SA. Trans R Soc S Aust 19:19–24

Tepper JGO (1896) Orthoptera. In: Spencer B (ed) Report on the work of the Horn scientific expedition to central Australia, part 2. Melville, Mullen and Slade, Melbourne, pp 151–153

Tietkins WH (1891) Journal of the central Australian exploring expedition, 1889. In: Bristow CE (ed), Government Printer, Adelaide

Tillyard RJ (1926) The insects of Australia and New Zealand. Angus and Robertson, Sydney

Timms BV (2001) Large freshwater lakes in arid Australia: a review of their limnology and threats to their future. Lakes Reserv Res Manag 6:183–196

Timms BV (2006) The large branchiopods of gnammas (rock holes) in Australia. J R Soc West Aust 89:163–173

Timms BV (2007) The biology of the saline lakes of central and eastern inland of Australia: a review with special reference to their biogeographical affinities. Hydrobiologia 576:27–37

Tindale NB (1953) On some Australian Cossidae including the moth of the Witjuti (witchetty) Grub. Trans R Soc S Aust 76:56–65

Tindale NB (1966) Insects as food for the Australian Aborigines. Aust Nat Hist 15:179–183

Tindale NB (1981) Desert aborigines and the southern coastal peoples: some comparisons. In: Keast A (ed) *Ecological biogeography of Australia*. Dr. W. Junk bv Publishers, The Hague, pp 1853–1884

Turner AJ (1914) Insecta: Lepidoptera Heterocera. Trans R Soc S Aust 38:455–459

Turpin M (2013) Semantic extension in Kaytetye flora and fauna terms. Aust J Linguist 33:488–518

Waite ER (1917) Results of the South Australian Museum expedition to Strzelecki and Cooper Creeks. September and October 1916. Trans R Soc S Aust 41:405–453

Warburton PE (1875) Journey across the western interior of Australia. Sampson, Low, Marston, Low, and Searle, London

Waterhouse GA (1914) Insecta: Lepidoptera Rhopalocera. Trans R Soc S Aust 38:455

Watts CHS, Humphreys WF (2003) Twenty-five new Dytiscidae (Coleoptera) of the genera *Tjirtudessus* Watts and Humphreys, *Nirripirti* Watts and Humphreys and *Bidessodes* Regimbart, from underground waters in Australia. Rec S Aust Mus 36:135–187

Watts CHS, Humphreys WF (2006) Twenty-six new Dytiscidae (Coleoptera) of the genera *Limbodessus* Guignot and *Nirripirti* Watts and Humphreys, from underground waters in Australia. Trans R Soc S Aust 130:123–185

Watts CHS, Humphreys WF (2009) Fourteen new Dytiscidae (Coleoptera) of the genera *Limbodessus* Guignot, *Paroster* Sharp and *Exocelina* Broun, from underground waters in Australia. Trans R Soc S Aust 133:62–107

Wells A (1993) Bugs and bug collectors of the northern territory: entomology and entomologists in the Northern Territory. State library of the Northern Territory occasional papers no. 40

White SA (1910) A record of the A.O.U. expedition to Eyre's Peninsula, October, 1909, with notes on ornithology, botany, and entomology. W. K. Thomas and Co., Printers, Adelaide

White SA (1914) Scientific notes on an expedition into the interior of Australia carried out by Capt. S.A. White, M.B.O.U., from July to October 1913. Trans Proc R Soc S Aust 38:407–474

Williams WD (1980) Australian freshwater life: the invertebrates of Australian inland waters, 2nd edn. Macmillan, Melbourne

Williams WD (1998) Biodiversity in salt lakes. In: McComb AJ, Davis JA (eds) Wetlands for the future. Contributions from INTECOL's V international wetlands conference, Gleneagles Publishing, Adelaide, pp 161–166

Wilson EO (1987) The little things that run the world (the importance and conservation of invertebrates). Conserv Biol 1:344–346

Withers PC, Edward DH (1998) Terrestrial fauna of granite outcrops in Western Australia. J R Soc West Aust 80:159–166

Yen AL (1987) A preliminary assessment of the correlation between plant, vertebrate and Coleoptera communities in the Victorian mallee. In: Majer JD (ed) The role of invertebrates in conservation and biological survey. Western Australian Department of Conservation and Land Management Report, Perth, pp 73–88

Yen AL (1989) Overstorey invertebrates in the Big Desert, Victoria. In: Noble JC, Bradstock RA (eds) Mediterranean landscapes in Australia: mallee ecosystems and their management. CSIRO Publishing, Melbourne, pp 285–299

Yen AL (1996) The contribution of the Horn expedition to our knowledge of terrestrial invertebrates in central Australia. In: Morton SR, Mulvaney DJ (eds) Exploring central Australia: society, the environment and the 1894 Horn expedition. Surrey Beatty and Sons, Chipping Norton, pp 230–244

Yen AL (2005) Insect and other invertebrate foods of Australian Aborigines. In: Paoletti MG (ed) Ecological implications of minilivestock. Science Publishers, Inc, Enfield, pp 367–387

Yen AL (2011) Insects and other invertebrates. In: Joyce EB, McCann DA (eds) Burke and Wills: the scientific legacy of the Victorian exploring expedition. CSIRO Publishing, Collingwood, pp 193–206

Yen AL (2014) The importance of recording local knowledge about edible insects in Oceania with particular reference to Australia. In: Durst P, Bayasgalanbat N (eds) Promotion of underutilized indigenous food resources for food security and nutrition ion Asia and the Pacific. UN FAO Office for Asia and the Pacific RAP Publication 2014/07, pp 78–91

Yen AL, Wainer J (2003) Scolopendrid centipedes caught by pitfall trapping in the Uluru-Kata Tjuta National Park, Northern Territory, including a record of an apparent 'outbreak'. Proc Roy Soc Victoria 115:55–65

Yen AL, Reid JRW, Wainer J (1996) A pitfall trap survey of ground dwelling invertebrates. In: Reidand JRW, Hobbs TJ (eds) Monitoring the vertebrate Fauna of Uluru National Park, Phase II – Final report. Consultancy Report to the Australian Nature Conservation Agency. CSIRO, Alice Springs, pp 139–159

Yen AL, Gillen J, Gillespie R, Vanderwal R, the Mutitjulu Community (1997) A preliminary assessment of Anangu knowledge of Central Australian invertebrates. Mem Mus Victoria 56:631–634

Subterranean Fauna of the Arid Zone

Stuart A. Halse

Introduction

Subterranean fauna can be divided into two broad groups – stygofauna are aquatic and occur in groundwater, while troglofauna are air-breathing and occur in the unsaturated zone from depths of a metre or so below the ground surface down to the water table. Defining exactly which species are covered by the term subterranean fauna is quite complex, because of the different life histories of many vertebrate and invertebrate species, and the habitat differences between caves and the much more extensive, but less studied underground matrix outside caves. However, a useful starting point for understanding the general characteristics of subterranean species is provided by various schemes that categorise species according to their dependence on the underground environment. These schemes are discussed in detail by Sket (2008), but, in summary, species occurring only in the aphotic zone of caves or deep underground are classified as troglobites or stygobites (Table 1). The terms troglophiles and stygophiles are applied to species found in parts of caves where there is some penetration of light or to species that use surface habitats for one (usually short) part of their life history. Occasionally, troglophilic or stygophilic species may have some surface populations and some wholly subterranean populations. The third category, trogloxenes and stygoxenes, is applied to primarily surface species that regularly make use of caves or underground habitats, often as a refugium during periods of adverse conditions (such as drought) in their usual surface habitat.

In this chapter, the terms subterranean fauna, troglofauna and stygofauna refer principally to troglobites, stygobites, troglophiles and stygophiles (Table 1). Species in these categories are clearly dependent on caves and other subterranean habitats for their survival. Trogloxenes and stygoxenes are mostly excluded from coverage, although there are occasions and situations in which subterranean habi-

---

S. A. Halse (✉)
Bennelongia Environmenatl Consultants, Jolimont, WA 6014, Australia
e-mail: stuart.halse@bennelongia.com.au

H. Lambers (ed.), *On the Ecology of Australia's Arid Zone*,
https://doi.org/10.1007/978-3-319-93943-8_9

Table 1 Characteristics of different types of species found underground

Subterranean species, troglofauna and stygofauna	
Troglobite/ stygobite	Occur in aphotic zone of caves or deep in the unsaturated zone
Troglophile/ stygophile	Occur in caves where there is some light or use surface habitats for one part of their life history (or some populations occur on surface in case of stygofauna)
Primarily surface species found underground	
Trogloxene/ stygoxene	Occasional use of caves or the unsaturated zone, often as a refugium in adverse conditions
Accidental	Occurrence at mouth of cave, fallen into drill hole or bore

tat is important for these species. Bats and cave-nesting birds are excluded from consideration, largely because this chapter deals with what is happening in the broad landscape outside caves. Aquatic invertebrates found in the bed of streams are also not treated as subterranean for the purpose of this chapter, although, globally, much study of stygofauna is conducted in stream beds (Hancock et al. 2005; Dole-Olivier et al. 2009). Similarly, there is little consideration of fish and reptiles, because nearly all subterranean fauna species in Australia are invertebrates, although some stygofauna fish and troglofaunal reptiles do occur (e.g. Aplin 1998; Larson et al. 2013).

The major difference between this chapter and most accounts of subterranean fauna is the focus on underground habitats other than caves. Globally, most subterranean fauna studies deal with caves. However, the arid zone of Australia has very few large caves; in fact, there are arguably only two large cave systems in the arid zone. These are on the Nullarbor Plain (Webb and James 2006) and around Camooweal, north-west of Mount Isa (Grimes 1988; Eberhard 2003) (Fig. 1). Despite their large size, both systems have relatively depauperate subterranean faunas (Richards 1971; Eberhard 2003) which is perhaps unsurprising given the lack of wider occurrence of caves. Other cave systems on the edge of the arid zone, such as the Judbarra/Gregory karst area in the Northern Territory, are also depauperate (Moulds and Bannick 2012) (Fig. 1). Largely as a result of the paucity of cave fauna and the traditional emphasis of subterranean fauna studies on caves, it is only during the last 20 years that the richness of the Australian arid zone subterranean fauna outside caves has begun to be appreciated (Guzik et al. 2010).

This chapter provides a summary of current information on subterranean fauna in the Australian arid zone, particularly in the western half of the arid zone where most richness appears to occur. Some of the main issues in contemporary subterranean fauna research are discussed, together with issues that are relevant to the conservation of that subterranean fauna. A recent account with greater focus on the evolution of subterranean fauna in Australia is provided by Humphreys (2016).

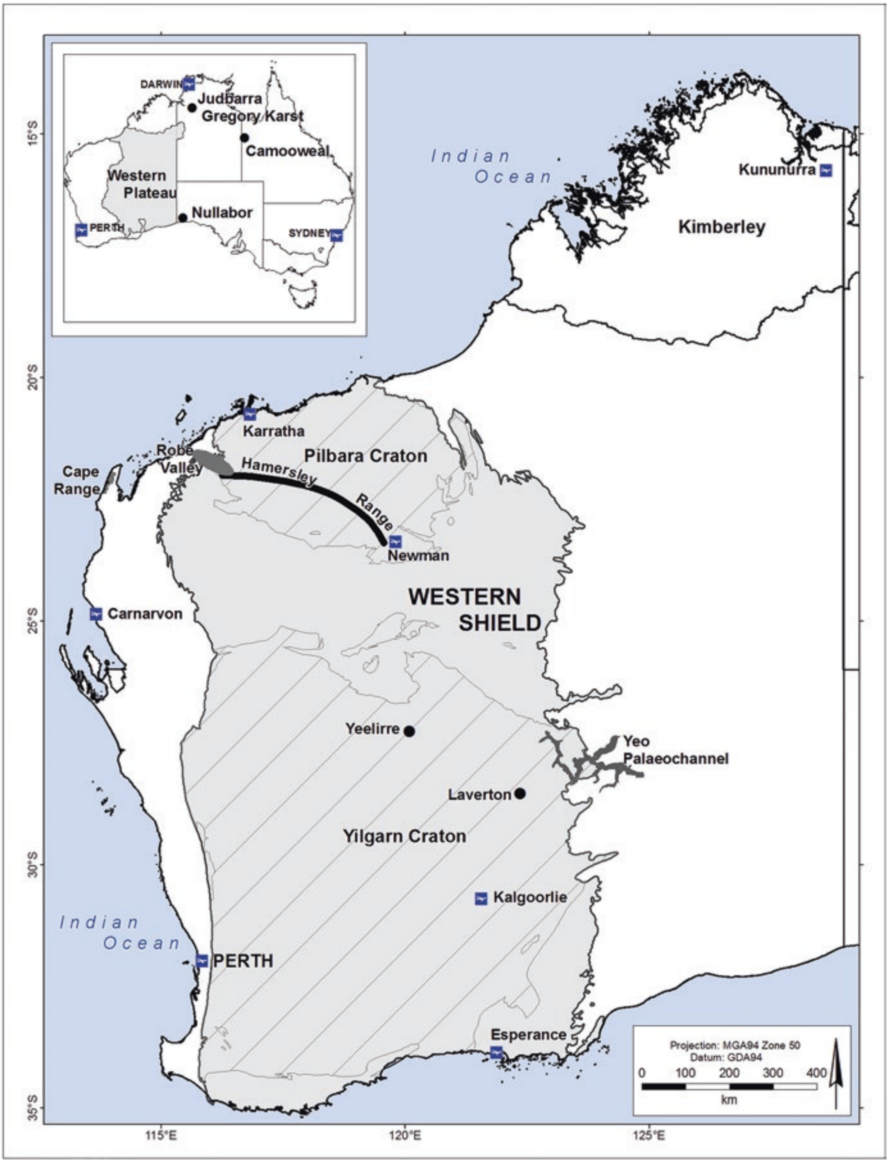


Fig. 1 Locations of the Western Shield, Pilbara and Yilgarn cratons (or regions) and other places mentioned in text

Subterranean Fauna Habitats

While many stygofauna species occur in groundwater below stream beds and in cave streams and ponds, most of this chapter deals with stygofauna in deeper regional aquifers that extend more widely across the landscape. The habitats of troglofauna outside caves are less well documented, but in general terms they comprise the habitat between the 'dry' ground surface and the water table. This habitat is often referred to as the vadose zone (e.g. Halse and Pearson 2014), although the term 'unsaturated zone' is also apt. Juberthie (1983) was the first to pay much attention to the unsaturated zone, although his focus was on the upper part of the zone, and he applied the term milieu souterrain superficial (MSS) to shallow detrital habitats across the landscape that support troglofauna (see also Mammola et al. 2016). Culver and Pipan (2008) applied the term shallow superficial habitats (SSH) to a wider variety of situations (including near-surface stygofauna habitat) but in doing so implied that caves comprised the major deep subterranean habitat. This is not the case in the Pilbara and Yilgarn regions of Western Australia, where stygofauna and troglofauna may be found tens of metres below the surface in various types of very small spaces that are widespread across the landscape. These small spaces are mostly what Howarth (1983) termed microcaverns (<5 mm in width) or, less commonly, mesocaverns (5–500 mm) (Fig. 2). A variety of other terms are used to describe the spaces, with the names often providing some information about their genesis [e.g. interstitial spaces in alluvium, vugs (or small spaces) in weathered rock, fissures in fractured rock].

The factors determining the occurrence of subterranean fauna are still in the early stages of investigation. While the size, pattern and quantity of spaces in a habitat is important for the occurrence of fauna, poor connectivity with the surface may constrain the number of species present (Halse et al. 2014), because most energy (as carbon) comes from the surface. Studies elsewhere suggest that the chemistry of the host substrate is not particularly important in most cases beyond its influence on habitat structure (Hahn and Fuchs 2009). The importance of spaces to the occurrence of subterranean fauna is most clearly documented for stygofauna, where the likelihood of species occurring is related in a positive way to the transmissivity of the aquifer (Maurice and Bloomfield 2012). At the same time, studies by Bradford et al. (2013) and others have shown there is currently poor understanding of how the finer details of habitat structure affect subterranean fauna occurrence. One example of fine-scale variation in occurrence, however, is provided by Hose et al. (2017) who showed differences in the abundance of stygofauna species in different alluvial substrates over vertical distances of less than 1 m. Such fine-scale control of distributions probably occurs in many species.

While predictions about the suitability of habitats for subterranean fauna at a fine scale tend to be unreliable, existing work enables some general observations to be made. Despite subterranean fauna occurring in a wide range of geologies in the arid zone, they tend to occur most abundantly in three broad geological units: karst (especially calcrete), alluvium and colluvium and mineralised or weathered iron

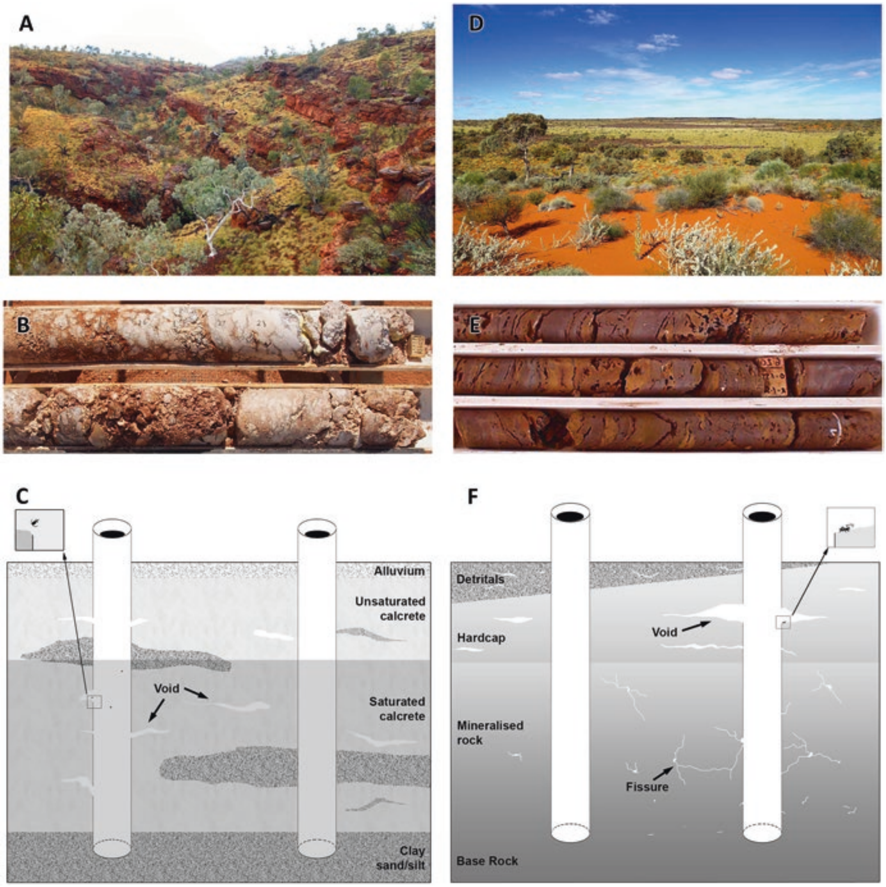


Fig. 2 Habitats in which subterranean fauna species occur. (**a**) Iron ore range in the Pilbara, with deep gullies and mesocaverns in hardcap; (**b**) drill core through saturated calcrete; (**c**) schematic illustration of subterranean habitat where calcrete is present; (**d**) Yilgarn palaeochannel containing calcrete below ground (red sand dune in foreground); (**e**) drill core through mineralised iron ore formation; and (**f**) schematic illustration of subterranean habitat in iron ore range

formations, especially banded iron formation and channel iron deposit. They are sometimes abundant in weathered volcanics and ultramafics but mostly occur in low numbers in other geologies.

The relationship between large numbers of stygofauna and calcrete bodies in palaeochannels in the Yilgarn region of Western Australia is well documented (Humphreys 2001, 2008; Guzik et al. 2010), with up to 75 species recorded from a single calcrete body (EPA 2016a). Another well-studied relationship is the occurrence of large numbers of troglofauna species in mineralised banded iron formations and channel iron deposits of the Pilbara, with more than 120 species being recorded from sections of banded iron formation in the Hamersley Range and up to 25 species being recorded from individual small mesas in the Robe Valley (Harvey et al. 2008; G. Humphreys and M. Curran, unpublished data). It should also be noted that it is not uncommon for a site to yield high numbers of stygofauna and low numbers of troglofauna or vice versa. This is sometimes the result of different geologies in the unsaturated zone and in the underlying groundwater aquifer; in other situations the flow of water may have kept spaces open in the aquifer, whereas they have been filled by fine sediment in the unsaturated zone.

Environmental Parameters

While physical habitat structure, connectivity and the extent of surface connection are determinants of subterranean fauna occurrence across the broad landscape matrix, some of the factors critical to subterranean fauna occurrence in caves are equally important across the landscape. These include the absence of light, stable temperatures and, in the non-saturated zone, high relative humidity (Culver and Pipan 2008). Differences in relative humidity are probably a key factor distinguishing between the habitats of soil fauna and subterranean fauna in the arid zone, with subterranean habitats probably usually being very close to saturated (Fig. 3), while surface habitats in the Pilbara and Yilgarn are often quite dry as a consequence of annual pan evaporation being 3000–5000 mm.

Groundwater in much of the arid zone is saline, and salinity is another factor potentially controlling the occurrence of species in groundwater, in the same way as it does in surface systems (Pinder et al. 2005). While it has been widely thought that stygofauna in the Pilbara and Yilgarn are unlikely to occur at salinities much above seawater concentration (35,000 mg L^{-1} or 50,000 μS cm^{-1}) (e.g. Watts and

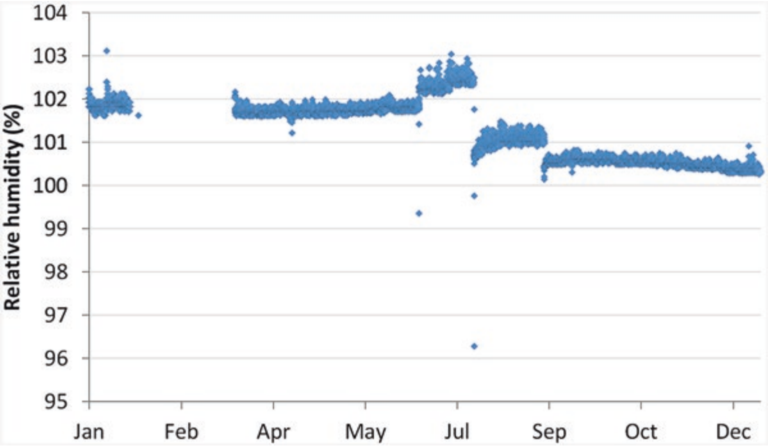


Fig. 3 Relative humidity through the year at a depth of 15 m in an iron ore mesa in the Pilbara. Measuring humidity near saturation is technically difficult, and the data are interpreted as showing 100% relative humidity throughout the year

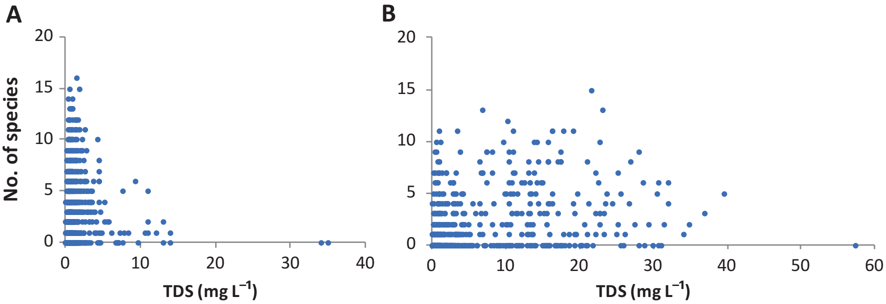


Fig. 4 Comparative salinity tolerances of stygofauna in the Pilbara and Yilgarn as shown by number of species per sample in relation to total dissolved solids (TDS). (**a**) Pilbara and (**b**) Yilgarn

Humphreys 2006), there are recent records of stygofauna in the northern Yilgarn at salinities of approximately 100,000 mg L^{-1} (Outback Ecology 2012). Despite these records suggesting some stygofauna species are strongly salt-adapted, most species are restricted to salinities of less than 10,000 mg L^{-1} in the Pilbara (Halse et al. 2014) and 25,000 mg L^{-1} in the Yilgarn (Humphreys et al. 2009) (Fig. 4). The broader environmental tolerances of stygofauna in Australia have been reviewed by Korbel and Hose (2011).

Subterranean Fauna of the Western Shield

Sampling of stygofauna outside caves in the arid zone began only in the late 1990s, when Bill Humphreys and colleagues extended their coastal sampling at Cape Range into the Pilbara and Yilgarn regions of Western Australia (Pesce et al. 1996; Humphreys 1999, 2001). Troglofauna sampling began about 10 years later, with the collection of schizomids and other troglofauna in the Robe Valley in the Pilbara (Harvey et al. 2008). Examples of the fauna collected are shown in Fig. 5.

As the amount of sampling of both stygofauna and troglofauna has increased, the richness of these two groups in arid parts of Western Australia has become ever more apparent. For example, Humphreys (2008) reported the occurrence of 560 stygofauna species on the Western Shield (principally the Pilbara and Yilgarn regions) (Fig. 1). This was followed by Eberhard et al. (2009) estimating, based on a regional sampling program, that 500–550 stygofauna species occur in the Pilbara alone, after which Guzik et al. (2010) estimated that 4140 subterranean fauna species, comprising 2680 stygofauna and 1460 troglofauna species, occur in the western half of Australia, mostly in the arid zone. More recent work suggests that even Guzik et al.'s (2010) large figure underestimates the richness of the fauna.

Halse (2015) proposed, based on a combination of sampling results and extrapolation based on the pattern of increasing richness seen with additional sampling, that nearly 3000 species of subterranean fauna occur in the Pilbara (Table 2). While they

Fig. 5 Species of subterranean fauna. (**a**) *Billibathynella* sp. (syncarid), (**b**) *Lagynochthonius* sp. (pseudoscorpion), (**c**) *Haifameira pori* (copepod), (**d**) Lathrobiina sp. (beetle), (**e**) *Gomphodella yandii* (ostracod), (**f**) Stenoniscidae gen. nov. sp. (isopod), (**g**) *Mangkurtu kutjarra* (spelaeogriphacid), (**h**) *Limbodessus* sp. (beetle), (**i**) *Nocticola* sp. (cockroach), (**j**) Linyphiidae sp. (spider), (**k**) *Draculoides* sp. (schizomid), (**l**) Hydrobiidae sp. (snail), and (**m**) Japygidae sp. (dipluran)

Table 2 Numbers of subterranean fauna species in the Pilbara, as collected by Bennelongia Environmental Consultants (BEC) or estimated to be present based on extrapolation of the collecting results to date by researchers, BEC and other environmental consultants

	No. of species	
Faunal group	Collected by BEC	Estimated
Stygofauna		
Crustacea		
Amphipoda	106	200
Isopoda	31	75
Syncarida	70	300
Copepoda	130	250
Ostracoda	194	300
Others	4	4
Hydracarina	23	40
Annelida	74	150
Mollusca	5	10
	637	1329
Troglofauna		
Isopoda	81	200
Pseudoscorpiones	66	150
Schizomida	59	120
Araneae	53	130
Palpigradi	18	40
Diplopoda	24	50
Chilopoda	51	120
Symphyla	38	80
Pauropoda	27	60
Diplura	90	200
Thysanura	47	100
Blattodea	27	40
Hemiptera	23	50
Coleoptera	69	150
Others	7+ (mostly Diptera)	21
	680	1511

do not represent systematic sampling, the results of surveys for environmental impact assessments suggest that the Yilgarn has similar stygofauna richness to that in the Pilbara but fewer troglofauna species. Therefore, it is considered likely that more than 4500 stygofauna and troglofauna species occur in the Pilbara and Yilgarn and that approximately 5500 subterranean species occur in the western half of Australia. By way of context, the known vascular plant richness in the Pilbara is less than 1800 species, with approximately 15% of these being endemic to the region (Erickson and Merritt 2016). Nearly all stygofauna and troglofauna species in the Pilbara (and Yilgarn and elsewhere) are endemic to the region in which they occur (Humphreys et al. 2009; Halse et al. 2014).

New comparisons of the richness of subterranean fauna in the Western Shield with other parts of the world are not made here, because there are substantial differences in the habitats that have been sampled in different countries, what species are treated as subterranean and the way in which numbers of species have been determined (Culver et al. 2013). However, both Halse et al. (2014) and Guzik et al. (2010) provide some comparisons between the richness of stygofauna in the Pilbara and western half of the arid zone and the richness of assemblages in other parts of the world. Halse et al. (2014) suggested the Pilbara has higher known density of stygofauna species than any other region in the world, except the Dinaric karst in south-eastern Europe, while Guzik et al. (2010) suggested arid Australia is uniquely rich in stygofauna compared with other areas of the world. Few easy comparisons of troglofauna richness can be made, because regional inventories are rarely compiled, but, with an estimated 1511 species, the Pilbara is likely to be one of the richest regions in the world for troglofauna. Only 995 troglofauna species have been recorded in the well-studied Dinaric karst (Sket et al. 2004), which is widely regarded as an area of global importance for troglofauna.

Stygofauna

A detailed account of the stygofauna of the Pilbara is given by Halse et al. (2014). Information on the Yilgarn is less consolidated, and the first moderately comprehensive overview is provided here, although general information is also available in Humphreys (2001) and Humphreys et al. (2009).

There is relatively little overlap in composition of stygofauna assemblages below the stream bed and in deeper groundwater aquifers of the Pilbara (Halse et al. 2002, 2014). This is probably because the groundwater associated with the alluvium of the ephemeral rivers and creeks of the Western Shield is poorly connected to regional groundwater (Dogramaci et al. 2012). Thus, while some species typical of the streambed fauna are found in regional aquifers, such as darwinulid ostracods, the candonid ostracod *Candonocypris tenuis*, many cyclopoid copepods and possibly phreatoicid isopods (Knott and Halse 1999; Schön et al. 2010; Pinder et al. 2010), the reverse rarely occurs.

The stygofauna assemblages of the Pilbara and Yilgarn show similar patterns at higher taxonomic levels, despite some differences in the proportions of the major groups (Fig. 6). Further comments on six of the groups are made here. First, based on the number of animals collected, copepods dominate stygofaunal communities of both the Pilbara and Yilgarn, comprising approximately 60% of the fauna in the Yilgarn and 40% in the Pilbara. However, copepod species are often represented by large numbers of animals, and, based on species richness, copepods comprise 44% of the fauna in the Yilgarn and 20% in the Pilbara (Halse et al. 2014; S. Halse, unpublished data). Complementing this overall picture, there appears to have been explosive speciation of harpacticoid copepods in some calcretes of the Yilgarn (Karanovic and Cooper 2011, 2012), where copepod species may represent almost half of the species at a site. As already noted, global comparisons are difficult to make, because of differences in habitats sampled and analytical methods, but cope-

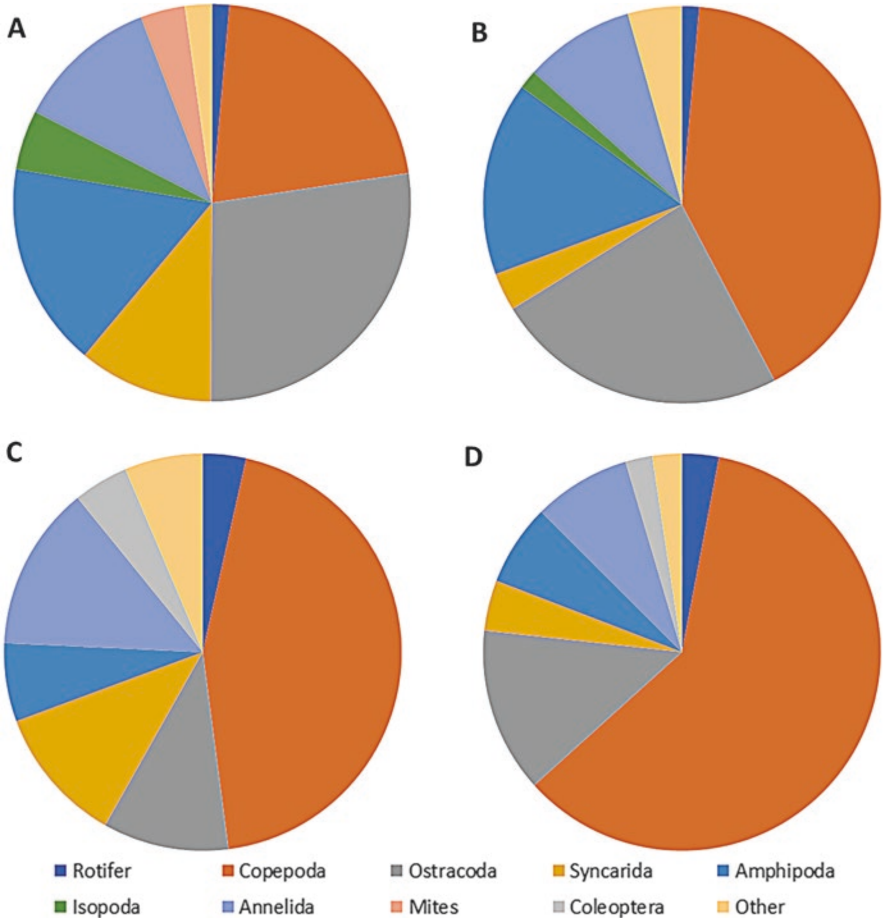


Fig. 6 Proportions of stygofauna in the Pilbara and Yilgarn belonging to different taxonomic groups. (**a**) Pilbara species, (**b**) Pilbara abundance, (**c**) Yilgarn species, and (**d**) Yilgarn abundance

pods may be regarded as comprising 17% of the species in a typical stygofauna community elsewhere (Eberhard et al. 2005) or 20–40% of the species in European communities (Galassi et al. 2009). The diversity of copepods in the Pilbara conforms to global patterns, while the diversity in the Yilgarn is relatively high.

Ostracods represent 24% and 13%, respectively, of the stygofaunal animals in the Pilbara and Yilgarn (Fig. 6) and 30% and 10% of the species in these regions. The greater contribution of ostracod species in the Pilbara reflects the enormous radiation of candonid ostracods in this region, consisting of 11 described endemic genera and more than 108 collected species (Reeves et al. 2007; Karanovic 2007; S.A. Halse, unpublished data). By global standards, where ostracods typically constitute about 3% of species in groundwater communities (Eberhard et al. 2005), both the Pilbara and Yilgarn are rich in ostracods.

Another outstanding characteristic of the stygofauna of the Yilgarn is the occurrence of more than 90 described species of dytiscid beetle in it and nearby regions (Watts and Humphreys 2009; Eberhard et al. 2016). In contrast, there is only one described beetle species in the Pilbara (Watts and McRae 2013), and this disparity, together with the difference in abundance of candonid ostracods, forms the clearest indications of the biogeographic differences between the Pilbara and Yilgarn. Despite their diversity, beetles are not a dominant component of the Yilgarn fauna in terms of either animal abundance or species richness. Beetles represent 0.01% and 2.2%, respectively, of the animals in the Pilbara and Yilgarn and 0.01% and 4.5% of the species in these regions. (Far more sites, including some outside the Yilgarn, have been sampled for beetles than for other stygofaunal groups which is why a larger number of species have been described than their proportional representation in the Yilgarn suggests.)

Amphipods are common in most stygofauna communities, typically representing about 19% of species globally. They represent 16% and 7%, respectively, of the animals in the Pilbara and Yilgarn (Fig. 6) and 17% and 20% of the species in these regions (Halse et al. 2014; S.A. Halse, unpublished data). Much of the focus of Yilgarn and Pilbara stygofauna research has been on amphipods (Finston et al. 2004, 2007; Cooper et al. 2007; Bradford et al. 2010, 2013; King et al. 2012), and comparisons of the results of this research with that from the northern hemisphere provide some insights into the different factors structuring communities in Australia and Europe.

Syncarids comprise 3.1% and 4.1%, respectively, of the stygofaunal animals in the Pilbara and Yilgarn and 11% of the stygofaunal species in both regions. This is a substantially larger proportion of the stygofauna community than is typically represented elsewhere by syncarids (Eberhard et al. 2005). Despite the relatively high number of species present and some recent morphological (e.g. Cho 2005; Cho and Humphreys 2010) and genetic work (e.g. Guzik et al. 2008), there is relatively poor understanding of the diversity and distributions of syncarids in the Pilbara and Yilgarn, especially for the family Bathynellidae (Perina et al. 2018).

Oligochaetes represent 9% and 8%, respectively, of the stygofaunal animals in the Pilbara and Yilgarn (Fig. 5) and 11% and 8% of the species, compared with a global average of 2% of the species in stygofauna communities (Eberhard et al. 2005). Many oligochaetes are quite widespread, and the proportion of stygobitic species in groundwater communities is often quite low (Creuze des Chatelliers et al. 2009), which may have affected global calculations. However, the greater number of stygal species in the Pilbara and Yilgarn is mostly attributable to the collection of relatively large numbers of enchytraeid species, despite phreodrilids and other oligochaete groups also occurring (Pinder 2008; Brown et al. 2015). Only 11% of the stygofaunal oligochaete species listed by Creuze des Chatelliers et al. (2009) are enchytraeids, which are considered to be a predominantly terrestrial family with unstable taxonomy and uncertain ecological attributes, whereas they comprise 31% of Pilbara and 50% of Yilgarn oligochaete species.

Troglofauna

Information on the occurrence of troglofauna outside caves comes almost entirely from environmental impact assessment surveys associated with mining proposals and is strongly biased towards the sampling of hard rock geologies. Areas of calcrete have usually been sampled at low intensity, if at all, because of the difficulty maintaining open holes without casings of soft substrata. Halse and Pearson (2014) have provided an analysis of the taxonomic composition of troglofauna in the Pilbara, but the first account of the overall composition of Yilgarn troglofaunal assemblages is presented here.

One of the peculiarities of the information on troglofauna in the Pilbara and Yilgarn is that there has been no attempt to assess the occurrence of troglofaunal mites and collembolans. Both groups occur as subterranean fauna in other parts of the world (Ortuño et al. 2013; Kováč et al. 2016) and have been observed in Pilbara and Yilgarn samples (Greenslade 2002). Leaving aside mites and collembolans, there are substantial differences between the troglofaunal assemblages of the Pilbara and Yilgarn, with isopods dominating the Yilgarn fauna and several of the groups that are prominent in the Pilbara (cockroaches, schizomids, dipterans) being absent, or nearly so, from the Yilgarn (Fig. 7). The occurrence of 10 groups is considered in detail.

Based on the number of animals collected, isopods comprise 6% and 43% of the troglofauna abundance in the Pilbara and Yilgarn, respectively. The difference between the regions is reduced somewhat when species richness is examined, with isopods comprising 12% of troglofauna species in the Pilbara and 30% of those in the Yilgarn. Comparisons of these proportions with typical troglofaunal communities elsewhere in the world are difficult to make, because of differences in the habitats sampled (cave or broader unsaturated zone), the completeness of lists and whether lists include all troglofauna species or only troglobites. Nevertheless, the Yilgarn appears to have an unusually high proportion of isopods compared with other parts of the world, such as the Balkan Peninsula and various high-yielding sites where, in both cases, 12% of species are isopods (Culver and Sket 2000; Sket et al. 2004). On the other hand, in the small fauna of Portugal, isopods occur in proportions similar to the Yilgarn (26% of species; Reboleira et al. 2013). More than 72 troglofauna isopod species have been recorded in the Yilgarn, including 20 troglomorphic species listed by Javidkar et al. (2016) that are not included in Fig. 7. This is nearly three times as many isopod species as recorded from Brazilian caves (Campos-Filho et al. 2014), albeit that very few Yilgarn isopods are described (Taiti 2014).

Hemipterans, mostly belonging to the family Meenoplidae, are very abundant in the Pilbara and to a lesser extent the Yilgarn, representing 23% and 10%, respectively, of all animals, but only 3.4% of the troglofauna species in each region (Fig. 7). Some troglophilic meenoplid species are widespread in the Pilbara and Yilgarn. Other potentially troglobitic species appear to have small ranges, but further taxonomic and ecological work is required to confirm their status as troglobitic.

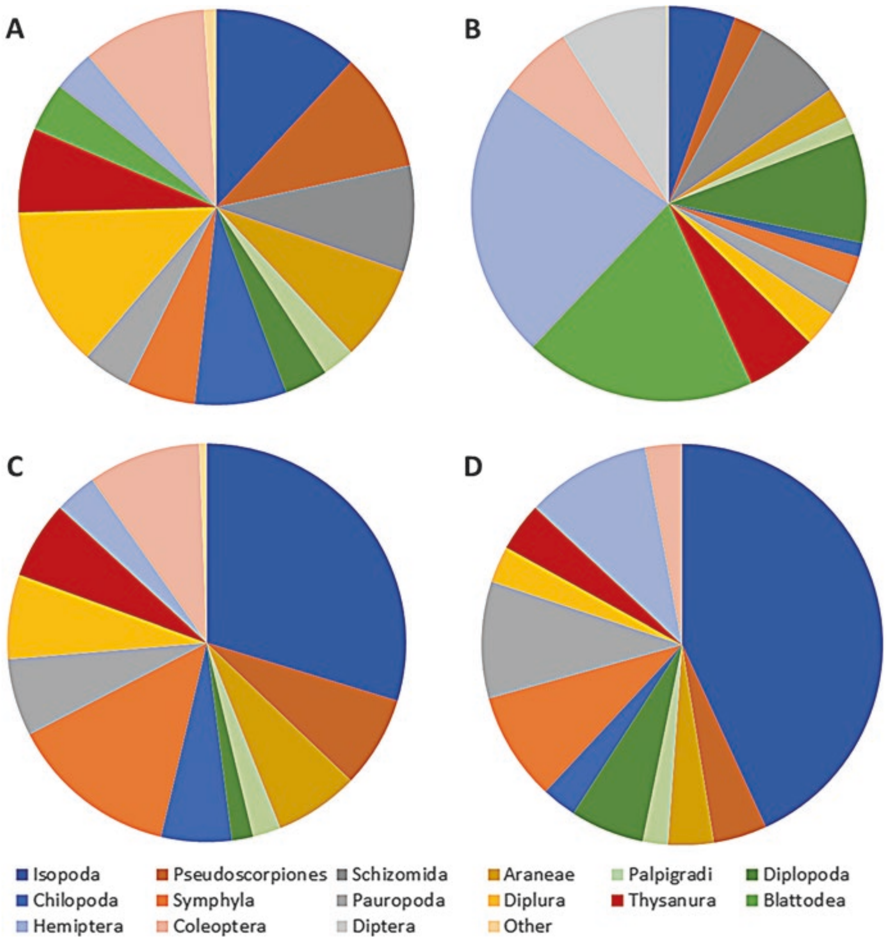


Fig. 7 Proportions of troglofauna in the Pilbara and Yilgarn belonging to different taxonomic groups. (**a**) Pilbara species, (**b**) Pilbara abundance, (**c**) Yilgarn species, and (**d**) Yilgarn abundance

Culver and Pipan (2008) considered troglobitic hemipterans to be more common in shallow subterranean habitats than caves, although meenoplid species considered to be troglobitic are found in caves of northern Australia (Hoch 1993; Moulds and Banninck 2012).

Cockroaches, mostly belonging to the family Nocticolidae, are also very abundant in the Pilbara, where they represent 19% of animals but only 4% of all troglofauna species. However, cockroaches are one of the many groups in which use of genetic species concepts is likely to substantially increase the number of species recognised (Trotter et al. 2017). No cockroaches have been collected from the Yilgarn. Elsewhere, cockroaches often occur in low numbers (Roth 1991; Moulds and Banninck 2012), and their diversity in the unsaturated zone of the Pilbara appears to be comparatively high.

Table 3 Median linear range (recalculated from Halse and Pearson 2014) of troglofauna species in the Pilbara and the main geologies from which the groups are known in the Pilbara and Yilgarn

Troglofauna group	Median linear range (km)	Major habitats
Isopoda	1.8	Mineralised rock, detritals (calcrete)
Pseudoscorpiones	5.3	Mineralised rock, detritals (calcrete)
Schizomida	2.6	Mineralised rock
Araneae	2.2	Mineralised rock (calcrete)
Palpigradida	21	Mineralised rock, detritals (calcrete)
Diplopoda	4.5	Mineralised rock, detritals (calcrete)
Chilopoda	6.2	Mineralised rock, detritals (calcrete)
Symphyla	3.2	Detritals, mineralized rock (calcrete)
Pauropoda	6.6	Detritals, mineralized rock (calcrete)
Diplura	4.5	Mineralised rock, detritals (calcrete)
Thysanura	3.7	Mineralised rock, detritals (calcrete)
Blattodea	6.1	Mineralised rock
Hemiptera	68	Mineralised rock, detritals (calcrete)
Coleoptera	8.7	Mineralised rock, detritals
Diptera	159	Mineralised rock

Millipedes are relatively abundant in both the Pilbara and Yilgarn, representing 9% and 6% of all troglofaunal animals, respectively, in these regions (Fig. 7). However, this is largely the result of the widespread occurrence of the circum-tropical, troglophilic *Lophoturus madecassus* (see Car et al. 2013), and millipedes comprise only 3.5% and 1.7% of the species present, respectively, in the two regions. In comparison, millipedes comprise 10% of the fauna in the Balkan Peninsula (Sket et al. 2004) and 8% of the fauna at selected sites around the world that are rich in troglofauna (Culver and Sket 2000).

Schizomids occur moderately often in caves and the unsaturated zone across Northern Australia (e.g. Harvey 2001) as well as in the tropics more generally (Monjaraz-Ruedas 2013). However, in iron ore ranges of the Pilbara, they are found with a diversity that appears to be exceptionally high for the group, and they comprise 7% of all animals and 9% of all species in Pilbara troglofaunal assemblages (Fig. 7). Some of the diversity of schizomids in the Robe Valley of the Pilbara was documented in detail by Harvey et al. (2008), while Harms et al. (2016) have discussed issues around species delineation in the Hamersley Range. At least in Australia, the occurrence of schizomids is indicative of a taxonomically rich troglofauna community. As with cockroaches, schizomids are absent from the Yilgarn.

Diplurans usually comprise a small to moderate proportion of troglofaunal assemblages (1.1% in the Balkan peninsula, Sket et al. 2004; 1.4–6% in superficial subterranean habitats, Culver and Pipan 2008; 7% in Portugal, Reboleira et al. 2013). An unpublished report by Markus Koch in 2009 highlights the richness of diplurans in Western Australia, especially in the Pilbara, Yilgarn and Kimberley regions. However, troglofaunal dipluran species tend to occur at low abundance and comprise only 2.9% and 3.0% of animals in the Pilbara and Yilgarn, respectively, despite accounting for 13% and 7% of species. In fact, diplurans are the most species-rich troglofaunal group in the Pilbara, although some species are certainly troglophiles and the exact proportion of troglobitic species is unclear. The estimated median linear range of 4.5 km for Pilbara species (Table 3) suggests the proportion of troglobites may be quite high.

Pauropods, symphylans and, perhaps to a lesser extent, palpigrads provide even greater difficulty distinguishing troglofauna from surface species, because they occur in soil and lack eyes and pigment. While troglobitic palpigrads and symphylans are regularly recorded elsewhere in the world (e.g. Sket et al. 2004), there are few records of troglobitic pauropods anywhere (Vandel 1965). However, Halse and Pearson (2014) suggested that at least some of the pauropod species collected from the unsaturated zone in the Pilbara are likely troglobites, because of their small ranges and, more particularly, the hostile surface soil conditions in the hot, arid Pilbara. More documentation of the surface soil faunas of pauropods, symphylans and palpigrads would help determine the status of species collected in subterranean sampling (see Trajano and Bichette 2010). Based on current interpretations of surface and subterranean status, it is considered that all three groups are relatively species-rich in subterranean habitats of the Yilgarn and Pilbara. Pauropods, symphylans and palpigrads are thought to comprise 2.8%, 2.3% and 1.5% of all troglofaunal animals in the Pilbara and 9%, 9% and 2.0% of Yilgarn animals, respectively (Fig. 7). As a result of most species being collected at low abundance, these animals represent 4.9%, 5.6% and 2.6% and 6.3%, 13.6% and 2.3% of all troglofaunal species, respectively.

Compared with other parts of the world, the low proportions of beetles in the troglofauna assemblages of the Pilbara and Yilgarn are quite startling. It is also a contrast to the relative richness of stygofaunal beetles in the Yilgarn. Only 6% and 3% of troglofaunal animals and 10% and 9% of species are beetles in the Pilbara and Yilgarn, respectively. Typically, beetles comprise about one-third of the species in troglofaunal communities (30% at selected species-rich sites around the world, Culver and Sket 2000; 39% in the Balkan Peninsula, Sket et al. 2004; approximately 40% in Tennessee, Niemiller and Zigler 2013). While further taxonomic investigations are likely to substantially increase the number of beetles known from the Pilbara and Yilgarn (e.g. Baehr and Main 2016; Table 2), beetles are likely to continue to be poorly represented compared with other parts of the world.

Species Delimitation

In addition to the capacity for study of subterranean fauna in the Pilbara and Yilgarn to provide new insights into evolutionary and biogeographic processes (see Humphreys 2016), the potential for mining and groundwater abstraction to threaten the persistence of subterranean species is an important driver of stygofauna and troglofauna research. The process of identifying species as units for conservation (whether or not formally described), and, more particularly, the ranges of those species, is a fundamental step in assessing the likely conservation impacts of mining and groundwater developments.

There are challenges for both morphologists and geneticists when it comes to delimiting species in subterranean habitats. Identifying species through use of traditional morphological characters can be difficult, because of the occurrence of both convergent evolution on some characters (Ornelas-Garcia et al. 2008) and relaxed selection pressure on others that results in phenotypic plasticity, especially in relation to segmentation and setae on left and right sides of animals (Karanovic et al. 2013). In addition, the mostly low numbers in which species are collected, and high proportions of immature animals, means that the number of suitable specimens for morphology is usually very small. Consequently, species descriptions are occasionally based on single immature or damaged animals, making it difficult to achieve certainty when trying to align subsequently collected specimens with the described species.

Genetic recognition of species can also be challenging, because the likelihood of very limited dispersal capacity below ground means genetic structuring within a species is to be expected. Consequently, there may be almost as much intraspecific as interspecific variation in genes used for species discrimination (e.g. CO1; Bradford et al. 2010), which can cause problems in determining the number of species present (Ferguson 2002; Ross et al. 2008). The extent of sequence variation appears to differ among taxonomic groups, with insects being relatively conservative (Leys et al. 2003; Guzik et al. 2009), while arachnids and, particularly, crustaceans show greater variation (Harvey et al. 2008; Finston et al. 2007, 2011). Some variation in crustaceans in calcrete bodies is likely to be the result of successive isolation events for animal populations in refugia within the calcrete, followed by expansion events as higher water levels expand the area of saturated calcrete and permit wider gene flow. More generally, high intraspecific variability in subterranean fauna is often accompanied by low nucleotide diversity (Guzik et al. 2009; Bradford et al. 2013), and it is likely that accurate genetic delimitation of species will often require the use of multiple genes (Bazin et al. 2006; Asmyhr and Cooper 2012; Bradford et al. 2013) and collection of a large number of samples across the species' range (Bergstein et al. 2012). However, adequate sampling is usually difficult to achieve when access to the species' habitat is via pre-existing drill holes that probably cover only part of the species' range and, in fact, may often not intersect the species' preferred microhabitat (Fig. 2).

The way in which sampling and identification effort may affect the recognition of troglofauna species was illustrated by Harms et al. (2016), who showed that limited sampling led to eight species being recognised in the schizomid genus *Draculoides* from a small part of the Hamersley Range. Applying the results of barcoding with the CO1 gene and a small amount of additional sampling led to 15 species being recognised. However, further sampling in the same area and phylogenetic analysis using CO1 results reduced this to 12 species. This changing number of species highlights the complexity of delimiting species units in the subterranean environment, especially when the broad biological characteristics of the environment are still being investigated and there is a poor ecological and life-history framework in which to interpret results. Genetic data may provide no clearer guidance about species boundaries than morphological information, and, in such situations, use of a combination of genetics and morphology likely provides better-informed taxonomic decisions (De Queiroz 2007; Javidkar et al. 2016).

Species Distributions

As a group, subterranean fauna species are characterised by small ranges. This is especially so for troglofauna species (Halse and Pearson 2014), which in the Pilbara appear to have ranges that are mostly at least an order of magnitude smaller than those of stygofauna species (Eberhard et al. 2009; Halse et al. 2014). Linear ranges of 1–2 km appear to be moderately common among arid-zone troglofauna species in Australia (Table 3), while existing data suggest only about 5% of Pilbara stygofauna species are likely to have linear ranges of <30 km (Halse et al. 2014). There is probably less difference, however, between ranges of stygofauna and troglofauna species in the Yilgarn, particularly in calcretes.

Perhaps the best-known generalisation about the pattern of occurrence of subterranean fauna species is the 'calcrete island hypothesis' of Steve Cooper and others to explain the restricted distributions of many stygofauna species in calcrete bodies of the Yilgarn (Cooper et al. 2002, 2007). It also seems to apply to troglofauna species in Yilgarn calcretes (Javidkar et al. 2016). Under this hypothesis, most species in calcretes of the Yilgarn region are expected to be restricted to individual calcrete bodies that may have linear ranges of only tens of kilometres at most. The area between calcrete bodies, which includes intervening sections of the palaeochannel valleys hosting the calcretes, is considered to be unsuitable for stygofauna and troglofauna, because of high salinity (Humphreys et al. 2009), lack of suitable voids and spaces or otherwise inhospitable habitat for a variety of reasons. A series of papers by Tomislav Karanovic on the copepods of the Yeelirrie calcrete illustrate the extreme levels of geographic replacement and local endemism that may occur, with some species appearing to have linear ranges of <5 km (Karanovic and Cooper 2011, 2012; Karanovic et al. 2015).

Another apparent generalisation is that mineralised and weathered iron ore formations provide rich troglofaunal habitat. The occurrence of rich troglofauna communities in iron ore ranges in Australia is analogous to the occurrence of troglofauna in iron ore mining areas of Brazil (Silva et al. 2011), although in Brazil the animals have mostly been collected from caves, rather than from microcaverns across the iron ore deposit (Fig. 2). While iron ore formations are used extensively by troglofauna, the factors affecting the extent to which different types of deposits are used are still being studied and, for example, the reasons why banded iron formations in the Pilbara support greater numbers of troglofauna species than banded iron formations in the Yilgarn are not understood. Pilbara communities are more complex in structure and, as already mentioned, support groups such as schizomids and cockroaches that are absent from the Yilgarn.

In terms of species ranges, the microcaverns comprising most of the spaces in vuggy banded iron and other rock formations are unlikely to provide many pathways for long-distance lateral dispersal (Fig. 2). Therefore, the troglobitic species found in rock habitats would be expected to have smaller ranges than species inhabiting various types of detritals (scree and alluvium/colluvium) where the potential for dispersal through the matrix is likely greater. Despite this, based on current understanding of the habitats occupied by species, the ranges of troglofauna species in the Pilbara are not strongly determined by the type of geology in which the species occur (Table 3). Probably the most important factor is whether species are troglophilic and have a surface dispersal phase (rather than the lateral below-ground dispersal of troglobites), but intrinsic biological differences among groups may also affect ranges.

The finding that stygofaunal syncarids in alluvial aquifers in New South Wales display some genetic structuring over distances of 50 m in an apparently homogeneous alluvial aquifer (Asmhyr et al. 2013) highlights that lateral movement through the substrate by subterranean species is limited in many habitats. Furthermore, it may be vertically constrained by the physical structure of the substrate or its chemistry (Hose et al. 2017). With the limited information about subterranean habitats that is available from the surface (albeit often augmented with data from drill holes), it is usually difficult to determine whether species ranges are constrained by subtle habitat variation acting as barriers to reduce movement (Guzik et al. 2009; Trontelj et al. 2009) or innate life-history characteristics. This latter phenomenon is widely recognised in trapdoor spiders (Bond et al. 2001; Cooper et al. 2011) and, given the considerable variation in species' ranges between different taxonomic groups, may also be important in subterranean fauna.

Conservation Challenges

There are three issues that make it challenging to put together an appropriate program for the conservation of subterranean fauna in the Australian arid zone. These issues apply in other regions as well. The first issue is that the small ranges of subterranean fauna species make them particularly vulnerable to even single development projects where subterranean habitat is removed. The second issue is the limited information about the ecology and distribution of subterranean species across the arid zone as a whole. There has been only one regional survey to identify the local areas of high species richness (Halse et al. 2014), as well as to identify the extent to which different geologies are used by subterranean species. The third issue is perhaps the biggest challenge. It is the low level of awareness of subterranean fauna among policymakers and the public at large. There is no impetus to protect species that people know little about and which have poorly documented ecological roles.

Species Ranges in Relation to Project Impacts

Large mining operations may have open mine pits that extend 20 km or more, with annual dewatering requirements of up to 150 gigalitres and substantially larger areas of drawdown than the mine pits themselves (e.g. EPA 2015). In some cases, the pits may be hundreds of metres deep (e.g. EPA 2002). There may also be requirements for mine processing water or, where dewatering produces more water than can be used, the excess may be reinjected below ground. Irrigation projects in the arid zone are another potential user of large amounts of groundwater. All of these developments may pose a conservation threat to subterranean species. Given that many troglofauna and stygofauna species, respectively, have linear ranges of 1–2 km and < 30 km (and sometimes <5 km), such developments have the potential to threaten significant numbers of species through direct loss of habitat. There is also potential for reduction in stygofauna populations, and perhaps even extinction of species under some circumstances, as a result of changes in water chemistry associated with mining and irrigation. Potential changes include increased salinity, reduced carbon and nutrient inputs as a result of mining and increased nutrient loads as a result of irrigated agriculture (Hancock et al. 2005; Humphreys 2009; Nevill et al. 2010).

Documenting Distributions and Managing Threats

While assessments of the potential impacts of development on subterranean fauna usually focus on threats to species, another important conservation value to consider is the overall richness and biological uniqueness of the subterranean fauna assemblage in a development area. Regional surveys provide a framework of information that enables the relative value of assemblages to be assessed, as well as enabling prediction of the likely values of an area in advance of survey.

Regional surveys also help provide information on the distributional characteristics of species of different taxonomic groups, sometimes enabling a species' range to be predicted from that of related species. This type of information will be refined over time as more ecological and life-history studies of species are undertaken. The other important aspect of distributions, particularly from the viewpoint of predicting and managing impact, is the vertical occurrence of species. This may largely be controlled by the geological preferences of the species or, in the case of stygofauna, their salinity tolerance. Current sampling methods provide relatively unreliable information about the depths at which animals occur, although use of packers and other new techniques would improve the quality of information obtained when sampling (Sorensen et al. 2013).

In many situations, the threat to species is likely to be partial, whereby a considerable amount (but not all) of habitat is lost or the quality of the habitat is affected by development. If the biology of the species is well understood, then its likely impacts can be reduced or mitigated through management actions. One scenario where better information may allow mining to proceed without threat to species is where the vertical distribution of suitable habitat for a subterranean species can be shown to extend deeper than the mine pit or the extent of groundwater drawdown. However, sometimes the process of mining, groundwater abstraction or reinjection will alter conditions in the deeper 'refuge', rendering it unsuitable for the species. Sound ecological understanding is critical to decision-making in such situations.

Awareness of Subterranean Fauna

Of the government agencies in Australia, the Western Australian Environmental Protection Authority has responded most strongly to the threats to subterranean fauna, with stygofauna featuring in assessments in the arid zone as early as 1997 (EPA 1997, 1998) and troglofauna in 2006 (EPA 2006, 2007). This is largely a reflection of the richness of subterranean fauna on the Western Shield and the large amount of mining that occurs in Western Australia.

A series of guidelines on subterranean fauna assessment has been released in Western Australia, with the most recent describing the principles of assessment (EPA 2016b). Elsewhere in Australia, the Queensland Government released a subterranean fauna assessment guideline in 2014, while South Australia released a discussion document in 2015 (Goonan et al. 2015). Subterranean fauna have been identified as an issue requiring assessment in many development projects in New South Wales (e.g. Eco Logical 2015), but the framework for assessment is less formal than in Western Australia and Queensland.

Maintaining or increasing agencies' interest in the conservation of subterranean fauna would be assisted by clearer demonstration of the ecological services provided by these animals. There has been greater effort in this regard for stygofauna (e.g. Danielopol et al. 2003; Steube et al. 2009; Griebler and Avramov 2015) than for troglofauna, where the focus has been more taxonomic and biogeographic. However, troglofauna are likely to provide similar ecological services to those provided by soil fauna (e.g. Lavelle et al. 2006), albeit at greater depth. Plant roots, especially of trees, extend much deeper than the zones occupied by soil fauna and probably often rely on subterranean fauna to maintain a suitable environment.

Concluding Remarks

In summary, the arid zone of Western Australia contains very significant stygofaunal and troglofaunal biodiversity at the global scale. Largely because the animals are mostly tiny, and live underground, they have usually been overlooked in conservation planning, and their scientific importance has frequently been underestimated compared with surface plants and animals. While the large, iconic Karijini National

Park in the Pilbara is probably uniquely rich in troglofauna, there is no information whatsoever about the species within it.

The historical lack of interest in subterranean fauna is currently being redressed to some extent by research funding agencies, with many interesting research results emerging. In terms of management, both stygofauna and troglofauna provide taxonomic challenges when determining what comprises a species. Legislation for protecting fauna uses species as the operational unit, which means taxonomy will continue to be an important component of subterranean fauna research. New genetic techniques, such as environmental DNA, may assist in documenting the distributions of rare or 'difficult to collect' species, while more intensive studies of individual species and how particular microhabitats are used by subterranean fauna will provide the basis for informed management of subterranean fauna and for mitigation of threats to them. It is also important that research and reviews focus on providing more information about the environmental services provided by subterranean fauna and the sensitivity of these services to the loss of different types of species.

References

Aplin KP (1998) Three new blind snakes (Squamata, Typhlopidae) from north western Australia. Rec West Mus 19:1–12

Asmyhr MG, Cooper SJB (2012) Difficulties barcoding in the dark; the case of crustacean stygofauna from Eastern Australia. Invertebr Syst 26:583–591

Asmyhr MG, Hose G, Graham P, Stow AJ (2013) Fine-scale genetics of subterranean syncarids. Freshw Biol 59:1–11

Baehr M, Main D (2016) New genera and species of subterranean anilline Bembidiini from the Pilbara, north-western Australia (Insecta: Coleoptera: Carabidae: Bembidiini: Anillina). Rec West Aust Mus 31:59–89

Bazin E, Glemin S, Galtier N (2006) Population size does not influence mitochondrial genetic diversity in animals. Science 312:570–572

Bergsten J, Bilton DT, Fujisawa T, Elliott M, Monaghan MT, Balke M, Hendrich L, Geijer J, Herrmann J, Foster GN, Ribera I, Nilsson AN, Barraclough TG, Vogler AP (2012) The effect of geographical scale of sampling on DNA barcoding. Syst Biol 61:851–869

Bond JE, Hedin MC, Ramirez MG, Opell BD (2001) Deep molecular divergence in the absence of morphological and ecological change in the Californian coastal dune endemic trapdoor spider *Aptostichus simus*. Mol Ecol 10:899–910

Bradford T, Adams M, Humphreys WF, Austin AD, Cooper SJB (2010) DNA barcoding of stygofauna uncovers cryptic amphipod diversity in a calcrete aquifer in Western Australia's arid zone. Mol Ecol Resour 10:41–50

Bradford TM, Adams M, Guzik MT, Humphreys WF, Austin AD, Cooper SJ (2013) Patterns of population genetic variation in sympatric chiltoniid amphipods within a calcrete aquifer reveal a dynamic subterranean environment. Heredity 111:77–85

Brown L, Finston T, Humphreys G, Eberhard S, Pinder A (2015) Groundwater oligochaetes show complex genetic patterns of distribution in the Pilbara region of Western Australia. Invertebr Syst 29:405–420

Campos-Filho IS, Araujo PB, Bichuette ME, Trajano E, Taiti S (2014) Terrestrial isopods (Crustacea: Isopoda: Oniscidea) from Brazilian caves. Zool J Linnean Soc 172:360–425

Car CA, Short M, Huynh C, Harvey MS (2013) The millipedes of Barrow Island, Western Australia (Diplopoda). Rec West Aust Mus Suppl 83:209–219

Cho J-L (2005) A primitive representative of the Parabathynellidae (Bathynellacea, Syncarida) from the Yilgarn Craton of Western Australia. J Nat Hist 39:3422–3433

Cho J-L, Humphreys WF (2010) Ten new species of the genus *Brevisomabathynella* Cho, Park and Ranga Reddy, 2006 (Malacostraca, Bathynellacea, Parabathynellidae) from Western Australia. J Nat Hist 44:993–1079

Cooper SJB, Hinze S, Leys R, Watts CHS, Humphreys WF (2002) Islands under the desert: molecular systematics and evolutionary origins of stygobitic water beetles (Coleoptera: Dytiscidae) from Central Western Australia. Invertebr Syst 16:589–598

Cooper SJB, Bradbury JH, Saint KM, Leys R, Austin AD, Humphreys WF (2007) Subterranean archipelago in the Australian arid zone: mitochondrial DNA phylogeography of amphipods from Central Western Australia. Mol Ecol 16:1533–1544

Cooper SJB, Harvey MS, Saint KM, Main BY (2011) Deep phylogeographic structuring of populations of the trapdoor spider *Moggridgea tingle* (Migidae) from southwestern Australia: evidence for long-term refugia within refugia. Mol Ecol 20:3219–3236

Creuzé d, Châtelliers M, Juget J, Lafont M, Martin P (2009) Subterranean aquatic Oligochaeta. Freshw Biol 54:678–690

Culver DC, ad Pipan T (2008) Superficial subterranean habitats – gateway to the subterranean realm? Cave Karst Sci 5:5–12

Culver DC, Sket B (2000) Hotspots of subterranean biodiversity in caves and wells. J Cave Karst Stud 6:11–17

Culver DC, Trontelj P, Zagmajster M, Pipan T (2013) Paving the way for standardized and comparable biodiversity studies. Subterranean Biol 10:43–50

Danielopol DL, Griebler C, Gunatilaka A, Notenboom J (2003) Present state and future prospects for groundwater ecosystems. Environ Conserv 30:104–130

De Queiroz K (2007) Species concepts and species delimitation. Syst Biol 56:879–886

Dogramaci S, Skrzypek G, Dodson W, Grierson PF (2012) Stable isotope and hydrochemical evolution of groundwater in the semi-arid Hamersley Basin of subtropical northwest Australia. J Hydrol 475:281–293

Dole-Olivier M-J, Malard F, Martin D, Lefébure T, Gibert J (2009) Relationships between environmental variables and groundwater biodiversity at the regional scale. Freshw Biol 54:797–813

Eberhard S (2003) Nowranie Caves and the Camooweal Karst Area, Queensland: hydrology, geomorphology and speleogenesis, with notes on aquatic biota. Helicitite 38:27–38

Eberhard SM, Halse SA, Humphreys WF (2005) Stygofauna in the Pilbara region, north-west Western Australia: a review. J R Soc West Aust 88:167–176

Eberhard SM, Halse SA, Williams MR, Scanlon MD, Cocking JS, Barron HJ (2009) Exploring the relationship between sampling efficiency and short range endemism for groundwater fauna in the Pilbara region, Western Australia. Freshw Biol 54:885–901

Eberhard SM, Watts CHS, Callan SK, Leijs R (2016) Three new subterranean diving beetles (Coleoptera: Dytiscidae) from the Yeelirrie groundwater calcretes, Western Australia, and their distribution between several calcrete deposits including a potential mine site. Rec West Aust Mus 31:27–40

Eco Logical (2015) Bylong coal project environmental impact statement: stygofauna impact assessment. Prepared for Hansen Bailey. Ecological Australia, Sutherland, NSW

EPA (1997) Extensions to exmouth water supply borefield. Bulletin 843. Environmental Protection Authority, Perth

EPA (1998) Newman satellite development; mining of Orebody 23 below the water table. Bulletin 888. Environmental Protection Authority, Perth

EPA (2002) Iron ore mine, downstream processing (direct-reduced and hot-briquetted iron) and port, Cape Preston, WA. Bulletin 1056. Environmental Protection Authority, Perth

EPA (2006) Gorgon gas development, Barrow Island Nature Reserve. Bulletin 1221. Environmental Protection Authority, Perth

EPA (2007) Mesa A/Warramboo iron ore project. Bulletin 1251. Environmental Protection Authority, Perth

EPA (2015) Increase in abstraction and reinjection at Cloubreak mine. Report 1547. Environmental Protection Authority, Perth

EPA (2016a) Yeelirrie uranium project. Report 1574. Environmental Protection Authority, Perth

EPA (2016b) Environmental factor guideline: subterranean fauna. Environmental Protection Authority, Perth

Erickson TE, Merritt DJ (2016) Introduction to plant diversity of the Pilbara. In: Erickson TE, Barrett RL, Merritt DJ, Dixon KW (eds) Pilbara seed atlas and field guide: plant restoration in Australia's arid northwest. CSIRO, Melbourne, pp 1–5

Ferguson JWH (2002) On the use of genetic divergence for identifying species. Biol J Linn Soc 75:509–516

Finston TL, Bradbury JH, Johnson MS, Knott B (2004) When morphology and molecular markers conflict: a case history of subterranean amphipods from the Pilbara, Western Australia. Anim Biodivers Conserv 27:83–94

Finston TL, Johnson MS, Humphreys WF, Eberhard SM, Halse SA (2007) Cryptic speciation in two widespread subterranean amphipod genera reflects historical drainage patterns in an ancient landscape. Mol Ecol 16:355–365

Finston TL, Johnson MS, Eberhard SE, Cocking JS, McRae JM, Halse SA, Knott B (2011) New genus and species of groundwater paramelitid amphipods from the Pilbara, Western Australia: a combined molecular and morphological approach. Rec West Aust Mus 26:154–178

Galassi DMP, Huys R, Reid JW (2009) Diversity, ecology and evolution of groundwater copepods. Freshw Biol 54:691–708

Goonan P, Jenkins C, Hill R, Klainig T (2015) Subsurface groundwater ecosystems: a briefing report on the current knowledge, monitoring considerations and future plans for South Australia. Environment Protection Authority, Adelaide

Greenslade P (2002) Systematic composition and distribution of Australian cave collembolan faunas with notes on exotic taxa. Helicite 38:11–15

Griebler C, Avramov M (2015) Groundwater ecosystem services: a review. Freshw Sci 34:355–367

Grimes KG (1988) The Barkly karst region, north-west Queensland. In: Pearson L (ed) 17th biennial conference of the Australian Speleological Federation, TROPICON, Lake Tinaroo, Cairns. Australian Speleological Federation, pp 16–24

Guzik MT, Abrams KM, Cooper SJB, Humphreys WF, Cho J-L, Austin AD (2008) Phylogeography of the ancient Parabathynellidae (Crustacea: Bathynellacea) from the Yilgarn region of Western Australia. Invertebr Syst 22:205–216

Guzik MT, Cooper SJB, Humphreys WF, Austin AD (2009) Fine-scale comparative phylogeography of a sympatric sister species triplet of subterranean diving beetles from a single calcrete aquifer in Western Australia. Mol Ecol 18:3683–3698

Guzik MT, Austin AD, Cooper SJB, Harvey MS, Humphreys WF, Bradford T, Eberhard SM, King RA, Leys R, Muirhead KA, Tomlinson M (2010) Is the Australian subterranean fauna uniquely diverse? Invertebr Syst 24:407–418

Hahn HJ, Fuchs A (2009) Distribution patterns of groundwater communities across aquifer types in south-western Germany. Freshw Biol 54:848–860

Halse SA (2015) Subterranean biodiversity in the Pilbara provides difficulties for environmental assessment. In: Abstracts, invertebrate biodiversity and conservation conference 2015, Fremantle. Society of Australian Systematic Biologists and Western Australian Museum, p 12

Halse SA, Pearson GB (2014) Troglofauna in the vadose zone: comparison of scraping and trapping results and sampling adequacy. Subterranean Biol 13:17–34

Halse SA, Scanlon MD, Cocking JS (2002) Do springs provide a window to the groundwater fauna of the Australian arid zone? In: Yinfoo D (ed) Balancing the groundwater budget: proceedings of an international groundwater conference, Darwin 2002. International Association of Hydrogeologists, pp 1–12

Halse SA, Scanlon MD, Cocking JS, Barron HJ, Richardson JB, Eberhard SM (2014) Pilbara stygofauna: deep groundwater of an arid landscape contains globally significant radiation of biodiversity. Rec West Aust Mus Suppl 78:443–483

Hancock PJ, Boulton AJ, Humphreys WF (2005) Aquifers and hyporheic zones: towards an ecological understanding of groundwater. Hydrogeol J 13:98–111

Harms D, Halse S, McRae J, Scanlon M, Curran M (2016) Biodiversity in complex subterranean systems: a tale of arachnids in arid Western Australia. In: Abstracts, international conference on subterranean biology 2016, Fayetteville, Arkansas. International Society for Subterranean Biology, p 36

Harvey MS (2001) New cave-dwelling schizomids (Schizomida: Hubbardiidae) from Australia. Rec West Aust Mus Suppl 64:171–185

Harvey MS, Berry O, Edward KL, Humphreys G (2008) Molecular and morphological systematics of hypogean schizomids (Schizomida: Hubbardiidae) in semiarid Australia. Invertebr Syst 22:167–194

Hoch H (1993) A new troglobitic plant hopper species (Hemiptera: Fulgoroidea: Meenoplidae) from Western Australia. Rec West Aust Mus 16:393–398

Hose GC, Fryirs KA, Bailey J, Ashby N, White T, Stumpp C (2017) Different depths, different fauna: habitat influences on 1 the distribution of groundwater invertebrates. Hydrobiologia 791:145–157

Howarth FG (1983) Ecology of cave arthropods. Annu Rev Entomol 28:365–389

Humphreys WF (1999) Relict stygofaunas living in sea salt, karst and calcrete habitats in arid northwestern Australia contain many ancient lineages. In: Ponder W, Lunney D (eds) The other 99%: the conservation and biodiversity on invertebrates. Royal Zoological Society of New South Wales, Sydney, pp 219–227

Humphreys WF (2001) Groundwater calcrete aquifers in the Australian arid zone: the context of an unfolding plethora of stygal biodiversity. Rec West Aust Mus Suppl 64:63–83

Humphreys WF (2008) Rising from down under: developments in subterranean biodiversity in Australia from a groundwater fauna perspective. Invertebr Syst 22:85–101

Humphreys WF (2009) Hydrogeology and groundwater ecology: does each inform the other? Hydrogeol J 17:5–21

Humphreys WF (2016) Australasian subterranean biogeography. In: Ebach MC (ed) Handbook of Australasian biogeography. CRC Press, Baca Raton, pp 269–293

Humphreys WF, Watts CHS, Cooper SJB, Leijs R (2009) Groundwater estuaries of salt lakes: buried pools of endemic biodiversity on the western plateau, Australia. Hydrobiologia 626:79–95

Javidkar M, Cooper SJB, King RA, Humphreys WF, Bertozzi T, Stevens MI, Austin AD (2016) Molecular systematics and biodiversity of oniscidean isopods in the groundwater calcretes of central Western Australia. Mol Phylogenet Evol 104:83–98

Juberthie C (1983) Le milieu souterrain: étendu et compositon. Mémoires de Biospéologie 10:17–65

Karanovic I (2007) Candoninae (Ostracoda) from the Pilbara region in Western Australia. Crustaceana Monogr 7:1–432

Karanovic T, Cooper SJB (2011) Molecular and morphological evidence for short range endemism in the *Kinnecaris solitaria* complex (Copepoda: Parastenocarididae), with descriptions of seven new species. Zootaxa 3026:1–64

Karanovic T, Cooper SJB (2012) Explosive radiation of the genus *Schizopera* on a small subterranean island in Western Australia (Copepoda : Harpacticoida): unravelling the cases of cryptic speciation, size differentiation and multiple invasions. Invertebr Syst 26:115–192

Karanovic T, Eberhard SM, Perina G, Callan S (2013) Two new subterranean ameirids (Crustacea : Copepoda : Harpacticoida) expose weaknesses in the conservation of short-range endemics threatened by mining developments in Western Australia. Invertebr Syst 27:540–566

Karanovic T, Djurakic M, Eberhard SM (2015) Cryptic species or inadequate taxonomy? Implementation of 2D geometric morphometrics based on integumental organs as landmarks for delimitation and description of copepod taxa. Syst Biol 65:304–327

King RA, Bradford T, Austin AD, Humphreys WF, Cooper SJB (2012) Divergent molecular lineages and not-so-cryptic species: the first descriptions of stygobitic chiltoniid amphipods (Talitroidea: Chiltoniidae) from Western Australia. J Crustac Biol 32:465–488

Knott B, Halse SA (1999) *Pilbarophreatoicus platyarthricus* n.gen., n.sp. (Isopoda: Phreatoicidae: Amphisopodidae) from the Pilbara region of Western Australia. Rec Aust Mus 51:33–42

Korbel KL, Hose GC (2011) A tiered framework for assessing groundwater ecosystem health. Hydrobiologia 661:329–349

Kováč Ľ, Parimuchová A, Miklisová D (2016) Distributional patterns of cave Collembola (Hexapoda) in association with habitat conditions, geography and subterranean refugia in the Western Carpathians. Biol J Linn Soc 119:571–592

Larson HK, Foster R, Humphreys WF, Stevens MI (2013) A new species of the blind cave gudgeon *Milyeringa* (Pisces: Gobioidei, Eleotridae) from Barrow Island, Western Australia, with a redescription of *M. veritas* Whitley. Zootaxa 3616:135–150

Lavelle P, Decaëns T, Aubert M, Barot S, Blouin M, Bureau F, Margerie P, Mora P, Rossi JP (2006) Soil invertebrates and ecosystem services. Eur J Soil Biol 42(Suppl 1):S3–S15

Leys R, Watts CHS, Cooper SJB, Humphreys WF (2003) Evolution of subterranean diving beetles (Coleoptera: Dytiscidae, Hydroporini, Bidessini) in the arid zone of Australia. Evolution 57:2819–2834

Mammola S, Giachino PM, Piano E, Jones A, Barberis M, Badino G, Isaia M (2016) Ecology and sampling techniques of an understudied subterranean habitat: the milieu souterrain superficiel (MSS). Sci Nat 103:1–24

Maurice L, Bloomfield J (2012) Stygobitic invertebrates in groundwater – a review from a hydrogeological perspective. Fr Rev 5:51–71

Monjaraz-Ruedas R (2013) A new species of *Protoschizomus* (Schizomida: Protoschizomidae) from a cave in Guerrero, Mexico. J Arachnol 41:420–424

Moulds T, Bannink P (2012) Preliminary notes on the cavernicolous arthropod fauna of Judbarra/Gregory karst area, northern Australia. Helictite 41:75–85

Nevill JC, Hancock PJ, Murray BR, Ponder WF, Humphreys WF, Phillips ML, Groom PK (2010) Groundwater-dependent ecosystems and the dangers of groundwater overdraft: a review and an Australian perspective. Pac Conserv Biol 16:187–208

Niemiller ML, Zigler KS (2013) Patterns of cave biodiversity and endemism in the Appalachians and interior plateau of Tennessee, USA. PLoS One 8:e64177

Ornelas-Garcia CP, Dominguez-Dominguez O, Doadrio I (2008) Evolutionary history of the fish genus *Astyanax* Baird & Girard (1854) (Actinopterygii, Characidae) in Mesoamerica reveals multiple morphological homoplasies. BMC Evol Biol 8:340. https://doi.org/10.1186/1471-2148-8-340

Ortuño VM, Gilgado JD, Jiménez-Valverde A, Sendra A, Pérez-Suárez G, Herrero-Borgoñón JJ (2013) The "alluvial mesovoid shallow substratum", a new subterranean habitat. PLoS One 8:e76311

Outback Ecology (2012) Lake Maitland uranium project: stygofauna assessment. Outback Ecology Services, Jolimont

Perina G, Camacho AI, Huey J, Horwitz P, Koenders A (2018) Understanding subterranean variability: the first genus of Bathynellidae (Bathynellacea, Crustacea) from Western Australia described through a morphological and multigene approach. Invertebr Syst 32:423–447

Pesce GL, de Laurentiis P, Humphreys WF (1996) Copepods from ground waters of Western Australia. I. The genera *Metacyclops*, *Mesocyclops*, *Microcyclops* and *Apocyclops* (Crustacea: Copepoda: Cyclopidae). Rec West Aust Mus 18:67–76

Pinder AM (2008) Phreodrilidae (Clitellata: Annelida) in north-western Australia with descriptions of two new species. Rec West Aust Mus 24:459–468

Pinder AM, Halse SA, McRae JM, Shiel RJ (2005) Occurrence of aquatic invertebrates of the wheatbelt region of Western Australia in relation to salinity. Hydrobiologia 543:1–24

Pinder AM, Halse SA, Shiel RJ, McRae JM (2010) An arid zone awash with diversity: patterns in the distribution of aquatic invertebrates in the Pilbara region of Western Australia. Rec West Aust Mus Suppl 78:205–246

Reboleira ASPS, Goncalves F, Oromi P (2013) Literature survey, bibliographic analysis and a taxonomic catalogue of subterranean fauna from Portugal. Subterranean Biol 10:51–60

Reeves JM, De Deckker P, Halse SA (2007) Groundwater ostracods from the arid Pilbara region of northwestern Australia: distribution and water chemistry. Hydrobiologia 585:99–118

Richards AM (1971) An ecological study of the cavernicolous fauna of the Nullarbor Plain Southern Australia. J Zool 164:1–60

Ross HA, Murugan S, Li WLS (2008) Testing the reliability of genetic methods of species identification via simulation. Syst Biol 57:216–230

Roth LM (1991) A new cave-dwelling cockroach from Western Australia (Blattaria: Nocticolidae). Rec West Aust Mus 15:17–21

Schön I, Martens K, Halse S (2010) Genetic diversity in Australian ancient asexual *Vestalenula* (Ostracoda, Darwinulidae) – little variability down-under. Hydrobiologia 641:59–70

Silva M, Martins R, Ferreira R (2011) Cave lithology determining the structure of the invertebrate communities in the Brazilian Atlantic rain forest. Biodivers Conserv 20:1713–1729

Sket B (2008) Can we agree on an ecological classification of subterranean animals? J Nat Hist 42:1549–1563

Sket B, Paragamian K, Tontelj P (2004) A census of the obligate subterranean fauna of the Balkan Peninsula. In: Griffith HI (ed) Balkan biodiversity. Kluwer Academic, Dordrecht, pp 309–322

Sorensen JPR, Maurice L, Edwards FK, Lapworth DJ, Read DS, Allen D, Butcher AS, Newbold LK, Townsend BR, Williams PJ (2013) Using boreholes as windows into groundwater ecosystems. PLoS ONE 8:e70264

Steube C, Richter S, Griebler C (2009) First attempts towards an integrative concept for the ecological assessment of groundwater ecosystems. Hydrogeol J 17:23–35

Taiti S (2014) New subterranean Armadillidae (Crustacea, Isopoda, Oniscidea) from Western Australia. Trop Zool 27:153–164

Trajano E, Bichuette ME (2010) Diversity of Brazilian subterranean invertebrates, with a list of troglomorphic taxa. Subterranean Biol 7:1–16

Trontelj P, Douady CJ, Fišer C, Gibert J, Gorički Š, Lefébure T, Sket B, Zakšek V (2009) A molecular test for cryptic diversity in ground water: how large are the ranges of macro-stygobionts? Freshw Biol 54:727–744

Trotter AJ, McRae JM, Main DC, Finston TL (2017) Speciation in fractured rock landforms: towards understanding the diversity of subterranean cockroaches (Dictyoptera: Nocticolidae: *Nocticola*) in Western Australia. Zootaxa 4232:361–375

Vandel A (1965) Biospeleology: the biology of cavernicolous animals. Pergamon Press, London

Watts CHS, Humphreys WF (2006) Twenty-six new Dytiscidae (Coleoptera) of the genera *Limbodessus* Guignot and *Nirripirti* Watts and Humphreys, from underground waters in Australia. Trans R Soc Aust 130:123–185

Watts CHS, Humphreys WF (2009) Fourteen new Dytiscidae (Coleoptera) of the genera *Limbodessus* Guignot, *Paroster* Sharp, and *Exocelina* Broun from underground waters in Australia. Trans R Soc S Aust 133:62–107

Watts CHS, McRae JM (2013) *Limbodessus bennetti* sp. nov.: first stygobitic Dytiscidae from the Pilbara region of Western Australia. Rec West Aust Mus 28:141–143

Webb JA, James JM (2006) Karst evolution of the Nullarbor plain, Australia. In: Harmon RS, Wicks C (eds) Perspectives on karst geomorphology, hydrology, and geochemistry. Geological society of America special paper, pp 65–78

On the Ecology of Australia's Arid Zone: 'Fire Regimes and Ecology of Arid Australia'

Eddie J. B. van Etten and Neil D. Burrows

Introduction

Although fire is a widespread phenomenon and major ecosystem disturbance at the global scale, fire is a relatively rare event in much of the arid lands as rainfall and productivity are generally too low to support the dense vegetation and continuous fuel needed to sustain fires (Pausas and Bradstock 2007; Pausas and Ribeiro 2013). There are exceptions to this, such as landscapes dominated by xerophytic perennial grasses, where infrequent periods with above-average rainfall can result in exceptional grass and herb growth or where invasive species, particularly alien grasses, enhance fuel loads (Greenville et al. 2009; Keeley et al. 2012; Balch et al. 2013). Changes in land management (e.g. reduction in grazing, land abandonment), climate change and increased atmospheric CO_2 concentrations have also been linked to increased fire activity in arid zones across the globe (Bond and Midgley 2012; Pausas and Fernández-Muñoz 2012; Bachelet et al. 2016).

When they occur, arid-zone fires are predominantly grass fires (Murphy et al. 2013). However, low-lying flow-on areas may support sufficient shrubby vegetation and fuel to sustain fire. At the limits of the arid zone, where rainfall and productivity are generally higher (e.g. semiarid transition zones), shrub-dominated vegetation can be dense enough to enable crown fires, which are typically intense and 'stand replacing' (Keeley et al. 2012; Dalgleish et al. 2015). In southern Australia, fire

---

E. J. B. van Etten (✉)
Centre for Ecosystem Management, School of Science, Edith Cowan University,
Joondalup, WA, Australia
e-mail: e.van_etten@ecu.edu.au

N. D. Burrows
Department of Biodiversity, Conservation and Attractions, Kensington, WA, Australia
e-mail: neil.burrows@dbca.wa.gov.au

H. Lambers (ed.), *On the Ecology of Australia's Arid Zone*,
https://doi.org/10.1007/978-3-319-93943-8_10

frequency and extent increase in a southerly direction across the arid to Mediterranean climate transition in line with increasing rainfall, productivity and vegetation cover (Pausas and Bradstock 2007).

In arid Australia, which comprises around 70% of the entire continent, fire is generally a more prevalent and important feature than in drylands of other parts of the globe (Morton et al. 2011). One explanation for this is that rainfall, although variable, is relatively high, averaging >180 mm per annum (Stafford Smith 2008; van Etten 2009). Further, much of arid Australia supports extensive meadows of the highly flammable perennial spinifex grass (*Triodia* spp.), a life form that is unique to Australia. Spinifex is well adapted to arid environments and to fire. As a fuel, it behaves more like a shrub as aboveground biomass accumulates slowly over time (Rice and Westoby 1999; Armstrong and Legge 2011; Nano et al. 2012b).

In this chapter we review fire regimes and some impacts of fire on the flora and fauna of arid Australia. The review is structured around the major vegetation types in arid Western Australia, described in Table 1 and mapped in Fig. 1 as 'Spinifex', 'mulga', '*Acacia* scrub', 'eucalypt woodlands', 'mallee' and 'chenopod shrubland'. These types were derived by amalgamating vegetation units mapped at the 1:3 M scale (Beard et al. 2013) into major types based on general similarities in their structure, fuel characteristics and fire regimes. These vegetation types are broadly consistent with the Murphy et al. (2013) classification of vegetation by fire regimes based on the National Vegetation Information System (NVIS) mapping but with two important distinctions for Western Australia: (1) we recognise arid/semiarid eucalypt woodlands as being different from temperate woodlands (as per Gosper et al. 2016); and (2) *Acacia* shrublands are split into mulga woodlands/shrublands (dominated by *Acacia aneura s.l.*) and other *Acacia* shrublands/woodlands (non-mulga), which we refer to as '*Acacia* scrub'. The broad vegetation types found in the Western Australian arid zone also occur in other arid Australian regions, so we cite relevant literature from these areas. We also update recent reviews of arid Australian fire ecology (e.g. Nano et al. 2012b; Allan and Southgate 2002) and identify critical knowledge gaps and future research priorities.

Determining Fire History in Remote Arid Regions

A firm knowledge of fire history is important for interpreting ecological, economic, cultural and social influences of landscape fires and for determining appropriate fire management. The remoteness and vastness of Australia's arid zone make satellite products a cost-effective means for near real-time detection of active fires (hotspots), for mapping fire footprints (scars) and for reconstructing fire histories (Burrows and Christensen 1990; Allan and Southgate 2002; Turner et al. 2008; Avitabile et al. 2013). Remote-sensing technology is developing rapidly, and today the most commonly used satellites for detecting and mapping fires are Terra and Aqua (carrying the MODIS instrument), Landsat and Himawari. Each of these satellites has strengths and weaknesses in terms of resolution, bands, frequency of overpass, data accessibility and

Table 1 A summary of the broad vegetation types of arid Western Australia (WA) and associated fuel type and typical fire frequencies

Major vegetation type (and common names used in this chapter)	Description	Beard et al. (2013) mapped units	Main bioregions (IBRA) and WA area (km^2)	Dominant fuel type	Fire frequency (and intervals)
Hummock grassland ('Spinifex grassland' or 'Spinifex')	Dominated by *Triodia* spp. with open, sparse tree and/or shrub layers (*Eucalyptus, Corymbia, Acacia, Hakea, Grevillea*). Sometimes without emergent trees or shrubs. Common on a range of landforms and soils (sand dunes, plains, rocky and hilly country, mountain ranges)	30, 34, 35, 36, 37, 38, 39, 40, 41, mosaics 110, 111, 112, 116, 117, 118	GSD, GVD, Gibson Desert, LSD, Pilbara, Gascoyne, Murchison 925,000 km^2	Spinifex hummocks	Frequent fire (5–15 years) depending on rainfall
Mulga woodland ('mulga')	Low open woodland and occasionally shrubland dominated by *Acacia aneura* (*sensu lato*) and associated *Acacia* (e.g. *A. pruinocarpa, A. eremaea, A. victoriae*). Mostly on fine-textured soils of valley plains, often with hardpan. Understorey of very open shrubs (*Eremophila, Atriplex, Senna*) and mostly sparse perennial bunch/tussock grasses. After rain, many ephemerals occur, such as daisies, mulla mulla (*Ptilotus* spp.) and annual grasses	8, 44, mosaic 119	Murchison, Gascoyne, GVD, Pilbara 367,000 km^2	Ground fuel, mostly annual herbs and grasses	Infrequent fire (50+ years) following exceptional rainfall events
Acacia shrubland ('*Acacia* scrub')	Open to dense shrubland (occasionally with very sparse trees or mallee) dominated by *Acacia* other than *A. aneura s.l.,* such as bowgada (*A. linophylla*), snakewood (*A. xiphophylla*), *A. ramulosa, A. sclerosperma* and *A. coriacea* on red sand dunes and sandplains. On yellow sandplains, a mix of *Acacia, Allocasuarina* and *Melaleuca*. Typically open understorey of low shrubs and ephemeral forbs and grasses following rains	9, 13, 14, 15, 20, mosaics 103, 106, 107, 108	Carnarvon, Yalgoo, Mallee 275,000 km^2	Ground fuel, mostly grasses; dense shrub layer in semiarid zones	As above, although dense shrublands in semiarid areas can burn at 20–30 year intervals

(continued)

Table 1 (continued)

Major vegetation type (and common names used in this chapter)	Description	Beard et al. (2013) mapped units	Main bioregions (IBRA) and WA area (km^2)	Dominant fuel type	Fire frequency (and intervals)
Eucalyptus woodland ('eucalypt woodland')	Low to tall open woodland of *Eucalyptus* with open understorey of low shrubs on alluvial surfaces, drainage lines and valleys. Common overstorey species: Salmon gum (*E. salmonophloia*), York gum (*E. loxophleba*), gimlet (*E. salubris*), coolibah (*E. victrix*) and red morel (*E. longicornis*). Common understorey species: jam wattle (*Acacia acuminata*), *Melaleuca*, saltbushes (*Atriplex*) and bluebush (*Maireana*); occasional bunch or tussock grasses (e.g. *Themeda, Astrebla*) in northern regions	4, 5, 31, 32, mosaics 102, 104	Coolgardie, Pilbara, Avon Wheatbelt 121,000 km^2	Patchy litter on ground; some grasses and herbs	Infrequent fire (100+ years) possibly following exceptionally high rainfall
Mallee shrublands ('mallee')	Open shrubland of *Eucalyptus* (mallee, many species) over open to dense understorey of shrubs (*Melaleuca*, *Acacia*) and occasional grasses (hummock grasses or tussock grasses)	16, 17, mosaic 109	Mallee, Avon Wheatbelt, Coolgardie – mostly confined to SW semiarid to arid zones 55,000km^2	Ground fuel – mostly patchy litter but some grass	Infrequent fire (20–30 years) usually following above-average rainfall
Halophytic shrublands ('chenopod shrubland')	Open to dense shrubland dominated by chenopods such as samphires (*Tecticornia*), bluebush (*Maireana*) and saltbush (*Atriplex*) around salt lakes, saline surfaces and/or alkaline soils. May have very sparse tree layer, including myall (*A. papyrocarpa*), snakewood and *E. oleosa* (giant mallee)	42, 43, 45, 46. 47, 48, 49, 50, mosaics 105, 120	Nullarbor, Carnarvon 202,000 km^2	Vegetation largely non-flammable	Largely fire independent, non-flammable

Vegetation types are an amalgamation of Beard et al. (2013) vegetation units, with mixed types and mosaics included with vegetation type most similar in terms of structure, fuel properties, fire behaviour and typical fire frequency

IBRA refers to the Interim Biogeographic Regionalisation for Australia (Thackway and Cresswell 1997) as per Fig. 1 (*GSD* Great Sandy Desert, *GVD* Great Victoria Desert, *LSD* Little Sandy Desert)

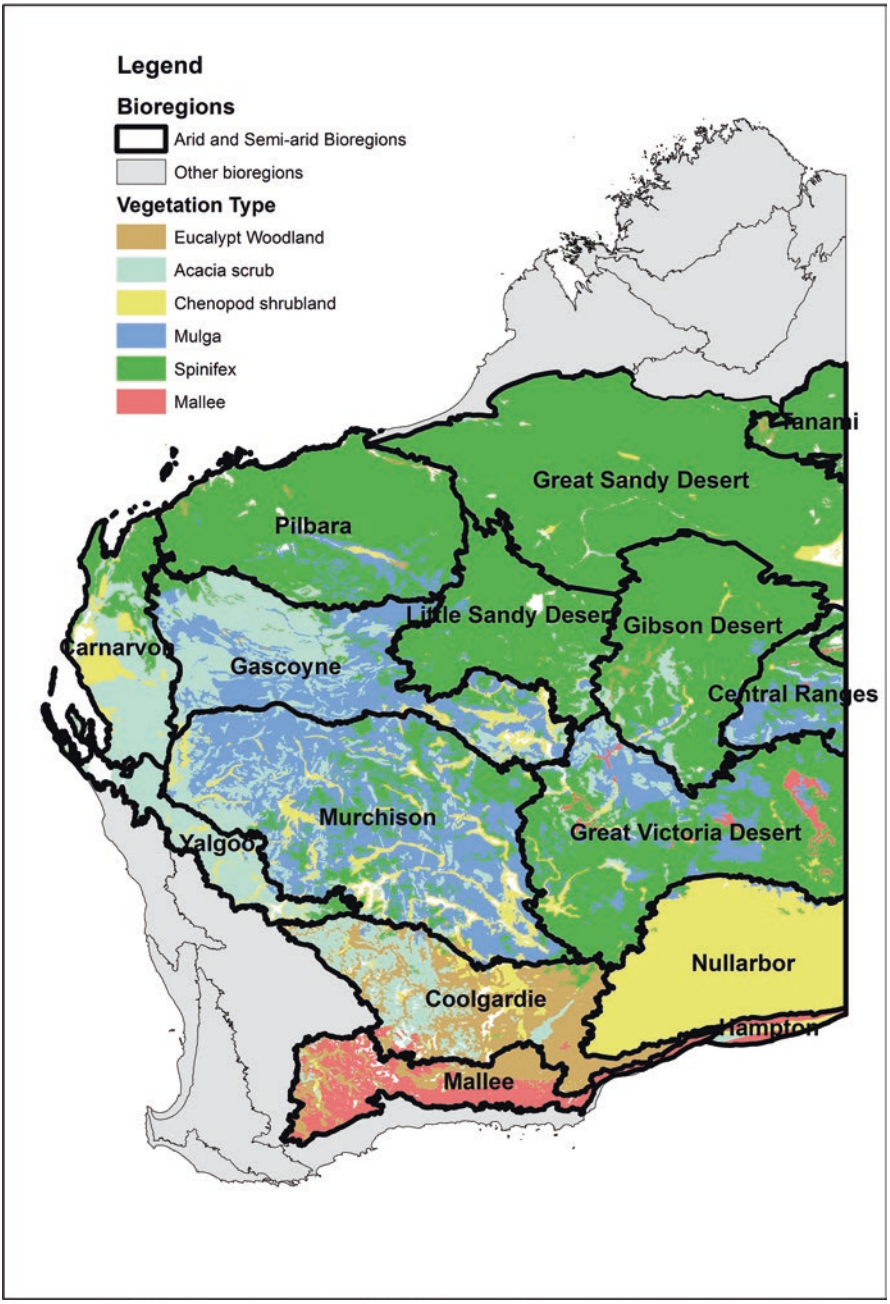


Fig. 1 Map of major vegetation types of the Western Australian arid zone based on fire characteristics. Types are defined and described in Table 1. Arid and semiarid IBRA (Interim Biogeographic Regionalisation for Australia) bioregions are shown

Plate 1 1953 aerial photography near Lake Mackay in the Western Desert clearly showing fire scars from traditional Aboriginal burning

cost. Unlike the tropical savannas, fire scars in the arid zone are generally detectable for several years or more before the vegetation regenerates. With the exception of some military- and special-purpose weather satellites, satellite imagery only became available from 1972 following the launch of Landsat 1. Prior to that, black and white aerial photography flown at irregular intervals is available for much of arid Australia since the 1940s. As well as being of variable resolution and quality, it is costly to acquire but of considerable historical value. Burrows and Christensen (1990) used early (1953) black and white aerial photography to describe and quantify fire patterns in a part of the Western Desert that was occupied by Aboriginal people living a traditional lifestyle at the time of the photography (Plate 1).

Important changes in ecosystem structure, function and composition can develop in the absence of fire over scales of many decades to centuries, especially so for those vegetation types which uncommonly experience fire (Gosper et al. 2013a, b; Knuckey et al. 2016). Therefore, much recent research has focussed on developing methodologies to establish the age of long-unburnt vegetation. Clarke et al. (2010) and Gosper et al. (2013c) used allometric relationships between stem diameter and plant age of dominant species (mallee and gimlet, respectively) to infer fire age of sites, which revealed some as being older than 200 years. More recently, Callister et al. (2016) successfully constructed models between vegetation structure and remotely sensed reflectance data to estimate time since fire in mallee vegetation of up to 100 years. Trees of the generally fire-sensitive conifer genus *Callitris* grow widely in arid Australia and can be aged by stem ring counts (e.g. O'Donnell et al. 2010). However this technique has some pitfalls, because *Callitris* can regenerate between fires and survive low-intensity fires, growth rings are not always annual and it can be difficult to obtain complete stem cores in very old trees (Cohn et al. 2011; Pearson et al. 2011; Prior et al. 2011). Carbon dating of charcoal in soil and under bark is a promising technique requiring further development. In many remote Aboriginal communities, a rich oral history exists of the traditional use of fire which gives great insight to prehistorical fire regimes in parts of the arid zone (e.g. Burrows et al. 2009; Rangeland NRM 2013).

Fuel Characteristics and Fire Regimes of Arid Australian Ecosystems

Spinifex Grasslands

Spinifex grasslands are characterised by the dominance of perennial hummock grasses, primarily of the genus *Triodia*. They cover about 2.1 million km^2 (~27%) of the continent including pastoral, Aboriginal and conservation lands as well as large tracts of unallocated crown land (Allan and Southgate 2002). Spinifex grasslands occur on a diversity of landforms including sandplains, dune fields, gibber plains and rocky hills in the semiarid and arid regions of the remote and sparsely populated parts of Australia. Annual average rainfall ranges from about 225 mm to 350 mm, the seasonality of which varies from predominantly summer rainfall in the north to winter rainfall in the south. This strongly affects the seasonality of fire, with most fires in the northern arid zone being confined to August to November (when this area is typically dry) compared with the southern arid zone where fires mostly occur in spring and summer (Turner et al. 2008; Nano et al. 2012b). Rainfall is highly variable and long periods of hot, dry weather are common (van Etten 2009). Mature spinifex grasslands are generally structurally simple, with a discontinuous ground cover dominated by *Triodia* hummocks and a diversity of scattered low shrubs and trees, including *Eucalyptus*, *Allocasuarina*, *Acacia*, *Senna*, *Callitris*, *Hakea* and *Grevillea* (Beard et al. 2013).

The combination of accumulation of flammable vegetation, the physical structure of the hummocks and the often extreme fire weather conditions make spinifex grasslands highly flammable (Griffin and Allan 1984; Burrows and Christensen 1990; Gill et al. 1995; Allan and Southgate 2002). Historically, lightning and deliberate burning by Aboriginal people were the main causes of fire. Today, most fires are started by lightning, although human-caused ignitions are significant near settlements, along vehicle travel routes and on pastoral leases where burning is sometimes carried out to manage browse (Edwards et al. 2008). While many *Triodia* species are fire sensitive (readily killed by fire, regenerate from seed; see section 'Response of dominant plant species'), spinifex grassland communities are fire dependent; fires at appropriate temporal and spatial scales are essential for their persistence and health (Suijendorp 1981; Latz 1995; Allan and Southgate 2002).

Fuel Loads, Distribution and Dynamics

Spinifex is highly flammable due to its physical structure and, in the case of resinous species, its chemical composition. Burrows et al. (1991) have described it as an 'almost perfect' bushfire fuel. Being desiccation-tolerant, the perennial spinifex plant has a remarkable ability to survive under conditions of extreme moisture stress. Rather than having a substantial root system that accesses soil moisture at depth (as is the case with many woody plants in these environments), when under moisture stress, spinifex gradually slows down growth and gas exchange, maintains cell structure and integrity (i.e. does not wilt) and 'suspends' metabolism (Grigg et al. 2008). Under water stress the plant is straw-coloured and has the 'cured' appearance of an annual grass. Within a short time after sufficient rain, the plant takes up soil moisture and 'greens up'. Depending on its age and the proportion of dead material in the clump, the moisture content of clumps can range from about 14% to 75% of oven dry weight (Burrows et al. 2016).

After regeneration following fire and rain, spinifex plants develop through a variety of structural or architectural forms, starting as a small dome-shaped clump and, with age, taking on a 'donut-' or crescent-shaped structure as stolons grow more or less radially, and older, central parts of the plant die. Dead spinifex can persist behind the 'active growing front' of the plant for several years. Not only does the structure of the plant change with age but so does the proportion of dead material in the hummock. Dead spinifex can make a significant contribution to the plant's fuel properties mainly because it remains very dry for long periods on account of the very low relative humidity normally experienced in arid environments. Examples of how biomass and structure change with time since fire in five Western Australian arid bioregions are shown in Fig. 2. The rate of postfire change in biomass and structure, hence the minimum fire return interval, as based on fuel characteristics, varies depending on cumulative rainfall since the last fire (Allan and Southgate 2002) and local soil and landform conditions.

Although spinifex hummocks are the major component of the fuel load, the flush of annuals (grasses and forbs), which commonly develop between hummocks following wet times, can increase overall fuel loads and fuel continuity and thereby contribute to fire spread (Allan and Southgate 2002; Myers et al. 2005; Burrows et al. 2009). Consequently, annual variation in the areal extent of fires in spinifex-dominated landscapes is strongly and positivity correlated with antecedent rainfall in the 2 years prior to fire (Greenville et al. 2009). It is now widely recognised that probability of fire in spinifex is not only dependent on time since fire, with short fire intervals possible during periods of sustained high rainfall (Wright and Clarke 2007a; Turner et al. 2008). We note few attempts to formally model the combined effects of antecedent rainfall and time since fire in spinifex, although Avitabile (2014) showed the cover of *T. scariosa* growing under mallee in south-east Australia increased with time since fire during periods of below-average rainfall but responded more to amount of recent rainfall during periods of above-average rainfall.

Fires in spinifex grasslands are surface fires with fire intensity strongly influenced by fuel load and fire rate of spread (ROS). Fuel loads at maturity are variable but generally range from 10 t ha^{-1} in inland arid areas to over 20 t ha^{-1} in higher-rainfall monsoonal areas in northern Australia (Burrows et al. 1991; Russell-Smith et al. 1998). Burrows et al. (2009) studied spinifex fuel dynamics across several sites in the Western Deserts (Great Sandy, Little Sandy and Gibson Deserts) using a space-for-time approach and showed that fuel loads increased with time since fire, plateauing at about 10–12 t ha^{-1} some 18–20 years after fire (Fig. 2). Flammability of hummocks increases in line with the moisture content of their living leaves (which varies widely in response to rain), proportion of dead material in the hummock (which increases with age) and amount of resinous oils (which varies with species) (Lazarides 1997).

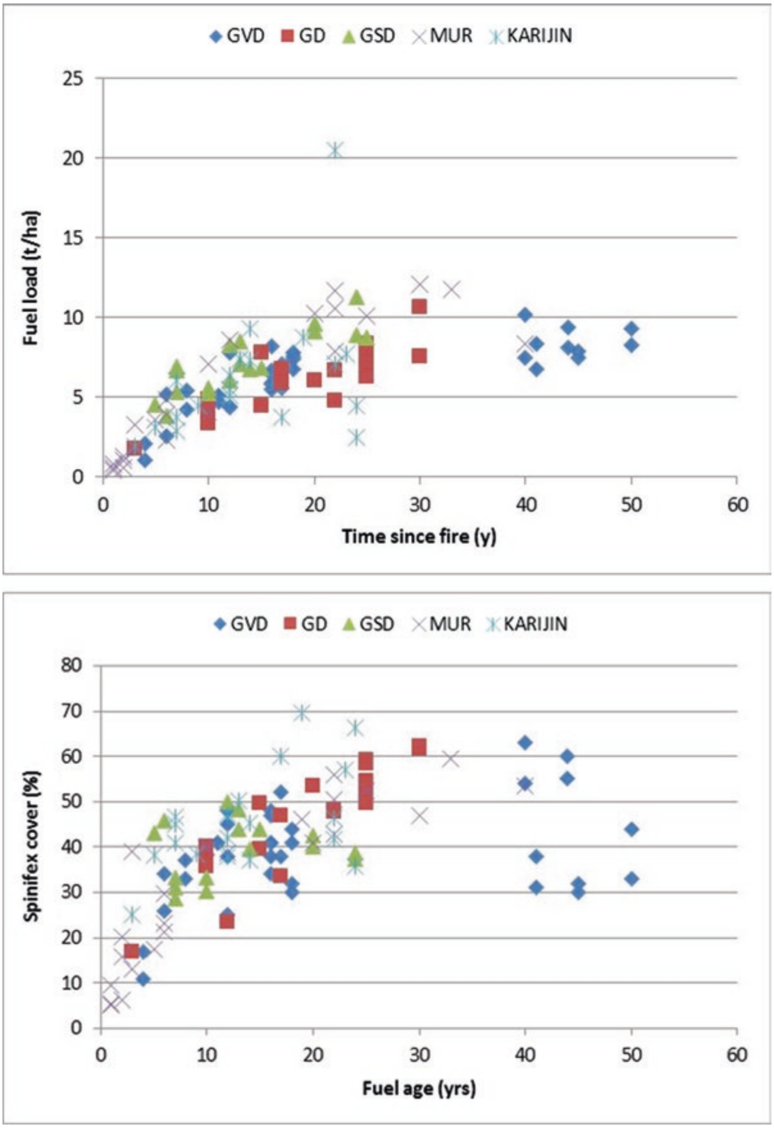


Fig. 2 Biomass (**a**) and structural change (**b**) in spinifex grasslands with time since fire in five Western Australian arid bioregions. *GVD* Great Victoria Desert, *GD* Gibson Desert, *GSD* Great Sandy Desert, *MUR* Murchison, *KARIJIN* Karijini National Park in Pilbara bioregion

Fire Behaviour

Although a structurally simple fuel, modelling the behaviour of fire in spinifex grasslands is challenging for a number of reasons. Spinifex is a perennial plant that is able to survive under a wide range of soil and plant moisture content conditions, unlike annual grasses that 'cure' once soils dry below wilting point. The spinifex grassland fuel array is discontinuous or patchy, giving rise to multiple thresholds to fire spread, and the structure and composition, especially the proportion of dead material, varies with time since last fire and cumulative rainfall. Notwithstanding these challenges, two fire behaviour models have been developed from empirical studies, the earliest of which was published by Griffin and Allan (1984). Later, Burrows et al. (1991, 2009, 2016) published updated versions of a two-step model that firstly determines the probability that thresholds for spread have been met or exceeded, and secondly, if they have, rate of spread and flame height can then be modelled using a linear relationship linking key fuel and weather variables. Key variables are wind speed, hummock moisture content, fuel cover and fuel load. Once the cover of spinifex exceeds about 30% and its biomass exceeds about 3–4 t ha^{-1}, it has the potential to sustain fire spread. For continuous fuels such as forest litter fuels, moisture content of extinction is the only threshold to fire spread once a cover of leaf litter has developed. Because of its discontinuity, or patchiness, mature spinifex fuels have at least three fire spread thresholds: (1) cover, *spinifex* fires rarely spread when the cover falls below about 30%; (2) fuel moisture content, when fully 'green', clumps may ignite if there is sufficient dead material present, and fire spread will be difficult to sustain when clump moisture content exceeds about 40% (Burrows et al. 2016); and (3) wind speed, which is probably the most important threshold (Williams et al. 2015). The wind speed threshold varies according to cover, moisture content and fuel load but is usually in the vicinity of 7–10 km h^{-1} (@ 2 m above ground) once moisture content and cover thresholds have been exceeded (Burrows et al. 2016). Fire is capable of spreading between 0.25 and 10 km h^{-1} generating intensities up to 30,000 kW m^{-1}. Flame height rarely exceeds 6 m, and spotting is not usually associated with spinifex fires, although short-distance spotting (up to 100 m) may occur in the presence of a eucalypt overstorey. Guides to predicting spinifex fire rate spread and flame height are provided by Burrows et al. (2016).

Fire Intervals

The minimum possible fire return interval based on fuel characteristics depends on cumulative rainfall and local soil and landform conditions that drive vegetation productivity but is usually in the range 5–10 years and generally shorter in northern latitudes, reflecting higher rainfall and conducive growing conditions in these regions (Allan and Southgate 2002; Greenville et al. 2009). However, fire intervals can be as short as 2–3 years when consecutive seasons of above-average rainfall promote rapid build-up of annual herbs and grasses (Wright and Clarke 2007a). Repeated fires at such short intervals can lead to structural and compositional changes to the vegetation, because some species are likely to be extirpated before replenishing their seed banks (refer to section 'Flora' below). Topographic and vegetation features can isolate and protect some patches of spinifex from large landscape fires, with reports of some patches being many decades old (Greenville et al. 2009).

Altered Fire Regimes

Following the departure of traditional Aboriginal burning practices, the fire regime throughout much of the spinifex grasslands has changed from one of predominantly small, patchy cool-season fires to large, intense hot-season fires (Latz and Griffin 1978; Burrows and Christensen 1990; Latz 1995; Allan and Southgate 2002). For example, over the period 2000–2002, ~500,000 km^2 of spinifex grassland was burnt by wildfire (Wright and Clarke 2007a), and hot summer wildfires commonly exceed 200,000 ha (Haydon et al. 2000; Allan and Southgate 2002; Burrows et al. 2009). This 'boom and bust' fire regime is now largely determined by rainfall (Fig. 4), which drives the rate of fuel accumulation (Griffin et al. 1983; Allan and Southgate 2002), with lightning as the dominant ignition source. This changed fire regime has been implicated in the decline of mammals and some bird species, as well as the contraction of fire-sensitive plants such as cypress pine (*Callitris* spp.) and mulga (Start 1986; Bowman and Latz 1993; van Leeuwen et al. 1995; Ward et al. 2014; see section 'Fire impacts and responses' below).

Mulga Woodlands

The structure of mulga vegetation typically comprises an open to moderately dense overstorey of low (2–10 m) trees of *Acacia aneura* or its close relatives (Maslin and Reid 2012), occasionally mixed with other *Acacia* species, and an understorey of sparse shrubs and herbaceous ground layer (Groves 1994). This ground layer mostly comprises grasses (perennial and annual) and forbs, which increase substantially in biomass and cover following big rains. This enhanced herbaceous layer, when dry, provides sufficient fuel to sustain ground fires. Fire frequency is therefore low to moderate, occurring every 20 to 100+ years (Murphy et al. 2013; Friedel et al. 2014), although Ward et al. (2014) reported return intervals as low as 3–10 years in a mulga woodland at Lorna Glen in the Gascoyne bioregion, a situation promoted by an extended period of above-average rainfall. There exist large expanses of mulga that have no record of fire, based on remote sensing and field observations, and are presumably very long unburnt (Hodgkinson 2002; Williams 2002; Turner et al. 2008; Ladbrook 2015).

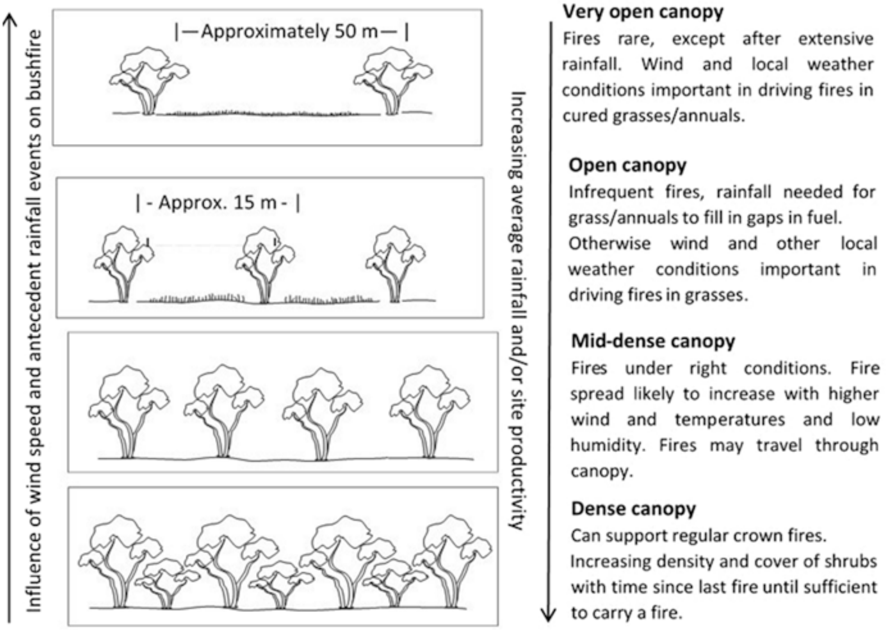
Fires in mulga communities are an integral component of the pulse-and-reserve response to major rain events typical of arid lands (Ludwig et al. 1996). Above-average rainfall, especially if spread across the seasons, results in rapid biomass accumulation, which leads to enhanced consumption (including fire), which, in turn, results in efficient resource feedback in terms of nutrient and carbohydrate replenishment and storage (which becomes important for driving the next pulse). However, the rainfall thresholds in terms of the amount and timing of rain required to produce sufficient fuel to enable fires in mulga remain unclear; such information would be vitally important to land managers, because it would enable the prediction of fire risk based on antecedent rainfall. Spatial redistribution of rainfall is also important and will mean such thresholds are unlikely simply a product of the amount of rain received. Mulga tend to grow in 'run-on' areas, which receive water from upslope and where flooding and sheet flow are common following heavy rainfall events (Ludwig et al. 1996). Sites receiving abundant surface runoff can be very productive and may at times produce large amounts of grassy fuels. Also grove-intergrove spatial arrangements, common to mulga on extensive plains, can result in highly patchy distributions of fuel following rain (Nano et al. 2012b). These patterns likely strongly influence fire behaviour (also likely to be very patchy; Nano et al. 2012b), with fires needing to move between patches of high fuel loads for them to be sustained over large areas, something typically only possible after exceedingly large rains.

Mulga on pastoral leases with a long history of grazing by domestic stock can survive for long periods, because grazing reduces the fuel load and hence the fire potential (Hodgkinson 2002; Edwards et al. 2008). Many areas have been so overgrazed that their perennial grass component has been lost or severely diminished (Burnside et al. 1995; Brandis 2008). Increased tree and shrub cover (especially of non-palatable species) following high grazing pressure may also suppress ground fuels. Beyond the pastoral areas, grazing and browsing by feral and native herbivores may influence the fire regime, especially where their numbers are artificially inflated by provision of permanent water points. Interactions between grazing and fire are discussed further below (section 'Fire-herbivore interactions').

Mulga is readily killed by fire and relies on a soil-stored seed bank for regeneration. The combination of fire and follow-up rain usually results in dense mulga regeneration, which can take as long as 15–20 years to reach maturity and up to 26 years to replenish seed banks (Ward et al. 2014). Fire-sensitive mulga can co-occur with flammable spinifex, provided fires in the surrounding landscape are of low intensity and occur at the cool time of the year. This is because the fuel load of spinifex beneath mulga groves is generally lower than that in the surrounding non-mulga landscape, so fire spread in the groves is less likely under cool conditions. Aboriginal people recognised this and would often protect valuable mulga groves by burning around them in the cool season (Burrows 2014). Where this is not practiced, regular large hot summer wildfires are extirpating mulga groves (Start 1986; Latz 1995; Ward et al. 2014).

Acacia *Scrub*

These are shrublands (occasionally woodlands) dominated by *Acacia* species other than mulga (although *A. aneura* can sometimes be a minor component in drier regions; Beard et al. 2013). They are typically found on sandplains and generally poorer soils compared with mulga and are widespread on the western side of the Western Australian arid zone (e.g. Carnarvon bioregion) and in the semiarid transition zone (e.g. Yalgoo and Coolgardie bioregions; Fig. 1). They are characterised by a mix of *Acacia* species (Table 1) with other shrub genera (*Allocasuarina, Melaleuca,*



Very open canopy
Fires rare, except after extensive rainfall. Wind and local weather conditions important in driving fires in cured grasses/annuals.

Open canopy
Infrequent fires, rainfall needed for grass/annuals to fill in gaps in fuel. Otherwise wind and other local weather conditions important in driving fires in grasses.

Mid-dense canopy
Fires under right conditions. Fire spread likely to increase with higher wind and temperatures and low humidity. Fires may travel through canopy.

Dense canopy
Can support regular crown fires. Increasing density and cover of shrubs with time since last fire until sufficient to carry a fire.

Fig. 3 Shrub/tree density influence on fire behaviour in arid shrubland vegetation. Distances between gaps determined from field and aerial photographs of *Acacia*-dominated vegetation across a climatic gradient from coastal to inland arid Western Australia. (Adapted from Ladbrook (2015))

Hakea, Callitris and *Grevillea*) also common (Knuckey et al. 2016). Structurally, they vary along a rainfall/productivity gradient from very dense shrublands around 2–4 m high capable of carrying a crown fire at maturity to moderately dense shrublands where crown fires are possible given strong winds, to more open shrubland, which only carries ground fire if sufficient fuel builds up following big rains (Fig. 3; Ladbrook 2015).

In the dense *Acacia* scrub of the Yalgoo and Coolgardie bioregions (described as 'thicket' by Beard et al. 2013), fuel primarily consists of live leaves and fine branches/twigs which continually, but slowly, accumulate over many decades as shrubs expand laterally and vertically (Dalgleish et al. 2015). Dead leaves and other plant material on the ground and in the canopy also slowly build up after fire to contribute about 40% of the fuel load after 30–50 years and increase the flammability of vegetation at these ages (Dalgleish et al. 2015; Kelso et al. 2015). Total fuel load stabilises around 20–25 t ha^{-1} after 60 years, with some evidence that senescence of shrubs may contribute to more patchy fuel arrays after this time (Parsons and Gosper 2011; Dalgleish et al. 2015).

The fire regime in dense *Acacia* scrub is closely linked to this fuel dynamic with burnt areas not recovering sufficiently to carry a subsequent fire for at least 20–30 years, which is consistent with the reported interval between fires of around 30–40 years for *Acacia* sandplain scrub in the Yalgoo bioregion (Parsons and Gosper

2011; Doherty et al. 2017). Overall, this suggests the overriding importance of time since fire in shaping the fire regime, although the role of pre-fire rainfall in promoting fire (either via extra fuel following deluges or lower fuel moisture following drought), as well as the importance of fire weather, needs further exploration. Fires tend to be intense crown fires, which are stand replacing (Dalgleish et al. 2015; Kelso et al. 2015) and can be large and dangerous. For example, the Boorabbin fire, in which three people lost their lives, burnt some 400 km^2 of mostly sandplain scrub in the 2007–2008 summer (Kelso et al. 2015); fires south of Mt. Gibson burnt 800 km^2 of mostly dense scrub in 2001–2002 (E. van Etten, unpubl.). Extreme fire weather conditions (very hot, dry and windy) prevailed during the Boorabbin fire (BoM 2008).

Eucalypt Woodland

Eucalypt woodlands occur along major streams and drainage lines throughout the arid zone of Australia but also form extensive stands in the Coolgardie and Yalgoo bioregions of Western Australia where species such as Salmon gum (*E. salmonophloia*), gimlet (*E. salubris*) and York gum (*E. loxophleba*) dominate on heavier soils in broad valley systems (Beard et al. 2013). These woodlands here generally have low fuel and exist in clearly delineated landscape mosaics with more flammable vegetation (e.g. *Acacia* scrub and mallee). Consequently, fires in these eucalypt woodlands are mainly limited to their margins where fires burn in from surrounding more flammable vegetation (Kelso et al. 2015; O'Donnell et al. 2011a; Prober et al. 2012; Gosper et al. 2016).

In contrast to eucalypt woodlands of temperate Australia where tussock grasses are the main fuel component (Lunt et al. 2012; Murphy et al. 2013), there are few grasses in these semiarid eucalypt woodlands, and fuel comprises mostly a thin, patchy cover of leaf litter and fine woody plant debris (Gosper et al. 2016). Such ground litter fuel, however, accumulates extremely slowly (O'Donnell et al. 2014) and for *E. salubris* woodland has been reported to peak and then decline after several decades (Gosper et al. 2013a). Ground fuels rarely reach a level and continuity where fires will readily spread, except perhaps when strong winds move flames across patches of ground fuels (O'Donnell et al. 2011a, 2014; Gosper et al. 2016). Consequently, fire is rare and of low intensity, with fire return intervals estimated at 300+ years and largely decoupled from temporal accumulation of fuel (O'Donnell et al. 2011a; Gosper et al. 2013c). The low and patchy ground cover in these semiarid woodlands has been hypothesised to be due to the intense competition exerted by the large eucalypt trees (which have extensive lateral roots) for moisture and nutrient resources (Yates et al. 2000) and is unlikely to reflect high grazing pressure as many areas are outside of pastoral leases (Prober and Wiehl 2011).

O'Donnell et al. (2011b) demonstrated the importance of a sequence of wet and dry years for promoting large fires in a semiarid landscape of eucalypt woodland, shrubland and mallee in the Coolgardie bioregion. It is therefore possible that grasses and other herbs will proliferate after flooding rains, which, when dry, would increase continuity of fuels and promote fire spread in these woodlands, which rarely burn otherwise, but this remains largely conjectural (O'Donnell et al. 2011b; Prober et al. 2012). Understanding the relative roles of rain, time and fire weather in enabling occasional fires in eucalypt woodlands requires study over long time frames to capture a representative amount of climatic variability.

Mallee

Mallee shrublands are characterised by an open overstorey of mallee eucalypts (tall, multi-stemmed shrubs resprouting from a large underground lignotuber, typically 10–40% cover) with either an open shrubby or grassy understorey (hummock or tussock grasses). On some soil types throughout the arid zone, a spinifex understorey can develop beneath the mallees sufficient to sustain fire at relatively frequent intervals (15–20 years). More commonly though, it is ground litter, comprising mostly eucalypt leaves and other plant debris, built up over many years (and sometimes decades) which is all important to sustain fires, although extra plant growth (both annual and perennial) following rainy periods will increase the likelihood of fire (Bradstock and Cohn 2002). Although most mallee fires are ground fires burning through the litter layer, fires do typically flare up and burn into the crowns of mallee eucalypts, aided by the accumulation of litter around the base of trees and presence of loose bark and dead material in mallee crowns (Bradstock and Gill 1993; Cruz et al. 2013). However, it is only where there are dense patches of mallee and/or shrubs (more common in southern semiarid parts of its distribution) that sustained crown fires tend to occur. Ground litter accumulates slowly after fire, but this accumulation plateaus after 20–30 years (Haslem et al. 2011) at around 5–10 t ha^{-1} (Bradstock and Cohn 2002). Fire return intervals are generally 20–100 years (Murphy et al. 2013), but for mallee of south-western Australia, these are typically 55–80+ years (O'Donnell et al. 2011a; Gosper et al. 2016).

In the absence of a spinifex-dominated understorey, fire behaviour in mallee is relatively complex and unpredictable due to the highly patchy nature of the multiple strata of fuel (mallee, shrubs, grasses and ground litter). Due to differences in these characteristics across its distribution, fire behaviour models need to be developed for different types of mallee vegetation. Cruz et al. (2013) successfully modelled fire behaviour in mallee with understorey of shrubs (which they called 'mallee-heath') and found that litter moisture content and wind are the most important variables influencing fire spread, with fuel load playing a minor role. Specifically, litter moisture needs to be below 7–8% for fire to be sustained in mature mallee stands (McCaw 1995; Cruz et al. 2013).

Avitabile et al. (2013) mapped fires over a large area of semiarid south-eastern Australia and found that ~40% of the mallee vegetation in this area had burnt over a 35-year period, mostly by a few very large fires. Although there was a general link between prior rainfall and these large fires, it could not account for all of them, suggesting time since fire also plays a role. Similarly, O'Donnell et al. (2011b) reported a weak link between the sequence of wet and dry years on fire probability in a semiarid region with mallee in south-west Australia but also demonstrated that fire intervals in mallee vegetation of this region moderately depend on fuel age (O'Donnell et al. 2011a). Future research should focus on the interactive effects of time since fire and rainfall variability in promoting fires in mallee vegetation.

Chenopod Shrublands

Fire is rare or absent in chenopod shrublands (Groves 1994; Murphy et al. 2013; Friedel et al. 2014). This is not surprising given the low flammability with most of the dominant species being succulent or semi-succulent (being adaptations to saline soils). Fires in chenopod shrublands have been reported and are damaging, but most seem to be at their boundaries where fires have burnt in from neighbouring fire-prone vegetation, especially following rain events when fuel levels may be atypically high and continuous (e.g. Ladbrook 2015). As fires are not commonplace in chenopod vegetation, very little research has been conducted but is required to understand the impacts of fire on this ecosystem.

Invasion by flammable exotic and native grasses and forbs has altered composition and structure of chenopod vegetation in some areas such as the Nullarbor Plain, resulting in very large and damaging summer bushfires, especially following above-average rainfall. As disturbances such as fire and grazing can promote the invasion of grasses, it may be possible that areas of chenopod shrubland are caught in a fire – grass cycle (D'Antonio and Vitousek 1992) – whereby loss of shrubs by fire results in colonisation by more annual grasses which in turn increases the susceptibility of these areas to further burning and so on. This appears to be a common situation across much of the Nullarbor where grazing by rabbits initiated the loss of shrub cover and promoted grass invasion and then large fires (Burnside et al. 1995). Burnt chenopod shrubland can experience major changes in composition and structure. For example, in the Western Australian Goldfields, vegetation dominated by chenopods such as *Maireana* and *Atriplex* spp. changes to a more open vegetation dominated by fire-tolerant species such as *Senna* spp. and *Acacia hemiteles* following fire (Burnside et al. 1995).

Landscape-Scale Fire Patterns

The extent and scale of landform, soil and vegetation heterogeneity in the arid zone is variable within and between bioregions. Today, very large dry-season fires are common and invariably involve a range of landforms and associated vegetation

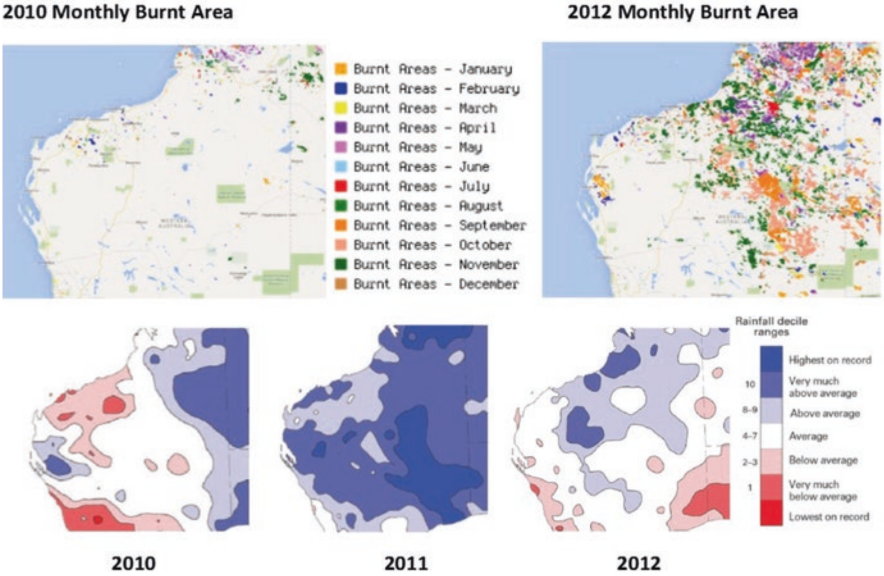


Fig. 4 Monthly burn area and annual rainfall deciles across arid-semiarid Western Australia for two contrasting periods: 2010 (generally dry) and 2012 (extended wet period) (Sources: FireWatch website (http://firewatch.landgate.wa.gov.au) and Bureau of Meteorology annual climate summaries for 2010, 2011 and 2012, respectively)

types (Haydon et al. 2000; Kelso et al. 2015). Embedded within the more flammable matrices of spinifex grasslands or dense *Acacia* scrub are landforms such as rock outcrops, playa lakes, gorges, breakaways and floodplain margins that often support sparse vegetation that rarely, or never, burns. These habitats are often refugia for fire-sensitive and fire-independent taxa such as *Ficus* spp., *Brachychiton* spp., vine thickets and some *Callitris* spp. (Bowman and Latz 1993). These fire-sensitive plant communities are often of conservation significance and, presently, are threatened by large, intense fires entering from adjoining vegetation types (Allan and Southgate 2002; Nano et al. 2012b). Further, if fire is adequately managed in the broader, more flammable landscape matrix, then these low-fuel areas can act as natural firebreaks, which help restrict fire size and protect refugia and long-unburnt stands of vegetation (O'Donnell et al. 2011a; Knuckey et al. 2016). Historically, this would have been achieved via frequent cool-season burning by Aboriginal people which resulted in a fine-scale mosaic of burnt patches that would have prevented or mitigated the development of large hot-season fires (Burrows and Christensen 1990; Bowman 1998). Rainfall drives vegetation growth, which, in turn, drives fire, so in the arid zone, large bushfires invariably follow seasons of above-average rainfall. At regional scales, large fires in arid Australia tend to be confined to wet years, irrespective of fuel dynamics of inherent vegetation (Turner et al. 2008; Fig. 4).

Invasive Species and Fire

Invasive plant species can drastically change species composition, habitat structure and ecosystem processes, including alteration of fire regimes. Where invasive species are promoted by fire and also increase fuel loads and/or flammability, a fire-weed cycle can be established, whereby fires lead to greater weed cover, which, in turn, promotes more fire, resulting in unnaturally high fire frequencies and loss of biodiversity (D'Antonio and Vitousek 1992). This is a worldwide phenomenon affecting many different types of ecosystems and primarily involves invasive C4 grasses (D'Antonio and Vitousek 1992; Brooks et al. 2004). In many arid regions across the globe, exotic grass invasion has dramatically increased fuel levels and fire incidence, intensity and spread (Balch et al. 2013).

In semiarid and arid regions of Australia, the main invasive grass of environmental concern is buffel grass (*Cenchrus ciliaris* L.; syn. *Pennisetum ciliare*), although it is valued as fodder by pastoralists (Marshall et al. 2012). Invasion of buffel grass in the absence of fire can cause profound changes to vegetation communities (e.g. Olsson et al. 2012). However, it often develops sufficient cover and biomass to carry fire relatively frequently, altering the natural fire regime to the detriment of the native biota (Miller et al. 2010; Clarke et al. 2005). Because it is a perennial species capable of surviving droughts, fire incidences become decoupled from the natural fluctuations in ground fuels due to rainfall variability (Clarke et al. 2005).

Fires in vegetation dominated by buffel grass are of enhanced intensity (McDonald and McPherson 2011) and severely damage overstorey trees and woody shrubs, as well as reducing the regenerative capacity of plants from seed and aerial buds (Miller et al. 2010; Schlesinger et al. 2013). This, combined with the competitive abilities of buffel grass, results in lowered native plant diversity (Clarke et al. 2005; Schlesinger et al. 2013). Animals, such as certain reptiles (which use bare ground for basking; Eyre et al. 2009) and ground-feeding birds (Young and Schlesinger 2015), are impacted by buffel grass invasion due to its homogenising effect on habitat. Buffel grass invasion strongly favours more productive arid ecosystems such as eucalypt woodland on drainage lines, floodplains and outwash plains (Friedel et al. 2014), meaning control efforts should be focussed on these areas. Weed and fire management in these areas is complicated as pastoralists rely heavily on these areas for livestock production, and in many instances they have promoted the establishment of buffel grass at the expense of native species.

Fire Impacts and Responses

Flora

Most perennial plant species in the Australian arid zone are able to regenerate following fire by resprouting, either from buds buried beneath stem bark in the case of trees (epicormics) or from belowground organs (Nano and Clarke 2011; Nano et al.

2012b; Clarke et al. 2015; Table 2). Resprouting species are more commonly found in arid environments with higher fire frequency (such as spinifex grasslands) and in more productive parts of the landscape, probably because short fire intervals and rapid recovery of burnt sites by resprouters disfavour plants regenerating by seed (Nano and Clarke 2011). About two-thirds of resprouting woody species studied across arid Australia are 'obligate resprouters' (depend on resprouting for postfire recovery), with the remainder being 'facultative resprouters' (i.e. they resprout but will also regenerate well from seed). Mallee and eucalypt woodlands are exceptions, with the majority of species in these vegetation types being facultative resprouters (Table 2), possibly reflecting their proximity to and association with the flora and fire regimes of temperate/Mediterranean climatic regions of southern Australia.

Plants that regenerate en masse after fire from seed ('seeders') generally account for around 40–60% of species (Table 2). However the proportion that are 'obligate seeders' (rely solely on seed for regeneration and don't resprout) is generally low but varies widely among vegetation types, being greatest in mallee but relatively uncommon in spinifex (Table 2; Nano and Clarke 2011). Obligate seeders with long juvenile periods are particularly vulnerable to short intervals between fires as there is insufficient time to replenish seed stores. Examples of species that have declined due to frequent 'hot' fires include *Callitris* (Bowman and Latz 1993) and mulga (Start 1986; Ward et al. 2014). Most arid-zone obligate seeders are however relatively short-lived and include small *Acacia* shrubs, native peas (e.g. *Gastrolobium, Indigofera, Mirbelia viminalis*) and fire ephemerals (e.g. *Keraudrenia* and species in the Gyrostemonaceae) which grow quickly and flower in years immediately after fire (Wright and Clarke 2007a; Nano and Clarke 2011; Knuckey et al. 2016). Many herbaceous ephemerals also have enhanced recruitment and presence immediately after fire (Suijendorp 1981; Wright and Clarke 2007a). These obligate seeders tend to build up a seed bank over time (mainly in soil), with seed germination often stimulated by the heat and/or smoke of fire (Erickson et al. 2016a, b).

Although synchronous postfire seedling recruitment is observed in many arid-zone species, some longer-lived woody species do not appear to accumulate a viable seed bank with time since fire but rather have fluctuating seed availability over time in response to rainfall events (Nano et al. 2012a, b). Not only are phenology and seed production favoured by high-rainfall periods but so is germination, suggesting inter-fire recruitment is a relatively common phenomenon for such species (Preece 1971; Auld 1995; Knuckey et al. 2016). Altogether these characteristics point to the prevalence of species with rain-cued recruitment in the Australian arid zone; species demonstrating such traits include relatively tall, long-lived and generally resprouting *Acacia,* as well as eucalypts (*Eucalyptus* and *Corymbia*), *Senna* and *Eremophila* (Wright and Clarke 2009; Nano et al. 2012b; Knuckey et al. 2016). However, more research is required on soil seed bank dynamics, seed longevity and recruitment bottlenecks for arid plant species as such information is clearly lacking compared with other ecosystems in Australia.

The above discussion points to weaknesses in the resprouter-seeder classification scheme (Table 2) when applied to the arid zone. The principal one is that it applies a dichotomy when there is clearly a range of fire responses from weak to strong among species and much within-species variability (Nano et al. 2012b; Clarke et al. 2015). For instance, resprouting can be ‘weak’ and variable for some species in that it tends to occur only in mature plants facing low-intensity fire and then mostly from basal buds (Wright and Clarke 2007b). At the other extreme, it can be consistently ‘strong’ with such plants being able to withstand repeated hot burns via prolific and enduring epicormic resprouting (Hodgkinson 1998). Similarly, seed germination may be strongly promoted by fire (via heat or smoke compounds) or be more cued to ample soil moisture and/or long storage (Erickson et al. 2016a). Overall, fire responses appear to be more weakly developed in arid Australia than in ecosystems in southern Australia subject to regular fire (e.g. heathland, dry sclerophyll forest); however, there appears to be a mix from strong to weak responses in all communities (Nano et al. 2012b). Future research needs to focus on patterns in the relative strengths of fire responses within and across the major vegetation types.

Some studies conducted at local scales in the Western Australian arid zone have revealed divergent fire response spectra from those generally found for that vegetation type (Table 2). For instance, dense *Acacia* scrub in the Yalgoo bioregion in south-western Australia and mulga woodlands in the eastern Goldfields and Pilbara have far greater proportions of obligate seeders and fewer obligate resprouters than typical *Acacia*-dominated vegetation (Table 2). This may reflect the more regular and hotter crown fires in the Western Australian examples (at least for the Yalgoo shrublands; Dalgleish et al. 2015) and a more predictable Mediterranean climate (for all except the Pilbara site). Semiarid eucalypt woodland in south-west Australia also has far more obligate seeders and fewer obligate resprouters than other eucalypt woodlands (which are mainly from tropical and temperate Australia). The prevalence of such strongly developed responses is difficult to explain given the rarity of fire in the ‘low-fuel’ Western Australian woodlands, but perhaps this is also a response to stand-replacing fires, albeit at a very low frequency (Gosper et al. 2016). However, misclassification or inconsistencies in assigning response types, as well as the different spatial scales, may also have contributed to differences found. Local (Western Australian) examples of mallee and spinifex are consistent with the general breakdown by response type for these vegetation types (Table 2).

Response of Dominant Plant Species

Triodia species, which dominate a large proportion of the arid zone, can be either seeders or resprouters, and species with divergent responses may co-exist at local and landscape scales. In the Pilbara, for instance, two very common species, *T. basedowii* (obligate seeder) and *T. wiseana* (facultative resprouter), can occupy the same site (Casson and Fox 1987). There has been no recent attempt to collate fire responses of *Triodia* species across Australia, or regionally, although the much-disputed and uncertain taxonomy in this genus (Hurry et al. 2012; Anderson et al. 2016) means that such a compilation would be difficult at present. Within some widespread species, there are differing responses between regions (e.g. Rice and Westoby 1999).

Table 2 Comparison of plant reproductive/recovery responses to fire (% of plant species) for major vegetation types of arid Australia based on (1) compilation of responses recorded from many sites across Australia ('continental'; data from Clarke et al. 2015) and (2) species present at particular localities in Western Australia

Vegetation type	Area/locality (sampling intensity)	R + S+ Facultative resprouters	R + S- Obligate resprouters	R-S+ Obligate seeders	R-S- Fire avoiders	No. of species examined	References
Spinifex	Continental	20.0	50.8	23.8	5.4	133	Clarke et al. (2015)
Spinifex	Marandoo, Pilbara (21 × 500 m^2 plots)	25.7	45.7	20.0	8.6	70	Van Etten and Fox 2004; Van Etten, unpubl
Acacia shrubland[a]	Continental	15.9	46.7	11.5	25.8	184	Clarke et al. (2015)
Acacia scrub	Mt Gibson, Yalgoo (40 × 400 m^2 plots)	9.7	16.1	61.3	12.9	62	Knuckey et al. (2016)
Mulga	Menangina, Eastern Goldfields (27 × 500 m^2 plots)	19.7	21.2	31.8	27.3	66	Fox (1985)
Mulga	West Angelas, Pilbara, (26 × 500 m^2 plots)	25.0	20.8	41.7	12.5	72	Fox (1985)
Mallee	Continental	35.4	3.3	57.1	3.8	215	Clarke et al. (2015)
Mallee	Lake King, Eastern Wheatbelt, Western Australia	38.6	0.8	60.6	0	?	Gosper et al. (2012)
Eucalypt woodland	Continental	47.6	40.4	7.3	4.7	235	Clarke et al. (2015)
Eucalypt woodland	Yellowdine (11 × 250 m^2 plots)	32.6	2.3	51.2	14.0	?	Gosper et al. (2013b)

R+ postfire resprouting – generation of new shoots from dormant buds after stem has been fully scorched by fire
R− no postfire resprouting
S+ postfire seeding – generation of a fire-resistant seed bank with postfire seed germination and seedling recruitment
S− no postfire seeding
[a] Clarke et al. (2015) combined mulga woodland/shrubland and shrubland dominated by other *Acacia* spp. into '*Acacia* shrubland'

Although it has been hypothesised that there will be more resprouting *Triodia* species in higher-rainfall and more productive parts of the arid zone due to high fire frequencies disfavouring seeders (Rice and Westoby 1999), this has also not been rigorously tested, and may not be the case as many seeders are known from relatively high-rainfall zones (Armstrong and Legge 2011). While some *Triodia* species reach reproductive maturity within 4 years of fire (Craig 1994), other species are relatively slow (up to 9 years to reach reproductive maturity; Westoby et al. 1988) and therefore vulnerable to short fire intervals. Although most *Triodia* species appear to be obligate seeders, with others tending to be facultative resprouters, it remains unclear to what degree fire stimulates germination of *Triodia* seed and how much of the soil seed bank may persist following fire. Cohn and Bradstock (2000) and Armstrong and Legge (2011) showed that most of the seed bank germinated after fire, whereas Bogusiak et al. (1990) and Wells (1999) found a minor effect of fire on seed germination with many seeds remaining ungerminated in the soil after fire, suggesting polymorphic germination responses within some species. Several studies have demonstrated a positive effect of smoke-derived compounds on *Triodia* seed germination (Wright and Clarke 2009; Erickson et al. 2016b), although the response can be inconsistent and is thought to depend on seed age/maturity, viability and timing. In many years, there appears to be little seed set with florets being empty or containing mainly unviable seed (Jacobs 1984; Erickson et al. 2016a,b).

An inconsistent germination response to fire within *Triodia* species may be a hedge-betting strategy as would be expected in regions of high rainfall variability and consequent irregular fire regimes. Wright et al. (2014) report on mast seeding in several *Triodia* species of central Australia in response to high-rainfall periods. They hypothesised that as fires also follow very wet periods, that mast seeding in *Triodia* is an evolved fire response to ensure abundant seed availability at the site during times of highest fire, and hence recruitment, probability. Seed masting in *Triodia*, and potentially other arid-zone species, and its link to rainfall and fire, is a phenomenon that requires further study, as it may unlock the key to understanding regeneration in these species and how they persist in a mostly dry, but highly variable, environment.

Mulga has been described as both an obligate seeder (R-/S+; Wright and Clarke 2007a; Ward et al. 2014) and a fire-sensitive ‘avoider’ which predominantly recruits within mature stands (R-/S-; Nano and Clarke 2011; Clarke et al. 2015). There are reports of resprouting within this species complex (e.g. Fox 1986; Wright and Clarke 2007b) but is likely to be limited to low-intensity fires. The variation in fire response across this species complex is not surprising given the range of subspecific taxa and their widespread distribution across landscapes and regions (Nano et al. 2012b). Ward et al. (2014) demonstrated that mulga at Lorna Glen (eastern Gascoyne region) is detrimentally affected by short fire intervals as it seems to require at least 20 years to establish an adequate soil seed bank to enable seedling regeneration. Others have observed that where fuel is sparser beneath the groves, mulga is able to avoid or survive frequent low-intensity ‘cool’ fires, but not ‘hot’ fires (Latz 1995; Burrows 2014). Mulga encapsulates the difficulty in classifying species into a single fire response type, and more study of the reproductive and regeneration ecology in this important species complex is needed.

There is little known about the fire response of chenopods, a dominant component of many arid shrublands and woodlands. Most species are fire sensitive, displaying no obvious fire adaptations (Hodgkinson and Griffin 1982), so could be classified as fire independent – i.e. fire plays no role in their ecology and could be harmful. There are a couple of exceptions, including *Maireana aphylla* and *M. sedifolia*, which are resprouters that tend to increase in dominance in chenopod shrublands following fire (Wilson et al. 1988; Burnside et al. 1995; Friedel et al. 2014).

Vegetation Changes

Distinct boundaries between mulga woodland/shrubland and spinifex grassland communities are found in many arid landscapes. Most studies report no or only very minor spatial shifts in such vegetation boundaries in response to fire or from the lack of it (Bowman et al. 1994; Nano and Clarke 2010; Fensham et al. 2011; Friedel et al. 2014). The general stability of these boundaries is believed to reflect soil/landform discontinuity with spinifex mostly on uplands and surrounding slopes and mulga on alluvium in valleys, drainage lines and other 'run-on' areas. Runoff received from areas upslope is believed to contribute to thickening of mulga vegetation at the boundary which may render it more stable through grass suppression (van Etten 1987).

Although distinct boundaries are often found in range- and basin-type topographies (such as the Hamersley Ranges in the Pilbara and MacDonnell Ranges in central Australia), Nano and Clarke (2008) point out that more complex spatial arrangements of mulga and spinifex communities exist, including mosaics, gradual transitions and even mixed communities (i.e. mulga with spinifex understorey). Some of these patterns cannot be adequately explained by edaphic differences and are structural rather than floristic in nature, so it is likely that fire is somehow responsible (Nano and Clarke 2008; Bowman et al. 2008). Complex mosaics and mixed communities, where two communities with extrinsically different fire regimes and responses co-occur (one fire-prone and resilient, the other fire sensitive), are thought to have been promulgated by past Aboriginal patch-burning practices, which would have promoted and then protected mulga stands from large fires (Bowman 1998). However, with the reduction or absence of such burning in many parts of the arid zone, conversion of mulga communities into spinifex grassland through repeated fires has been reported (Start 1986; Latz 1995; Allan and Southgate 2002). Understanding and predicting how boundaries and other spatial arrangements of mulga and spinifex become unstable and vulnerable to large fires is an important research area.

Some major changes in vegetation in response to altered fire regimes have been reported in the Australian arid zone (e.g. Bowman 1998) but little studied. For instance, on the Nullarbor Plain, the combined effect of fire and grazing (chiefly by rabbits) has reportedly converted large expanses of chenopod shrubland into open grassland with sparse shrubs (Burnside et al. 1995), although the evidence appears to be mainly anecdotal.

Fauna

The response of fauna to fire is broadly linked to postfire vegetation succession, particularly increasing cover and structural complexity of vegetation, attributes which tend to slowly recover in arid lands following burning. Fauna species have different habitat requirements (shelter, food, breeding sites), and therefore postfire vegetation dynamics tend to drive succession in animal species. This is generally the case for reptile species in spinifex grasslands (Masters 1996; Pianka 1996), mallee (Nimmo et al. 2012) and dense *Acacia* scrub (Doherty et al. 2015), and is thought to reflect differences in thermoregulatory requirements (e.g. some reptile species, such as the dragons, *Ctenophorus nuchalis* and *C. maculatus*, need or are able to bask in full sun for prolonged periods, common to newly burnt areas, whereas others, such as *C. isolepis* and *C. scutulatus*, need or prefer some shade). Letnic et al. (2004) also showed this is the case for reptiles in central Australian spinifex grassland but found the response in small mammals was more influenced by rainfall after fire. Consequently, they used a state-and-transition model involving various combinations of rainfall and fire events to explain the dynamics of small mammals.

There are many vertebrate species in arid Australian with seemingly no relationship with postfire seral stage or that have different fire age responses across their distributions (Driscoll and Henderson 2008; Nimmo et al. 2012, 2014; Doherty et al. 2015). This demonstrates that, overall, postfire dynamics in fauna are more complex than predicted by successional change in vegetation alone, with some species responding to multiple factors (e.g. combinations of grazing, drought, rain, invasive species and/or fire). Further, specific habitat features required by fauna may not necessarily change in gradual or predictable ways with fire age (Haslem et al. 2011), and some essential habitat features (such as tree hollows, food type, thick bark or dense litter) may only reappear after many decades without fire (Woinarski 1999; Haslem et al. 2011; Doherty et al. 2017). This points to the need to understand specific habitat requirements of fauna species and how these vary with fire regime, as well as the importance of maintaining at least some old vegetation in fire-prone landscapes.

The decline of medium-sized mammals across arid Australia has been attributed to several causes, with altered fire regimes regularly put forward as one of these (Woinarski et al. 2015). Specifically, this refers to a change in burning patterns since the departure of traditional Aboriginal practices which favoured a fine-grain mosaic of vegetation at different seral stages. This contrasts with the contemporary regime of very large, hot wildfires (refer to section 'Human use of fire and fire management'). Maintaining or reintroducing patch burning has appeal, because it was the pattern in place for thousands of years, mitigates against damaging effects of large wildfires (Burrows et al. 2009; Latz 1995; Bird et al. 2016) and provides diversity of seral stages and hence habitat diversity at fine scales. Although the biodiversity benefits of patch burning have been questioned by some (e.g. Parr and Andersen 2006), many studies of fauna-fire links at the landscape scale report at least some species with preference for vegetation of a particular fire age or a specific mix of fire ages. For example, Lundie-Jenkins (1993) reported that for the endangered rufous hare-wallaby, fine-scale seral diversity in spinifex grasslands is important. Pianka (1996), writing about the incredible richness of lizards in Australian deserts, noted that:

> One of the most important factors contributing to this is fire, which generates a patchwork of habitats at different states of recover, each of which favours a different subset of lizard species. Habitat specialised species can go locally extinct within a given habitat patch (fire scar) but persist in the overall system by periodic reinvasions from adjacent or nearby patches of suitable habitat of a different age. Such spatial-temporal regional processes facilitate local diversity.

Masters (1996) reported that a higher number of reptile species were trapped in mature spinifex and that fire mosaics maximise reptile diversity because of the preference by some species for earlier seral states. She also made the observation that recently burnt areas act as firebreaks and ensure that mature spinifex patches are always present. Langlands et al. (2012) studying the relationship between fire and spiders reported similar findings that different spider assemblages preferred different postfire states with about 50% of species restricted to a particular state. Similarly, Haydon et al. (2000) concluded that the patchwork of habitats at different stages of postfire recovery (seral states) played a vital role in the conservation of biodiversity in desert landscapes. Smith and Morton (1990), studying scorpions in the Tanami Desert, found that one species (*Lychas alexandrinus*) was caught most frequently 2–3 years after fire.

The relationship between patch burning and small mammals is similar, but perhaps not as pronounced. Masters (1993) found that patch-burning spinifex grasslands to create a diversity of seral states maximised the species diversity of small mammals by ensuring that suitable successional states were always present. She concluded that this was particularly important for species that are restricted in their distribution such as mulgara (*Dasycercus cristicaudata*). Letnic and Dickman (2005) working in the Simpson Desert found that while some species preferred long-unburnt spinifex and others preferred regenerating spinifex, the greatest capture rates were made at sites that received most rainfall. Like Masters (1996), they concluded that recently burnt patches were an important part of the mosaic because they reduced the extent of bushfires. Partridge (2008) working in the Purnululu National Park concluded that small-scale patchy spinifex fires were very important for *Pseudomys desertor* and *P. nanus*, which utilised long-unburnt patches for food and shelter.

Landscape heterogeneity driven by geomorphic-edaphic-vegetation patterns is also important for many animal species with fire potentially further enhancing this spatial complexity. For instance, Major Mitchell cockatoos (*Lophochroa leadbeateri*) require patches of old woodland with tree hollows for nesting but may also need recently burnt shrubland or spinifex nearby as seed of some pioneer plant species can provide an important food source (Nano et al. 2012b). Some species have large home ranges, which may need to be catered for in any patch-burning approach (i.e. may need to leave large continuous patches of their preferred seral stage). Patch burning per se covers a wide range of temporal and spatial scales, as well as a range of fire intervals. In addition to understanding traditional Aboriginal burning patterns, more landscape-scale studies are needed for a better scientific understanding of scale and biodiversity responses in relation to patch burning. Specifically, we need to know more about the patch sizes and spatial configuration of different fire ages to best maintain biodiversity within fire-prone arid landscapes.

Birds are a relatively well-studied group in the Australian arid and semiarid zones which demonstrates the above principles, with many bird species having distinct preferences for certain fire ages. In shrubland, mallee and mulga woodland, long-unburnt vegetation tends to be favoured by insectivores (such as the splendid fairy wren, *Malurus splendens*; inland thornbill, *Acanthiza apicalis*; rufous whistler, *Pachycephala rufiventris*; and grey shrike-thrush, *Colluricincla harmonica*). Generally these old patches have the greatest bird species richness, most likely in response to their greater within-patch complexity and/or food resources (Leavesley et al. 2010; Taylor et al. 2012; Watson et al. 2012; Davis et al. 2016). A smaller number of bird species, mostly granivores such as the zebra finch, favour recently burnt areas. However, there are a number of bird species that do not respond to fire age (mostly generalists and/or nectarivores, such as spiny-cheeked honeyeater, *Acanthagenys rufogularis*, and singing honeyeater, *Lichenostomus virescens*), and for some species their fire age preferences can vary throughout their range (Davis et al., 2016). At the landscape scale, Taylor et al. (2012) found bird species richness increased with proportion of long-unburnt vegetation, rather than the mix of fire ages which reflects the relatively large number of bird species favouring old vegetation.

Fire Regimes and Climate Change

Climate change, both in the past and future projections, for arid Australia is described in chapters 'Evolutionary History' and 'Feral Animals In The Semi-Arid And Arid Regions Of Australia; Origins, Impacts And Control' of this book. Predicted higher temperatures in coming decades, including more days with extreme temperatures, will directly affect fire weather, resulting in more days of high fire hazard. This increase in fire hazard will be compounded by predicted declines in humidity and increases in lightning and wind speeds over arid Australia (Cary et al. 2012). King et al. (2013) predicted rises in the average daily fire danger index of up to 20% by 2070 for central Australia. This may not necessarily translate to increases in fire incidence and extent as generally drier conditions will reduce fuel loads and connectivity, particularly in more open vegetation such as spinifex grasslands, eucalypt woodlands and open shrublands (Bradstock 2010; King et al. 2013). However, rainfall declines are predicted mainly for the southern arid zone, where relatively dense vegetation formations (such as mallee and dense shrublands, which tend to carry crown fire) may actually become more susceptible to fire due to overall lower fuel moisture levels. The expected increase in rainfall variability in the northern arid zone would tend to mean more pronounced and possibly more frequent wetter periods which may ultimately result in more fires following these times due to enhanced fuel levels. The shift to more variable rainfall therefore may mean more pronounced periods of larger fires with intervening times of fewer fires. The shifting seasonality of rainfall across arid Australia is also likely to alter seasonality of fires and perhaps fuel loads via changes in species composition. For instance, in the southern arid zone, increased incidences of summer rain may mean more C4 grasses which would increase fuel loads in woodlands and other open vegetation (e.g. Prober et al. 2012).

Fire-Herbivore Interactions

Given widespread pastoralism, especially in the woodlands and shrublands, across arid Australia, and the prevalence of medium-sized to large herbivores (both native and introduced), surprisingly few Australian studies have investigated the combined effects of grazing and fire. This contrasts with arid/semiarid regions of the USA and southern Africa where specific studies of interactive effects, including carefully designed manipulative experiments, are relatively common (e.g. Valone and Kelt 1999; Allred et al. 2011). There are two interactions of particular interest to fire managers.

Firstly, sustained grazing pressure can suppress fuel levels resulting in fewer and smaller fires, but no studies have quantified this impact in arid Australia. Furthermore, soil and vegetation degradation through overgrazing likely reduces overall productivity and the capacity to regenerate following rainfall leading to long-term reductions in fuel loads. Due to past overgrazing, particularly during times of sustained drought, the herbage that sustains livestock in many rangeland areas is now pulses of annual herbs following rainfall, with the important perennial grass component now missing or reduced (Brandis 2008). Also under high grazing pressure, other palatable plants will decrease, while unpalatable species (mostly woody species) will increase (Burnside et al. 1995), further changing fuel characteristics. Much of the impact associated with overgrazing stems from artificial water points (surface dams and bores), which tend to maintain high grazing pressure (combined effect of native, domestic and feral animals) well above carrying capacity during dry times (James et al. 1999). Judicious management of these watering points is the key strategy for limiting the negative effects of grazing. Over the last 10–15 years, there has been considerable change in the tenure and use of pastoral lands in Western Australia, with around one-third of leases either (being) converted to conservation tenure or now held by mining companies, nongovernment conservation organisations or Aboriginal groups with minor to no interest in grazing livestock (van Etten 2013). There is potential for fuel levels (and hence fire extent) to broadly increase with cessation or reduction in grazing on these lands, although this has not yet been demonstrated, and in fact it may take several decades of rangeland spelling before vegetation productivity and cover is replenished (Frank et al. 2013).

The second important interaction involves the postfire impacts of grazing. Grazing pressure on recently burnt areas can be profound, as new growth is often desirable and highly nutritious, with herbivores likely to move in from some distance to eat recently burnt vegetation (Letnic 2004). Such concentrated grazing likely reduces regeneration of grasses and other palatable species, accelerating the shift to woody, unpalatable species composition, as well as increasing other impacts of grazing such as loss of microbiotic crusts and enhanced erosion (Suijendorp 1981; Letnic 2004). Over the longer term, increased cover of woody plants likely further suppresses grasses which can lead to fewer fires and ultimately to a situation where fire can no longer occur (a state transition in ecological terms; Watson and Novelly 2012). Woody thickening is a widespread problem in arid and semi-lands and widely known for mulga vegetation, especially in eastern Australia, although this is largely reported as an impact of grazing alone (Noble 1997). The severity of grazing impacts on postfire regeneration would be expected to broadly decline with increasing fire patch size and the availability of other feed in the surrounding area (Allred et al. 2011).

Several authors have made the distinction between the impacts of grazing and browsing on vegetation, fuel and, thereby, fire (van Langevelde et al. 2003; Holdo et al. 2009). Grazing reduces grasses and therefore fuel loads; fires, when they occur, are of lower intensity and less damaging to woody vegetation. Increases in density and cover of trees and shrubs are the likely consequence and may lead to a change of state to a tree-dominated system (Fig. 5). Browsing, on the other hand, is defined as animals feeding on the leaves of trees and shrubs which can result in an increase in grass biomass (i.e. fuel), which, in turn, results in hotter and more frequent fires, which further negatively affects trees and shrubs. Therefore, browsing more likely leads to grass-dominant ecosystems, whereas grazing promotes woody plant dominance (Fig. 5). In arid Australia there are generally few browsers, although sheep may browse woody plants in time of extended drought. However, feral vertebrates such as goats and camels are predominately browsers and are increasing (Edwards et al. 2010). As these feral animals suppress woody plants when their densities are high, there is potential for indirect impacts in terms of increased fuel loads and fire hazard (Brim Box et al. 2016). However, browsers and grazers (including macropods) are usually both present in an area, and the interplay between them can be complex but will ultimately determine the impacts on vegetation structure and fuel loads (Holdo et al. 2009; Burrows, Chapter Feral animals in the semi-arid and arid regions of Australia; origins, impacts and control, this volume).

Although pastoral leases and grazing by cattle and sheep occur generally outside of spinifex country, Suijendorp (1981) did look at fire-grazing interactions in the west Pilbara where *Triodia pungens* can be partly palatable to livestock, especially when young; consequently, in this region, as in others, they burn this spinifex frequently. The outcome of this, however, has often been an increased dominance by hummock grasses and unpalatable shrubs to the detriment of more palatable, co-existing grasses and herbs. Deferral of grazing for 1 or 2 years after fire leads to re-establishment of these more palatable species (Burnside et al. 1995).

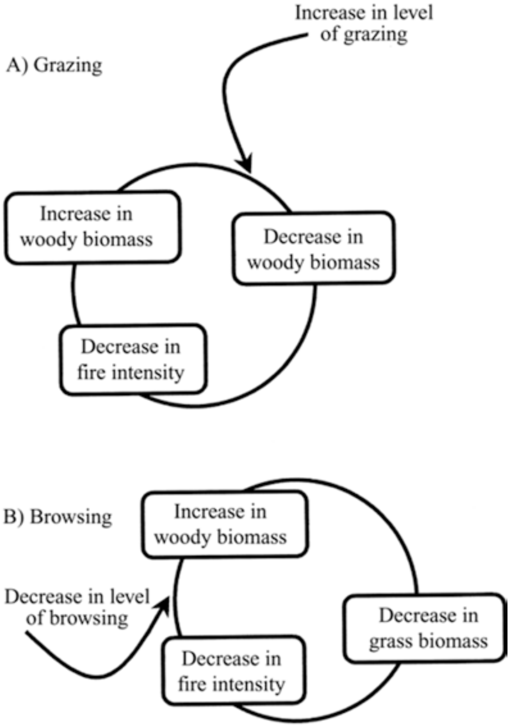


Fig. 5 Positive feedback mechanisms between grass biomass (fuel load) and fire intensity, triggered by (**a**) grazing and (**b**) browsing. A decrease in grass biomass leads to reduced fuel load which makes fire less intense and less damaging to trees, consequently resulting in an increase in woody vegetation. (From van Langevelde et al. 2003)

Human Use of Fire and Fire Management

Although lightning is responsible for most of the area burnt in remote areas, Edwards et al. (2008) found most fires in central Australia were started by people. Situations where humans light fires in the arid zone include pastoralist burning to promote palatable plants for livestock or to protect assets; Aboriginal people burning for ceremonies and/or resource enhancement; conservation/land managers burning to protect cultural or biodiversity assets; and accidental or arson fire, especially along access tracks/roads and around towns and infrastructure (Edwards et al. 2008; Turner et al. 2008). Edwards et al. (2008) note that relatively few areas have or are meeting formal fire management objectives.

While the pre-European fire regime has not been well quantified for many parts of arid Australia, there is sufficient evidence from ecologists (e.g. Jones 1969; Latz and Griffin 1978; Kimber 1983), and from Aboriginal people themselves, that fire was critical to their physical and spiritual wellbeing and that it was used widely and regularly. Using early (1953) aerial photographs from an area of the Great Sandy Desert, Burrows and Christensen (1990) quantified the extent of patch burning by Aboriginal people, who at the time had not been contacted by Europeans. The photography revealed a fine mosaic of burnt patches reflecting burning by local Aboriginal people prior to European contact (Plate 1). Given varying populations and circumstances of the Aboriginal people, the extent to which such patterns were ubiquitous across this vast area is uncertain. Following European settlement, wildfires, mostly caused by lightning, have led to fire sizes of millions of hectares, sizes unlikely to have occurred under Aboriginal occupation. Presently, there is a growing concern about the threat to assets that such fires pose – for example, the people and buildings of remote communities, biodiversity, air quality (as greenhouse gas emissions), cultural artefacts, pastoral properties, tourism and infrastructure associated with mining and other industries. To mitigate the threat, land managers are increasingly turning to the cool-season-prescribed burning of these discontinuous fuels. The current summer wildfire regime throughout most of the spinifex grasslands is likely to be a significant contribution to greenhouse gas emissions (carbon dioxide, methane and nitrous oxide; Burrows 2014). A return to traditional Aboriginal fire management, resulting in smaller, patchier fires lit in the cool season, may provide an opportunity for remote desert communities to contribute to reducing Australia's greenhouse gas emissions, to increasing carbon stocks, to conserving biodiversity and to improving ecosystem health. This is because such mild fires remove less stored carbon at both local and landscape scales compared with summer wildfires (Murphy et al. 2015; Williams et al. 2015; Plate 2). In addition to environmental benefits, substituting wildfires with traditional fire management has significant social and cultural benefits. Done at appropriate scales, good fire management can also provide training, employment and economic opportunities (Burrows 2014).

Prescribed burning for the purpose of biodiversity conservation, whether done via mosaics/patches or narrow strips/firebreaks, can be controversial, but there is consensus that such burning is useful as it can prevent or minimise landscape-scale wildfires and their impacts (Pastro et al. 2011; Burrows and Butler 2016). Such wildfires, which may burn for many days, can burn through and damage fire-sensitive vegetation and generally homogenise landscapes in terms of fire age and seral stages (Allan and Southgate 2002). The optimal or most appropriate spatial and temporal configuration of fire ages to maintain biodiversity in a given landscape is still a matter of debate and may not be obtainable in some areas as ideal fire age configurations can differ substantially and even conflict between biotic groups (Pastro et al. 2011; Kelly et al. 2015; Doherty et al. 2017). Traditional Aboriginal burning is believed to have resulted in a complex array of different fire ages, sizes and arrangements which did restrict fire extent (Burrows and Christensen 1990; Burrows et al. 2006). The call to reinstate Aboriginal burning practices, therefore, has merit but may only be achievable where there are ongoing links to land and traditional knowledge, as well as willing and adequately resourced participants. Pastro et al. (2011) argue that, in the absence of such complex burning practices, the best burning strategy may be to protect fire-sensitive vegetation and species via burning to maintain low-fuel strips or areas around these assets. This strategy can also be used to protect long-unburnt stands or habitat that may harbour unique or uncommon species (e.g. Knuckey et al. 2016).

There are many difficulties and constraints in achieving active fire management in arid areas, including remoteness, lack of people and resources and difficulties in access. Over many types of land tenure across arid Australia, there are no or very

Plate 2 Summer wildfires (**a**) tend to burn more biomass at local and landscape scales compared to controlled burns conducted in cool season (**b**)

few people living on the land (e.g. unallocated crown land and some pastoral leases), a situation that has generally worsened over time. This means a rapid suppression response is usually not possible, and so the tendency is to only deal with fires once they become major outbreaks and are generally difficult to control.

Conclusions

Three contrasting fire regimes predominate across arid Australia consistent with the structure and biomass of broad vegetation types as fuel for a bushfire. Firstly, spinifex grasslands are highly flammable and fire-prone and experience relatively regular fires (~every 5–15 years) in response to combined effects of fuel accumulation (time since fire) and antecedent rainfall. Fire at appropriate temporal and spatial scales is essential for their maintenance. They are also relatively well studied in terms of fire effects and behaviour, and there is growing evidence that large, hot-season spinifex fires are harmful to biodiversity and the environment with respect to greenhouse gas emissions. Fires in dense *Acacia* scrub and mallee are primarily linked to time since fire but experience less frequent burning (~every 30–80 years) because of the porous structure of the vegetation. When fires do occur, they are usually crown fires. Lastly, fire in open shrublands and eucalypt woodlands is relatively rare, because of the sparse and patchy nature of the vegetation and fuel. The role of fire in maintaining these ecosystems is questionable. These vegetation types occasionally burn following periods of high rainfall, which stimulates vegetation growth and, hence, fuel continuity; while they are able to recover from infrequent fire, there is little evidence that fire is essential for recruitment. Additionally, there are less common vegetation types which seem to be highly sensitive to fire and dramatically change in structure and species composition following even one-off burning (e.g. some chenopod shrublands, rocky uplands).

The arid and semiarid zones of Australia experience long periods of often severe fire weather. Low rainfall means long periods when the vegetation, especially dead material, is sufficiently dry to burn, and long periods of high temperatures, low humidity and strong winds ensure a large number of days when the fire danger rating is extreme, something which is expected to increase with climate change which may also increase the size and intensity of fires. Other future threats that are likely to alter fire regimes are the further spread and intensification of grassy weeds and introduced vertebrate browsers.

References

Allan GE, Southgate RI (2002) Fire regimes in the spinifex landscapes of Australia. In: Bradstock RA, Williams JE, Gill AM (eds) Flammable Australia: the fire regimes and biodiversity of a continent. Cambridge University Press, Cambridge, pp 145–176

Allred BW, Fuhlendorf SD, Engle DM, Elmore RD (2011) Ungulate preference for burned patches reveals strength of fire–grazing interaction. Ecol Evol 1:132–144

Anderson BM, Barrett MD, Krauss SL, Thiele K (2016) Untangling a species complex of arid zone grasses (*Triodia*) reveals patterns congruent with co-occurring animals. Mol Phylogenet Evol 101:142–162

Armstrong G, Legge S (2011) The post-fire response of an obligate seeding *Triodia* species (Poaceae) in the fire-prone Kimberley, north-West Australia. Int J Wildland Fire 20:974–981

Auld TD (1995) Soil seedbank patterns of four trees and shrubs from arid Australia. J Arid Environ 29:33–45

Avitabile SC (2014) Mallee HawkEye Project*:* final report 2011–2014. La Trobe University, Melbourne

Avitabile SC, Callister KE, Kelly LT, Haslem A, Fraser L, Nimmo DG, Watson SJ, Kenny SA, Taylor RS, Spence-Bailey LM, Bennett AF (2013) Systematic fire mapping is critical for fire ecology, planning and management: case study in the semi-arid Murray Mallee, South-Eastern Australia. Landsc Urban Plan 117:81–91

Bachelet D, Ferschweiler K, Sheehan T, Strittholt J (2016) Climate change effects on southern California deserts. J Arid Environ 127:17–29

Balch JK, Bradley BA, D'Antonio CM, Gómez-Dans J (2013) Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). Glob Chang Biol 19:173–183

Beard JS, Beeston GR, Harvey JM, Hopkins AJM, Shepherd DP (2013) The vegetation of Western Australia at the 1:3,000,000 scale, explanatory memoir, second edition. Conserv Sci W Aust 9:1–152

Bird DW, Bliege Bird R, Codding BF, Taylor N (2016) A landscape architecture of fire: cultural emergence and ecological pyrodiversity in Australia's Western Desert. Curr Anthropol 57(s13):s65–s75

Bogusiak A, Rice B, Westoby M, Friedel M (1990) Seedling emergence of hummock grasses in relation to the effects of fire. Rangel J 12:25–32

BoM [Bureau of Meteorology] (2008) Meteorological aspects of the Boorabbin Fire 28 December 2007 – 8 January 2008. Unpublished report by Western Australian Regional Office, Bureau of Meteorology, Perth, WA

Bond WJ, Midgley GF (2012) Carbon dioxide and the uneasy interactions of trees and savannah grasses. Philos Trans R Soc B Biol Sci 367:601–612

Bowman DMJS (1998) The impact of aboriginal landscape burning on the Australian biota. New Phytol 140:385–410

Bowman DMJS, Latz PK (1993) Ecology of *Callitris glaucophylla* (Cupressaceae) on the MacDonnell ranges, Central Australia. Aust J Bot 41:217–225

Bowman DMJS, Latz PK, Panton WJ (1994) Pattern and change in an *Acacia aneura* shrubland and *Triodia* hummock grassland mosaic on rolling hills in Central Australia. Aust J Bot 43:25–37

Bowman DMJS, Boggs GS, Prior LD (2008) Fire maintains an *Acacia aneura* shrubland—*Triodia* grassland mosaic in Central Australia. J Arid Environ 72:34–47

Bradstock RA (2010) A biogeographic model of fire regimes in Australia: contemporary and future implications. Glob Ecol Biogeogr 19:145–158

Bradstock RA, Cohn JS (2002) Fire regimes and biodiversity in semi-arid mallee ecosystems. In: Bradstock RA, Williams JE, Gill MA (eds) Flammable Australia: the fire regimes and biodiversity of a continent. Cambridge University Press, Cambridge, pp 238–258

Bradstock RA, Gill AM (1993) Fire in semi-arid mallee shrublands: size of flames from discrete fuel arrays and their role in the spread of fire. Int J Wildland Fire 3:3–12

Brandis AJ (2008) Rescuing the Rangelands: management strategies for restoration and conservation of the natural heritage of the Western Australian Rangelands after 150 years of pastoralism. Department of Environment and Conservation, Perth

Brim Box J, Nano CEM, McBurnie G, Waller DM, McConnell K, Brock C, Paltridge R, McGilvray A, Bubb A, Edwards GP (2016) The impact of feral camels (*Camelus dromedarius*) on woody vegetation in arid Australia. Rangel J 38:181–190

Brooks ML, D'Antonio CM, Richardson RM, Grace JB, Keeley JE, DiTomaso JM, Hobbs RJ, Pellant M, Pyke D (2004) Effects of invasive alien plants on fire regimes. Bioscience 54:677–688

Burnside D, Holm A, Payne A, Wilson G (1995) Reading the Rangeland: a guide to the Arid Shrublands of Western Australia. Department of Agriculture and Food, Western Australia

Burrows ND (2014) Potential for indigenous fire management in Central Australia to reduce greenhouse gas emissions and increase biosequestration. Report to the Department of Environment, Indigenous Carbon Farming Fund, Canberra, ACT

Burrows ND, Butler R (2016) A fire management plan for Matuwa (Lorna Glen) and Karara Karara (Earaheedy). Department of Parks and Wildlife Report, Perth, WA

Burrows ND, Christensen PES (1990) A survey of aboriginal fire patterns in the Western Desert of Australia. In: Nodvin SC, Thomas AW (eds) Fire and the environment: ecological and cultural perspectives, USDA Forests Service General Technical Report SE-69. Proceedings of an International symposium, Knoxville, Tennessee, pp 297–305

Burrows ND, Ward B, Robinson A (1991) Fire behaviour in spinifex fuels of the Gibson Desert Nature Reserve, Western Australia. J Arid Environ 20:189–204

Burrows ND, Burbidge AA, Fuller PJ, Behn G (2006) Evidence of altered fire regimes in the Western Desert region of Australia. Conserv Sci W Aust 5:272–284

Burrows ND, Ward B, Robinson A (2009) Fuel dynamics and fire spread in spinifex grasslands of the Western Desert. Proc R Soc Qld 115:69–76

Burrows N, Gill M, Sharples J (2016) A new fire spread model for spinifex grasslands. Paper presented at the 5th International fire behaviour and fuels conference, April 11–15, 2016, Melbourne, Australia

Callister KE, Griffioen PA, Avitabile SC, Haslem A, Kelly LT, Kenny SA, Nimmo DG, Farnsworth LM, Taylor RS, Watson SJ, Bennett AF, Clarke MF (2016) Historical maps from modern images: using remote sensing to model and map century-long vegetation change in a fire-prone region. PLoS One 11:e0150808

Cary GJ, Bradstock RA, Gill AM, Williams RJ (2012) Global change and fire regimes in Australia. CSIRO Publishing, Melbourne

Casson NE, Fox JED (1987) The post-fire regeneration responses of *Triodia wisena* and *T. basedowii*. Aust Rangel J 9:53–55

Clarke PJ, Latz PK, DE A (2005) Long-term changes in semi-arid vegetation: invasion of an exotic perennial grass has larger effects than rainfall variability. J Veg Sci 16:237–248

Clarke MF, Avitabile SC, Brown L, Callister KE, Haslem A, Holland GJ, Kelly LT, Kenny SA, Nimmo DG, Spence-Bailey LM, Taylor RS (2010) Ageing mallee eucalypt vegetation after fire: insights for successional trajectories in semi-arid mallee ecosystems. Aust J Bot 11:363–372

Clarke PJ, Lawes MJ, Murphy BP, Russell-Smith J, Nano CE, Bradstock R, Enright NJ, Fontaine JB, Gosper CR, Radford I, Midgley JJ (2015) A synthesis of postfire recovery traits of woody plants in Australian ecosystems. Sci Total Environ 534:31–42

Cohn JS, Bradstock RA (2000) Factors affecting post-fire seedling establishment of selected mallee understorey species. Aust J Bot 48:59–70

Cohn JS, Lunt ID, Ross KA, Bradstock RA (2011) How do slow growing, fire sensitive conifers survive in flammable eucalypt woodlands? J Veg Sci 22:425–435

Craig AB (1994) Aspects of post-fire regeneration in soft spinifex (*Triodia pungens*) communities near Newman, Western Australia. In: Australian Rangeland Society. 8th Biennial conference, Katherine, NT – working papers. Australian Rangeland Society, Perth, pp 47–50

Cruz MG, McCaw WL, Anderson WR, Gould JS (2013) Fire behaviour modelling in semi-arid mallee-heath shrublands of southern Australia. Environ Model Softw 40:21–34

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu Rev Ecol Syst 23:63–87

Dalgleish SA, van Etten EJB, Stock WD, Knuckey C (2015) Fuel dynamics and vegetation recovery after fire in a semiarid Australian shrubland. Int J Wildland Fire 24:613–623

Davis RA, Doherty TS, van Etten EJB, Radford JQ, Holmes F, Knuckey C, Davis BJ (2016) Conserving long unburnt vegetation is important for bird species, guilds and diversity: a case study in semi-arid shrublands. Biodivers Conserv 25:2709–2722

Doherty TS, Davis RA, van Etten EJB, Collier N, Krawiec J (2015) Response of a shrubland mammal and reptile community to a history of landscape-scale wildfire. Int J Wildland Fire 24:534–543

Doherty TD, van Etten EJB, Davis RA, Knuckey C, Radford JQ, Dalgleish SA (2017) Ecosystem responses to fire: incorporating data on birds, plants, mammals and reptiles to inform management strategies. Ecosystems 20:872–884

Driscoll DA, Henderson MK (2008) How many common reptile species are fire specialists? A replicated natural experiment highlights the predictive weakness of a fire succession model. Biol Conserv 141:460–471

Edwards GP, Allan GE, Brock C, Duguid A, Gabrys K, Vaarzon-Morel P (2008) Fire and its management in Central Australia. Rangel Jl 30:109–121

Edwards GP, Zeng B, Saalfeld WK, Vaarzon-Morel P (2010) Evaluation of the impacts of feral camels. Rangel Jl 32:43–54

Erickson TE, Barrett RL, Merritt DJ, Dixon KW (2016a) Pilbara seed Atlas & Field Guide: plant restoration in Australia's arid northwest. CSIRO Publishing, Melbourne

Erickson TE, Shackelford N, Dixon KW, Turner SR, Merritt DJ (2016b) Overcoming physiological dormancy in seeds of *Triodia* (Poaceae) to improve restoration in the arid zone. Restor Ecol 24:s64–s76

Eyre TJ, Wang J, Venz MF, Chilcott C, Whish G (2009) Buffel grass in Queensland's semi-arid woodlands: response to local and landscape scale variables, and relationship with grass, forb and reptile species. Rangel J 31:293–305

Fensham RJ, Powell O, Horne J (2011) Rail survey plans to remote sensing: vegetation change in the Mulga lands of eastern Australia and its implications for land use. Rangel J 33:229–238

Fox JED (1985). Fire in mulga – studies at the margins. In Ford JR (ed) Fire ecology and management of Western Australian ecosystems: proceedings of a symposium held in Perth, 10–11 May 1985. Western Australian Institute of Technology, Perth, pp 47–60

Fox JED (1986) Fire and its effects on Mulga (*Acacia aneura*) in Western Australia. In: Joss PJ, Lynch PW, Williams OB (eds) Rangelands: a resource under siege. Australian Academy of Science, Canberra, pp 45–46

Frank AS, Dickman CR, Wardle GM, Greenville AC (2013) Interactions of grazing history, cattle removal and time since rain drive divergent short-term responses by desert biota. PLoS One 8:e68466

Friedel M, Allan GE, Duguid A (2014) Do we know enough about vegetation dynamics to manage fire regimes in Central Australia? Ecol Manage Restor 15:128–132

Gill AM, Burrows ND, Bradstock RA (1995) Fire modeling and fire weather in an Australian desert. CALMSci Suppl 4:29–34

Gosper CR, Yates CJ, Prober SM (2012) Changes in plant species and functional composition with time since fire in two Mediterranean-climate plant communities. J Veg Sci 23:1071–1081

Gosper CR, Prober SM, Yates CJ (2013a) Multi-century changes in vegetation structure and fuel availability in fire-sensitive eucalypt woodlands. For Ecol Manag 310:102–109

Gosper CR, Yates CJ, Prober SM (2013b) Floristic diversity in fire-sensitive eucalypt woodlands shows a 'U'-shaped relationship with time since fire. J Appl Ecol 50:1187–1196

Gosper CR, Prober SM, Yates CJ, Wiehl G (2013c) Estimating the time since fire of long-unburnt *Eucalyptus salubris* (Myrtaceae) stands in the Great Western Woodlands. Aust J Bot 61:11–21

Gosper CR, Prober SM, Yates CJ (2016) Continental-scale syntheses of Australian pyromes – misclassification of south-western eucalypt woodlands misinforms management. J Biogeogr 43:858–861

Greenville AC, Dickman CR, Wardle GM, Letnic M (2009) The fire history of an arid grassland: the influence of antecedent rainfall and ENSO. Int J Wildland Fire 18:631–639

Griffin GF, Allan G (1984) Fire behaviour. In: Saxon EC (ed) Anticipating the inevitable: a patch-burn strategy for fire management at Uluru (Ayres Rock-Mt Olga) National Park. CSIRO Publishing, Melbourne, pp 55–68

Griffin GF, Price NF, Portlock HF (1983) Wildfires in Central Australia 1970– 1980. J Environ Manag 17:311–323

Grigg AM, Veneklaas EJ, Lambers H (2008) Water relations and mineral nutrition of Triodia grasses on desert dunes and interdunes. Aust J Bot 56:408–421

Groves RH (1994) Australian vegetation, 2nd edn. Cambridge University Press, Melbourne

Haslem A, Kelly LT, Nimmo DG, Watson SJ, Kenny SA, Taylor RS, Avitabile SC, Callister KE, Spence-Bailey LM, Clarke MF, Bennett AF (2011) Habitat or fuel? Implications of long-term, post-fire dynamics for the development of key resources for fauna and fire. J Appl Ecol 48:247–256

Haydon DT, Friar JK, Pianka ER (2000) Fire-driven dynamic mosaics in the great Victoria Desert, Australia. I. Fire geometry. Landsc Ecol 15:373–382

Hodgkinson KC (1998) Sprouting success of shrubs after fire: height-dependent relationships for different strategies. Oecologia 115:64–72

Hodgkinson KC (2002) Fire regimes in *Acacia* wooded landscapes: effects on functional processes and biological diversity. In: Bradstock RA, Williams JE, Gill MA (eds) Flammable Australia: the fire regimes and biodiversity of a continent. Cambridge University Press, Cambridge, pp 259–277

Hodgkinson KC, Griffin GF (1982) Adaptation of shrub species to fires in the arid zone. In: Barker WR, Greenslade PJM (eds) Evolution of the flora and flora of arid Australia. Peacock Publications, Frewville, pp 145–152

Holdo RM, Holt RD, Fryxell JM (2009) Grazers, browsers, and fire influence the extent and spatial pattern of tree cover in the Serengeti. Ecol Appl 19:95–109

Hurry CR, Walsh NG, Murphy DJ (2012) A taxonomic review of *Triodia bunicola* and *T. scariosa* (Poaceae: Chloridoideae), based on morphological and molecular data. Aust Syst Bot 25:304–312

Jacobs SWL (1984) Spinifex. In: Cogger HG, Cameron EE (eds) Arid Australia. Surrey Beatty & Sons, Chipping Norton, pp 131–142

James CD, Landsberg J, Morton SR (1999) Provision of watering points in the Australian arid zone: a review of effects on biota. J Arid Environ 41:87–121

Jones R (1969) Fire-stick farming. Aust Nat Hist 16:224–228

Keeley JE, Bond WJ, Bradstock RA, Pausas JG, Rundel PW (2012) Fire in Mediterranean ecosystems: ecology, evolution and management. Cambridge University Press, Cambridge

Kelly LT, Bennett AF, Clarke MF, McCarthy MA (2015) Optimal fire histories for biodiversity conservation. Conserv Biol 29:473–481

Kelso JK, Mellor D, Murphy ME, Milne GJ (2015) Techniques for evaluating wildfire simulators via the simulation of historical fires using the Australis simulator. Int J Wildland Fire 24:784–797

Kimber R (1983) Black lightning: aborigines and fire in Central Australia and the Western Desert. Archaeol Ocean 18:38–45

King KJ, Cary GJ, Bradstock RA, Marsden-Smedley JB (2013) Contrasting fire responses to climate and management: insights from two Australian ecosystems. Glob Chang Biol 19:1223–1235

Knuckey C, van Etten EJB, Doherty TS (2016) Effects of long-term fire exclusion and frequent fire on plant community composition: a case study from semi-arid shrublands. Austral Ecol 41:964–975

Ladbrook M (2015) Spatial and temporal patterns (1973–2012) of bushfire in an arid to semi-arid region of Western Australia. MSc thesis, Edith Cowan University, Australia. http://ro.ecu.edu.au/theses/1660

Langlands PR, Brennan K, Ward B (2012) Is the reassembly of an arid spider assemblage following fire deterministic? Austral Ecol 37:429–439

Latz P (1995) Fire in the desert: increasing biodiversity in the short term, decreasing it in the long term. In: Rose DB (ed) Country in flames: proceedings of the 1994 symposium on biodiversity and fire in North Australia. Department of the Environment, Sport and Territories, Canberra

Latz PK, Griffin GF (1978) Changes in aboriginal land management in relation to fire and to food. In: Hetzel BS, Frith HJ (eds) The nutrition of aborigines in relation to the ecosystem of Central Australia. CSIRO, Melbourne, pp 77–85

Lazarides M (1997) A revision of *Triodia* including *Plectrachne* (Poaceae, Eragrostideae, Triodiinae). Aust Syst Bot 10:381–489

Leavesley AJ, Cary GJ, Edwards GP, Gill AM (2010) The effect of fire on birds of Mulga woodland in arid Central Australia. Int J Wildland Fire 19:949–960

Letnic M (2004) Cattle grazing in a hummock grassland regenerating after fire: the short-term effects of cattle exclusion on vegetation in South-Western Queensland. Rangel J 26:34–48

Letnic M, Dickman CR (2005) The response of small mammals to patches regenerating after fire and rainfall in the Simpson Desert, Central Australia. Austral Ecol 30:24–39

Letnic M, Dickman CR, Tischler MK, Tamayo B, Beh C-L (2004) The responses of small mammals and lizards to post-fire succession and rainfall in arid Australia. J Arid Environ 59:85–114

Ludwig J, Tongway D, Hodgkinson K, Freudenberger D, Noble J (1996) Landscape ecology, function and management: principles from Australia's Rangelands. CSIRO Publishing, Melbourne

Lundie-Jenkins G (1993) Ecology of the rufous hare-wallaby, *Lagorchestes hirsutus* Gould (Marsupialia: Macropodidae) in the Tanami Desert, northern territory. I. Patterns of habitat use. Wildl Res 20:457–475

Lunt ID, Prober SM, Morgan JW (2012) How do fire regimes affect ecosystem structure, function and Diversity in grasslands and grassy woodlands of southern Australia. In: Bradstock RA, Williams JE, Gill MA (eds) Flammable Australia: fire regimes, biodiversity and ecosystems in a changing world. CSIRO Publishing, Melbourne, pp 253–270

Marshall VM, Lewis MM, Ostendorf B (2012) Buffel grass (*Cenchrus ciliaris*) as an invader and threat to biodiversity in arid environments: a review. J Arid Environ 78:1–12

Maslin BR, Reid JE (2012) A taxonomic revision of Mulga (*Acacia aneura* and its close relatives: Fabaceae) in Western Australia. Nuytsia 22:129–267

Masters P (1993) The effects of fire-driven succession and rainfall on small mammals in spinifex grassland at Uluru national park, northern territory. Wildl Res 20:803–813

Masters P (1996) The effects of fire driven succession on reptiles in spinifex grasslands at Uluru National Park, northern territory. Wildl Res 23:39–48

McCaw WL (1995) Predicting fire spread in western Australian mallee-heath. CALMSci Suppl 4:35–42

McDonald CJ, McPherson GR (2011) Fire behavior characteristics of buffelgrass-fueled fires and native plant community composition in invaded patches. J Arid Environ 75:1147–1154

Miller G, Friedel M, Adam P, Chewings V (2010) Ecological impacts of buffel grass (*Cenchrus ciliaris* L.) invasion in Central Australia – does field evidence support a fire-invasion feedback? Rangel J 32:353–365

Morton SR, Stafford Smith DM, Dickman CR, Dunkerley DL, Friedel MH, McAllister RRJ, Reid JRW, Roshier DA, Smith MA, Walsh FJ, Wardle GM, Watson IW, Westoby M (2011) A fresh framework for the ecology of arid Australia. J Arid Environ 75:313–329

Murphy BP, Bradstock RA, Boer MM, Carter J, Cary GJ, Cochrane MA, Fensham RJ, Russell-Smith J, Williamson GJ, Bowman DM (2013) Fire regimes of Australia: a pyrogeographic model system. J Biogeogr 40:1048–1058

Murphy BP, Edwards A, Meyer CP, Russell-Smith J (2015) Carbon accounting and savanna fire management. CSIRO Publishing, Melbourne

Myers B, Allan G, Bradstock RA, Dias L, Duff G, Jacklyn P, Landsberg J, Morrison J, Russell-Smith J, Williams R (2005) Fire management in the rangelands. Tropical Savannas CRC, Darwin

Nano CE, Clarke PJ (2008) Variegated desert vegetation: covariation of edaphic and fire variables provides a framework for understanding mulga–spinifex coexistence. Austral Ecol 33:848–862

Nano CE, Clarke PJ (2010) Woody–grass ratios in a grassy arid system are limited by multi-causal interactions of abiotic constraint, competition and fire. Oecologia 162:719–732

Nano CE, Clarke PJ (2011) How do drought and fire influence the patterns of resprouting in Australian deserts? Plant Ecol 212:2095–2110

Nano CEM, Bowland AE, Nano TJ, Raghu S, Pavey CR (2012a) Demographic hurdles to persistence in *Acacia peuce* (F. Muell.): effects of resources, fire and browsing on a threatened keystone tree species from arid Australia. J Arid Environ 80:17–26

Nano CEM, Clarke PJ, Pavey CR (2012b) Fire regimes in arid hummock grasslands and *Acacia* shrublands. In: Bradstock RA, Gill AM, Williams RJ (eds) Flammable Australia: fire regimes, biodiversity & ecosystems in a changing world. CSIRO Publishing, Melbourne, pp 195–214

Nimmo DG, Kelly LT, Spence-Bailey LM, Watson SJ, Haslem A, White JG, Clarke MF, Bennett AF (2012) Predicting the century-long post-fire responses of reptiles. Glob Ecol Biogeogr 21:1062–1073

Nimmo DG, Kelly LT, Farnsworth LM, Watson SJ, Bennett AF (2014) Why do some species have geographically varying responses to fire history? Ecography 37:805–813

Noble JC (1997) The delicate and noxious scrub: CSIRO studies on native tree and shrub proliferation in the semi-arid woodlands of eastern Australia. CSIRO, Canberra

O'Donnell AJ, Cullen LE, McCaw WL, Boer MM, Grierson PF (2010) Dendroecological potential of *Callitris preissii* for dating historical fires in semi-arid shrublands of southern Western Australia. Dendrochronologia 28:37–48

O'Donnell AJ, Boer MM, McCaw WL, Grierson PF (2011a) Vegetation and landscape connectivity control wildfire intervals in unmanaged semi-arid shrublands and woodlands in Australia. J Biogeogr 38:112–124

O'Donnell AJ, Boer MM, McCaw WL, Grierson PF (2011b) Climatic anomalies drive wildfire occurrence and extent in semi-arid shrublands and woodlands of Southwest Australia. Ecosphere 2:art127

O'Donnell AJ, Boer MM, McCaw WL, Grierson PF (2014) Scale-dependent thresholds in the dominant controls of wildfire size in semi-arid Southwest Australia. Ecosphere 5:art93

Olsson AD, Betancourt J, McClaran MP, Marsh SE (2012) Sonoran Desert ecosystem transformation by a C4 grass without the grass/fire cycle. Divers Distrib 18:10–21

Parr CL, Andersen AN (2006) Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. Conserv Biol 20:1610–1619

Parsons BC, Gosper CR (2011) Contemporary fire regimes in a fragmented and an unfragmented landscape: implications for vegetation structure and persistence of the fire-sensitive malleefowl. Int J Wildland Fire 20:184–194

Partridge TB (2008) Fire and fauna in Purnululu (Bungle Bungle) National Park, Kimberley, Western Australia. PhD thesis, Macquarie University, Australia

Pastro LA, Dickman CR, Letnic M (2011) Burning for biodiversity or burning biodiversity? Prescribed burn vs. wildfire impacts on plants, lizards, and mammals. Ecol Appl 21:3238–3253

Pausas JG, Bradstock RA (2007) Fire persistence traits of plants along a productivity and disturbance gradient in mediterranean shrublands of south-East Australia. Glob Ecol Biogeogr 16:330–340

Pausas JG, Fernández-Muñoz S (2012) Fire regime changes in the western Mediterranean Basin: from fuel-limited to drought-driven fire regime. Clim Chang 110:215–226

Pausas JG, Ribeiro E (2013) The global fire–productivity relationship. Glob Ecol Biogeogr 22:728–736

Pearson S, Hua Q, Allen K, Bowman DM (2011) Validating putatively cross-dated *Callitris* tree-ring chronologies using bomb-pulse radiocarbon analysis. Aust J Bot 59:7–17

Pianka ER (1996) Long-term changes in lizard assemblages in the Great Victoria Desert. In: Cody ML, Smallwood JA (eds) Long-term studies of vertebrate communities. Academic Press, New York, pp 191–201

Preece PB (1971) Contributions to the biology of Mulga. I.Flowering. Aust J Bot 19:21–38

Prior LD, McCaw WL, Grierson PF, Murphy BP, Bowman DM (2011) Population structures of the widespread Australian conifer *Callitris columellaris* are a bio-indicator of continental environmental change. For Ecol Manag 262:252–262

Prober SM, Wiehl G (2011) Resource heterogeneity and persistence of exotic annuals in long-ungrazed Mediterranean-climate woodlands. Biol Invasions 13:2009–2022

Prober SM, Thiele KR, Rundel PW, Yates CJ, Berry SL, Byrne M, Christidis L, Gosper CR, Grierson PF, Lemson K, Lyons T, Macfarlane C, O'Connor MH, Scott JK, Standish RJ, Stock WD, van Etten EJB, Wardell-Johnson GW, Watson A (2012) Facilitating adaptation of biodiversity to climate change: a conceptual framework applied to the world's largest Mediterranean-climate woodland. Clim Chang 110:227–248

Rangeland Natural Resource Management [NRM] (2013) Waru, kuka, mirrka wankarringu – lampaju (burning, bushfoods and biodiversity). Video (44 mins). https://www.youtube.com/watch?v=nKLD9LrySeU

Rice B, Westoby M (1999) Regeneration after fire in *Triodia* R.Br. Aust J Ecol 24:563–572

Russell-Smith J, Ryan PG, Klessa D, Waight G, Harwood R (1998) Fire frequency and fire-sensitive vegetation of the sandstone Arnhem plateau, monsoonal northern Australia: application of a remotely-sensed fire history. J Appl Ecol 35:829–846

Schlesinger C, White S, Muldoon S (2013) Spatial pattern and severity of fire in areas with and without buffel grass (*Cenchrus ciliaris*) and effects on native vegetation in Central Australia. Austral Ecol 38:831–840

Smith GT, Morton SR (1990) Response by scorpions to fire-initiated succession in arid Australian spinifex grasslands. J Arachnol 18:241–244

Stafford Smith DM (2008) The 'desert syndrome' – causally-linked factors that characterise outback Australia. Rangel J 30:3–14

Start AN (1986) Status and management of Mulga in the Pilbara region of Western Australia. In: Sattler (ed) The Mulga lands. Royal Society of Queensland, Brisbane, pp 136–138

Suijendorp H (1981) Responses of hummock grassland of northwestern Australia to fire. In: Gill AM (ed) Fire and the Australian biota. Australian Academy of Science, Canberra, pp 417–424

Taylor RS, Watson SJ, Nimmo DG, Kelly LT, Bennett AF, Clarke MF (2012) Landscape-scale effects of fire on bird assemblages: does pyrodiversity beget biodiversity? Divers Distrib 18:519–529

Thackway R, Cresswell ID (1997) A bioregional framework for planning the national system of protected areas in Australia. Nat Areas J 17:241–247

Turner D, Ostendorf B, Lewis M (2008) An introduction to patterns of fire in arid and semi-arid Australia, 1998–2004. Rangel J 30:95–107

Valone TJ, Kelt DA (1999) Fire and grazing in a shrub-invaded arid grassland community: independent or interactive ecological effects? J Arid Environ 42:15–28

van Etten EJ (1987) Environmental factors affecting the boundary between mulga (*Acacia aneura*) and hummock grassland (*Triodia* spp.) communities. MAppSc thesis, Curtin University of Technology, Australia

van Etten EJ (2009) Inter-annual rainfall variability of arid Australia: greater than elsewhere? Aust Geogr 40:109–120

van Etten EJB (2013) Changes to land tenure and pastoral lease ownership in Western Australia's central rangelands: implications for co-operative, landscape-scale management. Rangel J 35:37–46

van Etten EJB, Fox JED (2004) Vegetation classification and ordination of the central Hamersley ranges, Western Australia. J R Soc West Aust 87:63–79

van Langevelde F, van de Vijver CADM, Kumar L, van de Koppel J, de Ridder N, van Andel J, Skidmore AK, Hearne JW, Stroosnijder L, Bond WJ, Prins HHT, Rietkerk M (2003) Effects of fire and herbivory on the stability of savanna ecosystems. Ecology 84:337–350

van Leeuwen SJ, Start AN, Bromilow RB, Fuller PJ (1995) Fire and floristics of Mulga woodlands in the Hamersley Ranges, Western Australia. In: Page MJ, Beutel TS (eds) Ecological research and management in the Mulgalands. University of Queensland, Gatton College, pp 169–175

Ward BG, Bragg TB, Hayes BA (2014) Relationship between fire-return interval and Mulga (*Acacia aneura*) regeneration in the Gibson Desert and Gascoyne–Murchison regions of Western Australia. Int J Wildland Fire 23:394–402

Watson IW, Novelly PE (2012) Transitions across thresholds of vegetation states in the grazed rangelands of Western Australia. Rangel J 34:231–238

Watson SJ, Taylor RS, Nimmo DG, Kelly LT, Haslem A, Clarke MF, Bennett AF (2012) Effects of time since fire on birds: how informative are generalized fire response curves for conservation management? Ecol Appl 22:685–696

Wells G (1999) Biology and restoration ecology of spinifex grasses (*Plectrachne* and *Triodia* spp.) with special reference to the Argyle diamond mines (Western Australia). PhD thesis, University of Western Australia, Australia

Westoby M, Rice B, Griffin G, Friedel M (1988) The soil seed bank of *Triodia basedowii* in relation to time since fire. Aust J Ecol 13:161–169

Williams J (2002) Fire regimes and their impacts in the Mulga (*Acacia aneura*) landscapes of Central Australia. Unpublished report to Department of the Environment and Heritage, Canberra

Williams PR, Collins EM, Blackman M, Blackman C, McLeod J, Felderhof L, Colless L, Masters K, Coates S, Sturgess A, Martin G (2015) The influence of ignition technique on fire behaviour in spinifex open woodland in semiarid northern Australia. Int J Wildland Fire 17:607–612

Wilson AD, Hodgkinson KC, Noble JC (1988) Vegetation attributes and their application to the management of Australian rangelands. In: Tullier PT (ed) Vegetation science applications for rangeland analysis and management. Springer, Dordrecht, pp 253–294

Woinarski JCZ (1999) Fire and Australian birds: a review. In: Gill AM, Woinarski JCZ, York A (eds) Australia's biodiversity: responses to fire. Department of Environment and Heritage, Canberra, pp 56–101

Woinarski JC, Burbidge AA, Harrison PL (2015) Ongoing unraveling of a continental fauna: decline and extinction of Australian mammals since European settlement. Proc Natl Acad Sci 112:4531–4540

Wright BR, Clarke PJ (2007a) Fire regime (recency, interval and season) changes the composition of spinifex (*Triodia* spp.)-dominated desert dunes. Aust J Bot 55:709–724

Wright BR, Clarke PJ (2007b) Resprouting responses of *Acacia* shrubs in the Western Desert of Australia – fire severity, interval and season influence survival. Int J Wildland Fire 16:317–323

Wright BR, Clarke PJ (2009) Fire, aridity and seed banks. What does seed bank composition reveal about community processes in fire-prone desert? J Veg Sci 20:663–674

Wright BR, Zuur AF, Chan GC (2014) Proximate causes and possible adaptive functions of mast seeding and barren flower shows in spinifex grasses (*Triodia* spp.) in arid regions of Australia. Rangel J 36:297–308

Yates CJ, Hobbs RJ, Atkins L (2000) Establishment of perennial shrub and tree species in degraded *Eucalyptus salmonophloia* (salmon gum) remnant woodlands: effects of restoration treatments. Restor Ecol 8:135–143

Young L, Schlesinger C (2015) Habitat use and behaviour of birds in areas invaded by buffel grass (*Cenchrus ciliaris* L.) and in restored habitat. Wildl Res 41:379–394

Archaeology and Rock Art of the North-West Arid Zone with a Focus on Animals

Peter Veth, Jo McDonald, and Sarah de Koning

Introduction

In this paper we will focus on the Indigenous archaeology and rock art of the north-west arid zone of Western Australia. This includes the Little Sandy and Great Sandy Deserts (Western Desert) and the Pilbara uplands and arid coastline and archipelagos (Fig. 1). Remarkably, within just the last 5 years, some of the oldest and most comprehensive evidence has emerged for early occupation of Australia's deserts, including the use of dietary marine resources and production of figurative art (McDonald 2016; Veth et al. 2017a, b; Wood et al. 2016). We provide these new understandings of the art and archaeology of the north-west arid zone from the key sites of Lake Gregory (*Parnkupirti*), the Canning Stock Route (*Kaalpi*), the Dampier Archipelago (*Murujuga*) and Barrow Island. Initial occupation of the desert has been extended back to 50 ka, and we now have a better understanding of the fluctuations in arid zone occupation through the Holocene. Following a 15-year recording programme, Western Desert rock art provinces can now be contrasted with those from the Pilbara and specifically the Dampier Archipelago. We have previously provided a framework for major changes in art production as part of hunter-gatherer responses to climate change in the arid north-west (McDonald and Veth 2013a). Here we focus on the importance of desert fauna to people's subsistence and social strategies and describe how these have been depicted in art through time.

The figurative component of the extensive engraved and pigment art bodies recorded include endemic fauna, sometimes introduced (post-contact) fauna such as horses as well as combinations of human and animal forms – known as therianthropic figures. The classes of fauna depicted on the current coastline predictably

---

P. Veth (✉) · J. McDonald · S. de Koning
Centre for Rock Art Research and Management, M257 Archaeology, School of Social Sciences, Faculty of Arts, Business, Law and Education, The University of Western Australia, Crawley (Perth), WA, Australia
e-mail: peter.veth@uwa.edu.au

H. Lambers (ed.), *On the Ecology of Australia's Arid Zone*,
https://doi.org/10.1007/978-3-319-93943-8_11

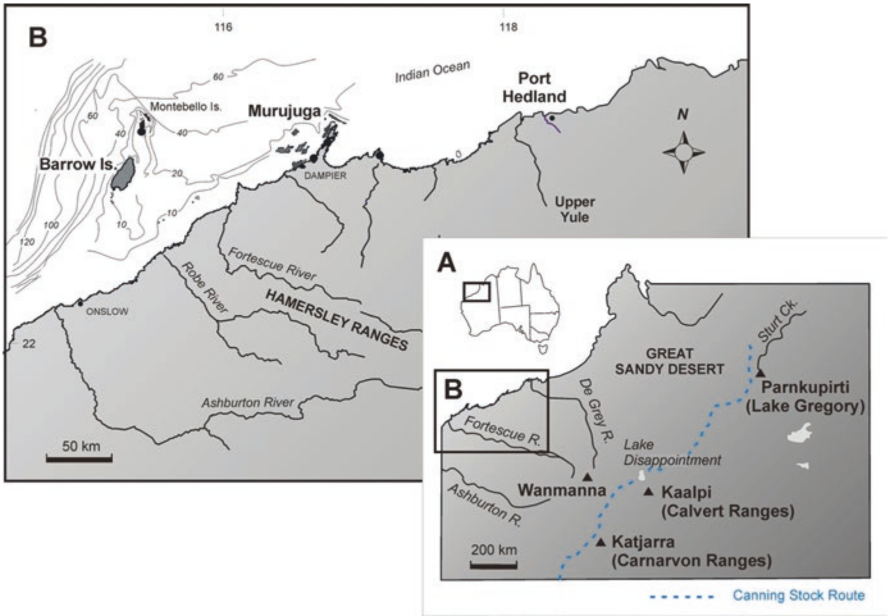


Fig. 1 Study areas within the north-west arid zone of Western Australia (Peter Veth)

reflect marine resources of the Indian Ocean, while hinterland assemblages depict faunal suites adapted to interior desert and xeric vegetation landscapes. Where more detailed analyses have been completed (e.g. *Murujuga*), we can illustrate that different species are being depicted in the art and that there are changes in species composition through time. While absolute dating of rock art is still nascent, multiphase models predict at least a terminal Pleistocene age (approx. 20,000 BP) for some of these figurative repertoire (McDonald 2015, 2016; McDonald and Veth 2013a; Mulvaney 2013). Changes in the dominant species depicted over time are likely due to shifts in precipitation and vegetation, the loss of coastal plains with sea-level rise and the extinction of species such as the thylacine. Perhaps less well known to the natural science community is the inherently dynamic archaeological record of Australian desert hunter-gatherers, whereby not only do settlement and mobility patterns change, but the rock art shows significant changes in style, theme, subjects and key fauna through time (Veth 2006; McDonald 2016).

50,000 Years of Aboriginal Occupation of the Western Australian Arid Zone

Sitting at the top of the Canning Stock Route, Lake Gregory (*Parnkupirti*) represents the discharge of a large coordinated drainage system into the arid zone from the south-east Kimberley. Positioned within the vast linear sand dunes of the Great

Sandy Desert, this wide and shallow basin was up to ten times larger when first occupied by people. Excavations along the palaeo-shoreline of *Parnkupirti* exposed a sequence of artefacts from an earlier pluvial phase extending back to 45–50 ka. When this was a mega-lake, it was likely full of fish, shellfish and water birds and surrounded by grazing macropods (Veth et al. 2009a). At the southern end of the Canning Stock Route, Serpent's Glen (*Karnatukul*) also demonstrates 50,000 years of occupation (McDonald et al. 2018), with changing artefact production and multiple phases of ochre use from different units. People were still using this shelter in the contact period, as documented by glass artefacts in the deposit and the use of pencil to outline earlier rock art motifs (O'Connor et al. 1998). This site is also part of an important ethnographic complex, indeed of such significance that the Birriliburu Native Title determination was held at this site with the Federal Court in 2008. This is the oldest known site for the Western Desert and one of the earliest for desert hunter-gatherers globally (Veth 2005). The most recent phase of pigment art here has been dated by plasma-oxidation pretreatment AMS, and this has provided a clear picture of art phases being produced in the millennium before contact (McDonald et al. 2014, 2018). Episodic and increasing use of this landscape through the mid- to late Holocene is documented both in the archaeology and rock art production (McDonald 2016; Veth et al. 2007, 2009).

There are now a number of Pilbara sites that record occupation from at least 45 ka – with ebbs and pulses in habitation coupled to climatic variations (Morse and Ryan 2009; Slack 2015). Across the North West Shelf, excavations at the Montebello and Barrow Islands have revealed an ancient and continuing reliance on marine resources including mangrove and rocky foreshore gastropods, Baler shell as well as terrestrial arid zone fauna, beginning from as early as 51.1 to 46.2 ka (Veth et al. 2007, 2014, 2017a, b). Occupation continues until 6.8 ka when the islands are cut off by rising waters, and then they are abandoned. The weakening of the Indonesian-Australian monsoon before the Last Glacial Maximum and then amelioration with rising sea levels (Field et al. 2017) by 14 ka with the re-initiation of the monsoon, and then islandisation by c. 7 ka, marks an evolving landscape with changing faunal compositions. Island assemblages show that marine and arid terrestrial faunal suites expand from between approximately 12 ka and 7 ka, when evidence for turtle, shark, porpoise, pelagic fish as well as over 40 species of dietary shellfish and tusk shellfish (*Dentalium*) beads are registered (Veth et al. 2017b). Located on the same plains as the Dampier Archipelago, the limestone caves and shelters here lack art. However, these have well-preserved remains of the same fauna as depicted in the rock art 100 km to the east (Fig. 1).

The Dampier Archipelago (*Murujuga* as it is known to its traditional custodians) juts into the Indian Ocean on the Pilbara coast. For much of human history, the jagged scree slopes would have represented interior uplands of the Abydos Plains between the Pleistocene-aged coastline and Pilbara uplands. Excavations on the outer islands (McDonald and Berry 2016) indicate a staggered loss of some terrestrial fauna and introduction of other marine elements (de Koning 2014). Ongoing excavations of a large rock shelter and several large midden and occupation sites on the Burrup Peninsula (McDonald field notes 2016; Lorblanchet 1983; Clune 2002) indicate occupation before the Last Glacial Maximum and then repeated occupations until contact with European pastoralists, whalers and pearlers.

Rock Art Traditions of the North West: Between the Desert and the Sea

Systematic surveys for rock art along the Canning Stock Route through the Great Sandy and Little Sandy Deserts have identified an early and extensive desert art province with geometric, track and simple figurative engravings followed by multiple phases of engraved and pigment art production with varying proportions of geometrics and figurative motifs (McDonald 2005, 2016; McDonald and Veth 2006a, b, 2012, 2013a). Within the most recent pigment phases, snakes are a common motif: this is *Jila* (water python) country where rainmaking and regeneration ceremonies accompany visits to named water sources, including mound springs, cisterns and rock holes (McDonald and Veth 2013b).

In the centre of the Canning Stock Route, ancient and continuing figurative art production can be found at the Carnarvon (*Katjarra*), Durba (*Jilakurru*) and Calvert (*Kaalpi*) Ranges as well as many other smaller sandstone outliers. Many of the more recent phases of art production include depictions of animals. The oldest art, which is difficult to date by chronometric techniques and which is dated through relative superimposition sequences, includes a large number of animal tracks, mainly bird (Fig. 2) and macropod, but also insects, such as centipedes, lizards and occasional human tracks. They are generally produced on horizontal panels, reflecting their 'natural' position in the landscape. These early tracks are found amongst a largely geometric repertoire. Occasionally, human faces, made up of arrangements of circles and arcs, are depicted. These motifs are always heavily patinated and geologically altered.

Different rock art phases in the Western Desert have diagnostic graphics (McDonald 2016) and represent behavioural systems, which are argued to be coupled with environmental changes. Significant changes in climate of importance to hunter-gatherers include pluvial conditions at the time of assumed colonisation (Veth et al. 2009), increasing aridity from 30 ka and especially during the Last Glacial Maximum between 22 and 18 ka (McDonald 2016; Veth et al. 2016a), and climatic amelioration by 14 ka, with warmer and then wetter conditions by the early Holocene (Reeves et al. 2013; Williams et al. 2015). Intensification of the El Nino Southern Oscillation 4–2 ka may have introduced stress to economic systems, while current conditions have prevailed since approximately 1.5 ka.

Desert hunter-gatherers are highly adaptable and will often alter their mobility to offset local and even regional resource stress (Veth 1993; Williams et al. 2015). Rock art is viewed as a way of socially mediating significant changes in environment and climate by signalling changing group cohesion, identity and boundary conditions (McDonald and Veth 2013a). Large-scale group-identifying behaviour may be shown through the depiction of geometric motifs such as concentric circles,

Fig. 2 Bush turkey tracks from *Kaalpi*, Western Desert. (Photo by Jo McDonald)

which represent both water sources and totemic sites – with imagery, which is understood – and which links groups over very large distances (McDonald and Veth 2012). Art produced in more fertile conditions – when groups become more territorially tethered to identified homelands – sees the development of figurative repertoires where human and animal motifs (Fig. 3) contain very high levels of social information in body design, headdress morphology and so forth (McDonald 2005, 2016). Animal depictions occupy an intriguing place in that they can represent prey, Ancestral Beings from the Dreaming, totems and regeneration sites (known in the West Pilbara as *Thalu*). They are also semiotic – depicted through their tracks – or shown with species-specific detail or more schematically (Fig. 4). The amount of information encoded in these different types of depictions can provide significant insight into the artists who produced them (Davidson 2018).

There are many shared elements amongst the rock art bodies between the Pilbara and Western Desert, and cultural connections are evidenced in both early and more recent phase art. Some early art, such as the archaic faces and climbing man motifs of *Murujuga*, reveal long-distance stylistic connections in deep time – far into the desert. Shared Dreaming narratives in the recent past such as the Two Lizard Men (*Wati Kutjarra*) and Seven Sisters (*Minyiburu*) demonstrate the chains of social connection (McDonald and Veth 2013a). The rock art of the Pilbara shows more distinct boundary-making behaviour, consistent with the presence of distinct language boundaries across this highly dissected arid landscape. This sits in contrast to the relatively homogeneous art of the desert – where social groups are represented by different dialect groups of the one language (McDonald and Veth 2013a; Tindale 1974; Wright 1968). The arid zone model, which integrates palaeoclimate, occupa-

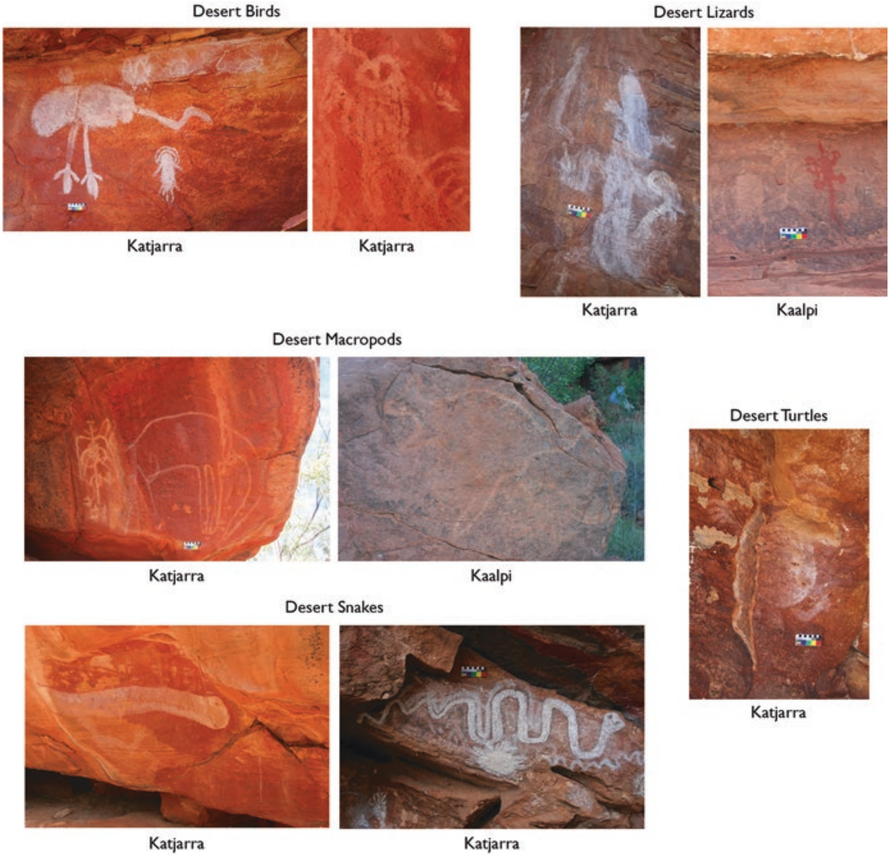


Fig. 3 Representations of desert animals – paintings and engravings from the Western Desert. (Photos by Jo McDonald)

tion and rock art phases from these different arid landscapes (McDonald and Veth 2006a, b, 2013a; McDonald 2016), can also be applied to the coastal Pilbara: although here there is considerable overprinting by coastal economies, which have been in place since 7 ka after stabilisation of sea levels (McDonald 2015). While some art phases are shared between the *Murujuga* and Pilbara art bodies, there are also some noticeable differences, such as the low number of early cupules in the former (Mulvaney 2013).

The 42 islands of the Dampier Archipelago host one of the world's largest concentrations of engravings estimated at greater than 1 M+ motifs. The National Heritage Listed Place (McDonald and Veth 2009) has at least seven art-style phases defined by the superimposition sequence (McDonald 2015; Mulvaney 2013, 2014) on highly resistant granophyre boulders (Pillans and Fifield 2013). In this locale, there is a clear transition from terrestrial fauna in the earliest assemblages to the most recent art having distinctively maritime themes (see discussion, below).

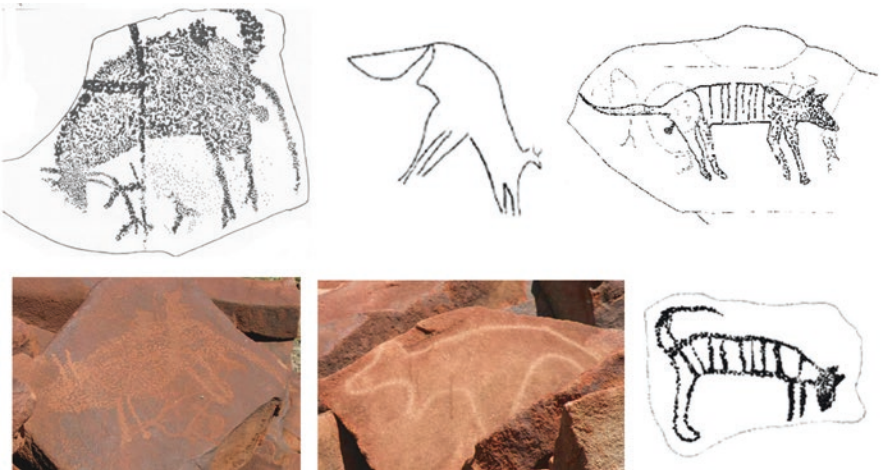


Fig. 4 Infilled and simple outline of macropod and thylacine engravings (*Murujuga*) (Jo McDonald, Michel Lorblanchet and Ken Mulvaney)

The softer calcarenite ridges of Port Hedland also house a major rock art province. This is a rich figurative assemblage of largely geometric engravings – but distinguished by depictions of Ancestral Beings, marine and terrestrial fauna and distinct shields and artefacts with desert designs. A recent research project has surveyed several major assemblages and provides high-quality data on faunal depictions within a maritime-desert setting (Harper 2016; McCarthy 1962). Unlike *Murujuga*, all of this art appears to post-date sea-level rise and stabilisation.

Subjects depicted across the Pilbara include multiple phases of engraved and painted macropods, lizards, snakes, water birds, tortoise, echidna, moles, quoll, bandicoot and the dingo (Fig. 5). Several of the art provinces have thylacine depictions (Fig. 6), and there are a number of provinces, which have remarkable therianthropes.

Analysis of Fauna from Rock Art Assemblages in the North-West Arid Zone and Proposed Style Phase Model

Where the desert meets the sea – at both *Murujuga* and Port Hedland – a cornucopia of marine fauna are depicted including whale, dugong, shark, turtle, pelagic fish, crab, crayfish and stingrays. There are also many depictions of humans in social/hunting scenes. Some of the associated material culture items depicted, and a variety of faunal depictions, have never been described in archaeological contexts from the Australian arid zone. Rock art assemblages from across the Pilbara and desert (see Fig. 7) include naturalistic animal depictions and animal tracks as a significant component. The proportional frequency of animals and their tracks range from 28%

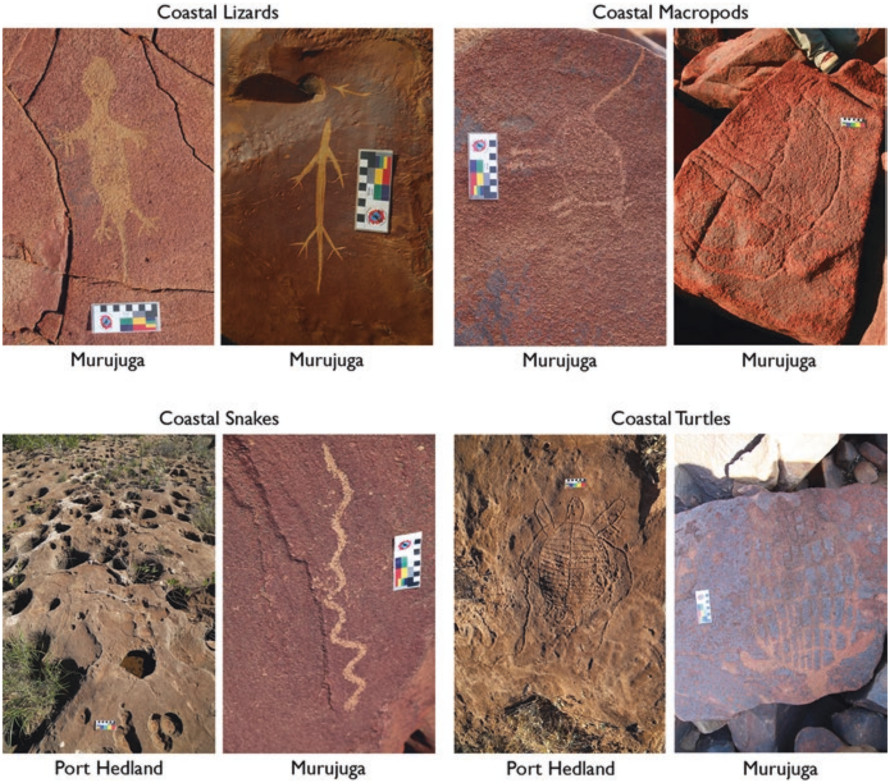


Fig. 5 Depictions of lizards, macropods, snakes and turtles from Murujuga and Port Hedland. (Photos by Jo McDonald and Sam Harper)

on the Pilbara coast and the Canning Stock Route and up to 45% in the Pilbara uplands (albeit from smaller assemblages). While there is a strong geometric presence, the zoomorphic depictions (ranging from 6% to 17%), when combined with human depictions, represent a significant figurative tradition amongst the western rangelands and arid coastline of north-western Australia. This has not generally been appreciated for the Australian arid zone.

X Axis Are Rock Art Study Areas

Western Desert rock art phases (Fig. 8), with projected age ranges (based on archaeological signatures), and behavioural correlates have been proposed (McDonald and Veth 2013a). These phases provide a chronological framework for diagnostic animal graphics and faunal depictions amongst these different styles. These are modelled ages which will certainly change with ongoing excavation and future direct dating programmes on the art.

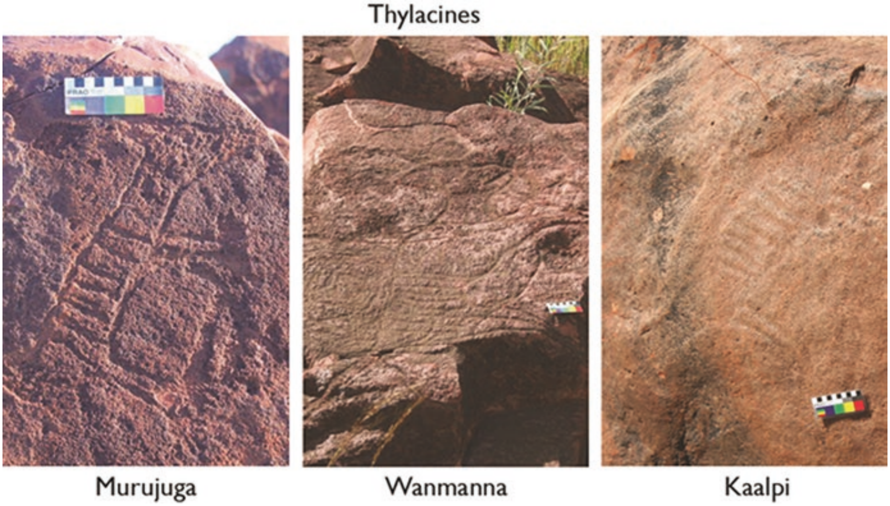


Fig. 6 Depictions of thylacine motifs from the Pilbara and Western Desert. (Photos by Jo McDonald)

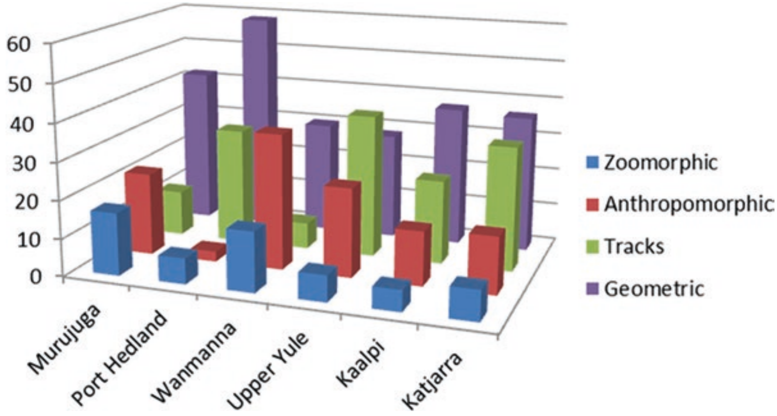
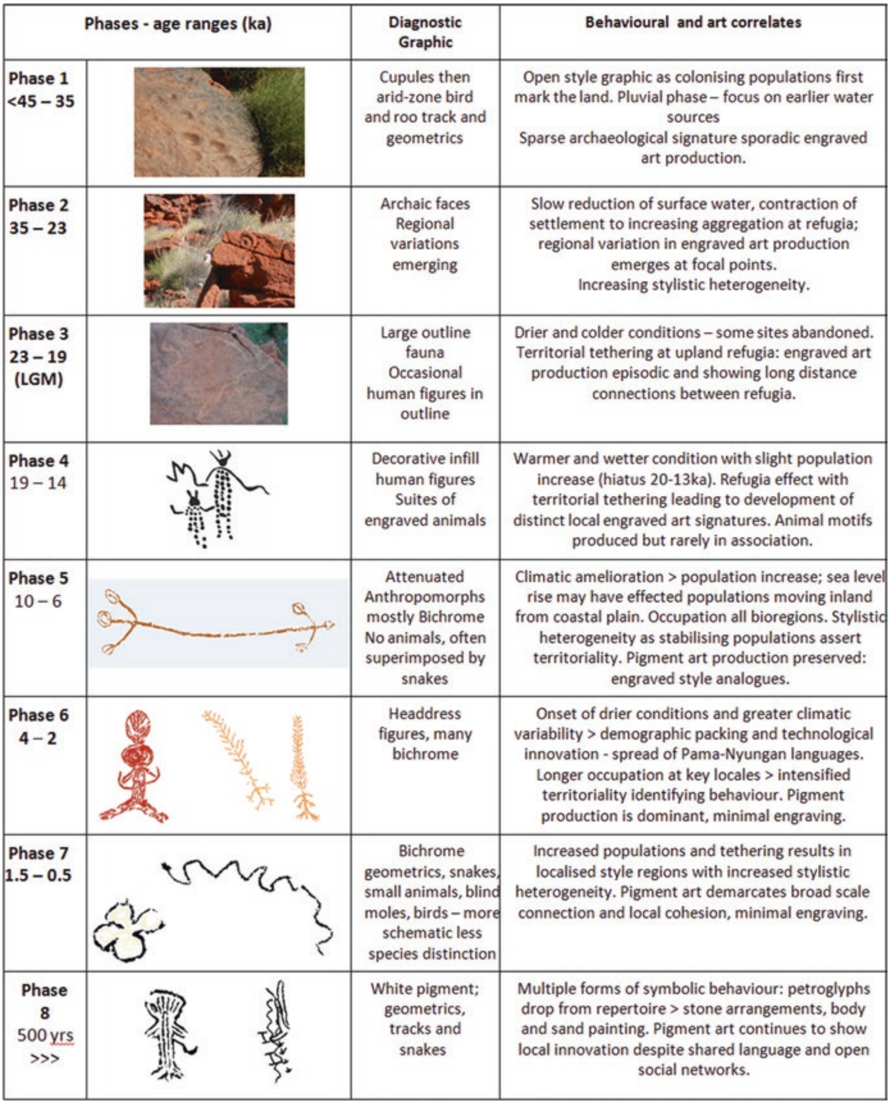


Fig. 7 Arid zone rock art by area and theme, showing variability between four broad categories. (Jo McDonald field data, Upper Yule from Wright 1968)



Phases - age ranges (ka)		Diagnostic Graphic	Behavioural and art correlates
Phase 1 **<45 – 35**		Cupules then arid-zone bird and roo track and geometrics	Open style graphic as colonising populations first mark the land. Pluvial phase – focus on earlier water sources Sparse archaeological signature sporadic engraved art production.
Phase 2 **35 – 23**		Archaic faces Regional variations emerging	Slow reduction of surface water, contraction of settlement to increasing aggregation at refugia; regional variation in engraved art production emerges at focal points. Increasing stylistic heterogeneity.
Phase 3 **23 – 19** **(LGM)**		Large outline fauna Occasional human figures in outline	Drier and colder conditions – some sites abandoned. Territorial tethering at upland refugia: engraved art production episodic and showing long distance connections between refugia.
Phase 4 19 – 14		Decorative infill human figures Suites of engraved animals	Warmer and wetter condition with slight population increase (hiatus 20-13ka). Refugia effect with territorial tethering leading to development of distinct local engraved art signatures. Animal motifs produced but rarely in association.
Phase 5 10 – 6		Attenuated Anthropomorphs mostly Bichrome No animals, often superimposed by snakes	Climatic amelioration > population increase; sea level rise may have effected populations moving inland from coastal plain. Occupation all bioregions. Stylistic heterogeneity as stabilising populations assert territoriality. Pigment art production preserved: engraved style analogues.
Phase 6 **4 – 2**		Headdress figures, many bichrome	Onset of drier conditions and greater climatic variability > demographic packing and technological innovation - spread of Pama-Nyungan languages. Longer occupation at key locales > intensified territoriality identifying behaviour. Pigment production is dominant, minimal engraving.
Phase 7 **1.5 – 0.5**		Bichrome geometrics, snakes, small animals, blind moles, birds – more schematic less species distinction	Increased populations and tethering results in localised style regions with increased stylistic heterogeneity. Pigment art demarcates broad scale connection and local cohesion, minimal engraving.
Phase **8** 500 yrs >>>		White pigment; geometrics, tracks and snakes	Multiple forms of symbolic behaviour: petroglyphs drop from repertoire > stone arrangements, body and sand painting. Pigment art continues to show local innovation despite shared language and open social networks.

Fig. 8 Western Desert art phases, with modelled age ranges, diagnostic animal graphics and behavioural correlates (Adapted from McDonald and Veth 2013a); *LGM* Last Glacial Maximum

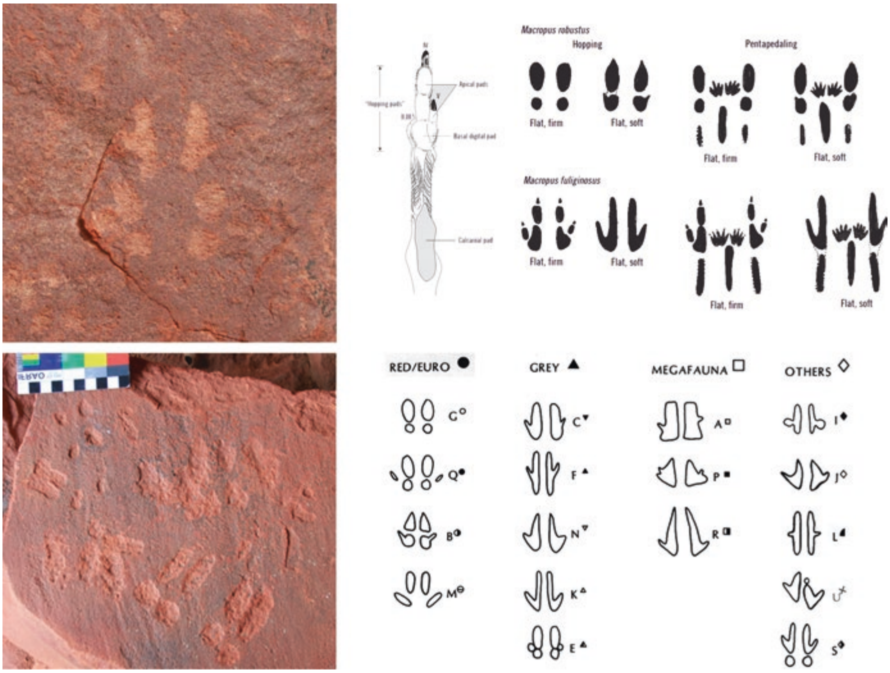


Fig. 9 Examples of Western Desert macropod tracks (right, photographs by Jo McDonald) with zoological foot shape, different gaits and some variety found in arid zone NSW engraved macropod tracks (left, from McDonald 1993)

The earliest arid zone style (Phase 1, in Fig. 8), comprising engraved tracks of various macropods, reptiles and birds, is part of a pan-Australian arid zone tradition (Maynard 1979; McDonald 1993, 2016). This early art production shows long-range connections across vast tracts of country – and also illustrates the detailed knowledge by early settlers of the desert of the different species of kangaroos. McDonald's early work in western New South Wales demonstrated that the key macropod species at the site were being depicted by artists – and that this accounted for much of the stylistic variability (McDonald 1993). It was also found that many of the tracks were narratives of macropod tracking and hunting – with different gaits (such as hopping, feeding, resting) often shown (Fig. 9).

A shift towards simple engraved outline fauna is modelled to occur during the Last Glacial Maximum and includes macropods, large snakes, large birds (probably emu) and reptiles. Post-Last Glacial Maximum engraved decorative infill figures are accompanied by a limited animal repertoire of snakes, lizards, quadrupeds and striped animals (dasyurids, bandicoot and thylacine) (Fig. 6). Later phases include pigment art, with a small number of engraved motifs being produced in the same styles (McDonald et al. 2014). This more recent art includes depictions of bush turkey (bustard), water birds, lizards, macropods and small quadrupeds. The pigment art produced in the last 1500 years, when climatic conditions approximate the present, includes depictions of snakes, moles, bandicoot, large water birds and reptiles sometimes in therianthropic form and described as Ancestral Beings (in the desert this art is created in thick white pigment and lacks some of the diagnostic detail of earlier phases).

The types of fauna depicted illustrate clear differences in ecology and also the time spans represented by these art bodies (Table 1). The *Murujuga* faunal depictions potentially extend back to 40 ka and cover the transition from arid plains to islands (McDonald 2015; Mulvaney 2014). This art has many examples, and in relatively equal numbers, of birds and bird tracks (29.8%, *N* = 1260) and macropods and their tracks (23.5%, *N* = 997) and then turtles (15.5%, *N* = 659) and fish (10.6%, *N* = 448). In contrast, the Western Desert site of *Kaalpi* is dominated by birds and their tracks (61%, *N* = 723). Macropods and tracks (15.1%, *N* = 176) and snakes (13.8%, *N* = 161) are the next most common, followed by a range of quadrupeds (5%, *N* = 58). The post sea-level stabilisation assemblage at Port Hedland is dominated by turtles, fish, stingray and other marine species (66.0%, *N* = 375). Snakes (8.6%, *N* = 49) and lizards (2.5%, *N* = 14) are relatively minor components, with birds present in very low numbers (0.7%, *N* = 4) and *no* macropods recorded within this sample.

Tracks and geometric motifs dominate arid zone art provinces, demonstrating the continuity of the earliest arid zone graphic traditions through time, as noted by many researchers (McDonald and Veth 2010, 2013a; Rosenfeld 1993; Smith et al. 2008). However, when one examines the details by location, it is apparent that there is not only discontinuity, both across space and through time, in motif preferences, but where motifs persist, there are other stylistic indicators illustrating changing modes of production. Tracks (mostly bird and macropod) and geometric motifs predominate within the Western Desert provinces; however, zoomorphic motifs, cupules and abraded grooves are completely absent from *Katjarra*. Conversely, tracks generally seem to be less important at *Murujuga* and *Wanmanna*, while zoomorphic motifs are present in higher proportions in both of these complexes, compared with both Port Hedland and the Western Desert sites.

In those provinces where there is pigment art production after the engraved traditions, distinct changes are witnessed through time. There are much higher proportions of geometric motifs being produced using pigment. Zoomorphs – which occur more rarely in the most engraved art phases– contribute to much greater proportions in the pigment art repertoires of the Western Desert (McDonald 2016). Interestingly, zoomorphic motif types also change from large terrestrial mammals and birds in the earlier engraved phases to include smaller mammals, snakes and a range of reptiles during the pigment phases.

Table 1 Terrestrial, avian and marine fauna by study areas: Pilbara coast (*Murujuga* and Port Hedland), Pilbara uplands (*Wanmanna* and Upper Yule) and Western Desert (*Kaalpi* and *Katjarra*)

	Dampier Archipelago		Port Hedland		Wanmanna		Upper Yule		Kaalpi		Katjarra	
	n	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
Animal part	282	*6.7*	96	*16.9*								
Bird	350	*8.3*	4	*0.7*	18	*20.5*	24	*11.4*	18		4	*1.2*
Bird track	910	*21.5*			18	*20.5*			705	*60.6*	105	*31.3*
Crustacean	8	*0.2*	5	*0.9*								
Dugong	18	*0.4*	1	*0.2*								
Fish	448	*10.6*	53	*9.3*								
Lizard	137	*3.2*	14	*2.5*	5	*5.7*	56	*26.7*	19	*1.6*	10	*3.0*
Macropod	482	*11.4*			34	*38.6*	30	*14.3*	15	*1.3*	2	*0.6*
Macropod track	515	*12.1*			6	*6.8*			161	*13.8*	146	*43.6*
Marine other	51	*1.2*	106	*18.7*								
Quadruped	202	*4.8*	1	*0.2*	4	*4.5*	14	*6.7*	58	*5.0*		
Snake	48	*1.1*	49	*8.6*			51	*24.3*	164	*14.1*	52	*15.5*
Stingray	29	*0.7*	99	*17.4*								
Thylacine	5	*0.1*			2	*2.3*			2			
Terrestrial other	65	*1.5*	33	*5.8*			27	*12.9*			1	*0.3*
Track unknown	31	*0.7*							49	*4.2*	2	*0.6*
Turtle	619	*14.6*	117	*20.6*	1	*1.1*	8	*3.8*	2	*0.2*	12	*3.6*
Turtle Trail	40	*0.9*										
Total	4240	*100.0*	568	*100.0*	88	*100.0*	210	*100.0*	1164	*100.0*	335	*100.0*

Murujuga Case Studies: Fauna of the Maritime Deserts of the North West

Recent analyses have demonstrated that the prehistoric Murujuga artists distinguished between the different species they were depicting in the art. Both macropods and turtles have been found to show species-specific traits – and to demonstrate changing foci and styles of production through time (de Koning 2014; Stewart 2016).

Turtles

Six sea turtle species (Australian flatback, green, hawksbill, leatherback, loggerhead, olive ridley) inhabit the waters around the islands of the Dampier Archipelago, where there are significant nesting rookeries. There is also one species of freshwater turtle (flat-shelled turtle). Using a zoological approach to create qualitative types for each species, de Koning (2014) has determined that species-level identification is possible from a large sample of engraved turtle motifs. More than half of a sample of 823 engravings from 40 sites could be identified to species (Fig. 10). Quantitative and qualitative characteristics were identified, some of which are used by zoologists in species description of this animal (Perrine 2003); however, the main criteria used by Western science are scute pattern and flipper shape. Other variables – such as body ratios – were equally effective in the archaeological analyses, and it is these characteristics which seem to have been deployed by Indigenous artists. There is morphological precision in the way these engravings were created, and it is suggested that these stylistic choices are a deliberate decision on behalf of the artist to represent the multiple species (de Koning 2014).

While the art of the Dampier Archipelago has not yet been directly dated (Mulvaney 2011; Pillans and Fifield 2013), a stylistic chronology which uses contrast state (a relative measure of weathering of the petroglyphs: Mulvaney 2014) and superimposition analysis has provided the general framework from which we understand how art production has changed through time (Fig. 11). This sequence commences during the Pleistocene, progresses through the insulation of the islands and formation of the Archipelago and continues up until European contact. A cornerstone of this sequence has been the observation that the earliest art includes terrestrial species (such as the emu), while the more recent art demonstrates a focus on maritime subjects (Mulvaney 2010, 2014; McDonald 2015; McDonald and Veth 2009). Some earlier faunal depictions, of large kangaroos and emu, almost certainly date to when the islands were landlocked during periods of lower sea levels when these range fauna were extant; today these larger species do not occur on any of the Pilbara islands.

De Koning's (2014) study demonstrated that almost 20% of the analysed turtle motifs fell within the oldest contrast states (i.e. contrast states 1 and 2). This would imply that turtles were already a part of the socioeconomic life across this art prov-

Fig. 10 Examples of the qualitatively distinctive species in the Murujuga rock art – turtles. (Source: de Koning 2014; CRAR+M Database)

ince during the terminal Pleistocene-early Holocene, when the islands were part of an inland range lying some distance from the sea (Ward et al. 2013). It is worth noting that the outer islands of the archipelago were proximal to the coastline by approximately 10 ka (McDonald and Berry 2016). Given the importance of coastal lifeways within Australia, the early maritime competencies demonstrated by the Pleistocene occupants of Barrow Island (around 100 kilometres to the west: Veth et al. 2014, 2016a, b) and the high mobility of arid zone hunter-gatherers (McDonald 2015; Veth et al. 2014), it would appear that the earliest coastal hunter-gatherer-fisher peoples of the Abydos Plain have depicted this abundant coastal food source – many kilometres inland from its maritime source. Marine elements were part of the artistic repertoire on the Dampier Archipelago from some of its earliest artistic productions. This new evidence agrees well with the emerging understanding of these early hybrid desert economies, whereby coastal groups had significant hinterland

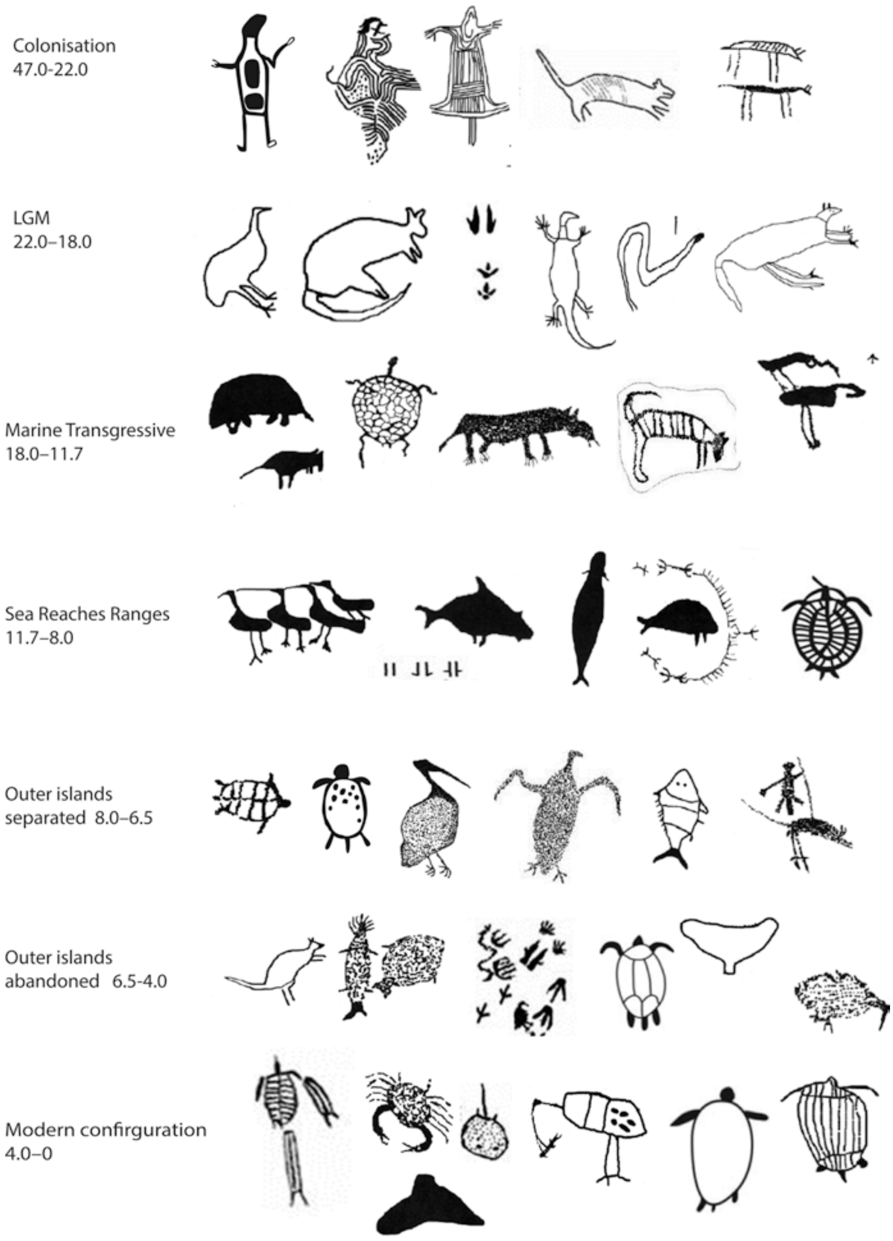


Fig. 11 Stylistic phases of Murujuga animals. (Following McDonald 2015, Fig. 3 which follows Mulvaney 2014, Fig. 10.2)

estates and portrayed prime resources both at their source and away from them. This is a common pattern in the placement of key animals within the northern hemisphere glacial refuges of Europe (e.g. David 2017).

Macropods

Eight species of macropod have been identified in engravings on the islands of the archipelago and in archaeological deposits prior to sea-level rise (Manne and Veth 2015; Stewart 2016). Three hundred engraved macropod motifs were analysed (Stewart 2016) to explore the high levels of stylistic heterogeneity identified previously in the Dampier Archipelago (McDonald and Veth 2009; Mulvaney 2014). Macropod motifs can be defined by head, ears, body, arm, paw, leg and tail shapes, along with the stance, gait and tail-to-body ratio. Multivariate analyses indicated that these attributes could distinguish between the zoological macropod species present and could also be used to understand the stylistic conventions that define the macropods within *Murujuga* rock art (Stewart 2016: Chap. 5).

The traits of eight Murujuga macropod types were analysed, and the traits of four species (*Macropus rufus, Macropus rufus robustus*, *Petrogale rothschildi* and *Bettongia lesueur*) had very strong representation. Traits from a number of lesser known species were also detected, but in lower numbers (Table 2). This research found that the *Murujuga* artists depicted both obvious species aspects and subtle traits reflecting intimate knowledge of the local macropod species (Stewart 2016: p. 127). It was also found that species habitat data could be correlated with climate reconstruction (Ward et al. 2013) within the broad temporal periods of the phased stylistic model (Table 2). The species representations in the different temporal phases have a demonstrable analogue to the faunal data recovered from excavations on the Montebello Islands (Veth et al. 1994) and from Barrow Island (Veth et al. 2016a, b). These results provide further support for the modelled art chronology (McDonald 2015; Mulvaney 2014).

Corroborative Archaeological Records for Faunal Depictions: The North West Shelf

Excavations on Barrow and Montebello Islands (Veth et al. 2007, 2014, 2016a, b) provide a record of northwest faunas from c. 51 ka until the mid-Holocene. Hunter-gatherers producing the art bodies from the Pilbara coast to the uplands were likely sharing the same cultural landscapes now drowned by rising sea levels (Manne and Veth 2015; Ward et al. 2015, 2016). The case for connecting palaeoeconomic and rock art records from adjacent areas of the North West is strengthened given the high levels of hunter-gatherer mobility deduced from Pleistocene-aged records

Table 2 Proportions of Murujuga macropod motifs and potential habitats through time (Stewart 2016: Table 6.7)

Contrast state	Macropod motif sample	Species representation	Habitat description
1		*Macropus rufus*	Widespread in harsh arid habitats
	2%	*Lagorchestes conspicillatus* *Bettongia lesueur*	Drier tropical regions with grasslands/shrubs Low vegetation habitats with dune edges or loamy soils
2		*M. rufus*	Widespread in harsh arid habitats
	24%	*M. robustus* *Petrogale rothschildi*	Widespread including arid habitats – but not the extreme arid zones Drier tropical regions with grasslands/shrubs
		L. fasciatus *B. lesueur* *L. conspicillatus*	Well-vegetated scrubland Low vegetation habitats with dune edges or loamy soils Drier tropical regions with grasslands/shrubs
3		*M. rufus* *M. robustus*	Widespread in harsh arid habitats Widespread, including arid habitats – but not extreme arid zones
		B. lesueur	Well-vegetated scrubland
	40%	*L. fasciatus* *P. rothschildi*	Drier tropical regions with grasslands/shrubs Harsh arid environments with rocky terrain
		L. conspicillatus and *Onychogalea unguifera*	Tropical/subtropical regions with relatively high rainfall
4		*P. rothschildi*	Harsh arid environments with rocky terrain
		M. robustus	Widespread including arid habitats – but not the extreme arid zones
	34%	*Macropus rufus*	Widespread in harsh arid habitats
		B. lesueur	Low vegetation habitats with dune edges or loamy soils
		O. unguifera *L. fasciatus* *L. conspicillatus* *L. hirsutus*	Tropical/subtropical regions with relatively high rainfall Well-vegetated scrubland Drier tropical regions with grasslands/shrubs Arid areas with hummock grasses and high plant diversity

(Veth 2005). The likely size of group territories for the Australian arid zone has been underestimated in previous archaeological and demographic studies, which have uncritically projected ethnographic boundaries into the deep past (Veth 2005; Veth et al. 2014). Palaeoeconomic and rock art data sets from the wider North West, and certainly from the drowned coastal plains, need to be better integrated. The fauna that people hunted and embodied in mythological and religious narratives will be visible in both dietary and ornamental remains, as well as symbolic expressions such as rock art.

From between 51 and 42 ka, four species of dietary and utilitarian shellfish were being transported inland from the Pleistocene shoreline to Boodie Cave on Barrow Island. From the same period and prior to the Last Glacial Maximum, terrestrial fauna from Boodie Cave and the Montebello Islands are dominated by arid zone species, including the spectacled hare wallaby (*Lagorchestes conspicillatus*) and euro (*Macropus robustus*) (Manne and Veth 2015). These larger macropods are consistent with prey targeted by male hunting parties, who may have used the cave as an inland bivouac. Post-Last Glacial Maximum, with rising sea levels and a more proximal coastline, the overall diet expands significantly to include 40 molluscan and 13 terrestrial species. The latter comprise largely small-to-medium game consistent with foraging by family groups of mixed gender and ages. Assemblages dating prior to abandonment of Barrow Island and the Montebellos by 7.0 ka are exceptionally rich and contain significant quantities of marine fauna including fish, turtle, marine mammal, crab and sea urchin, along with freshwater and marine molluscs. These economic fauna are precisely those depicted in the engravings from both *Murujuga* and Port Hedland, where our archaeological dietary evidence is less clear, because of the absence of suitable limestone caves to preserve this type of archaeological evidence.

The next step in ongoing analyses is to begin making correlations between suites of species represented in the rock art and the economic strategies of prehistoric hunter-gatherers of the North West, including innovations in hunting, trapping and netting. For example, there are turtle, dugong and fish remains associated with cooking hearth stones from Boodie Cave dated to c. 7 ka (Veth et al. 2014). There are depictions of people netting dugong, spearing turtle and fish and of course stone fish traps from the Dampier Archipelago (McDonald 2015; Veth 1993). Ongoing excavation programmes on *Murujuga*, Barrow Island and the Canning Stock Route are pushing back the early occupation sequences, recovering ancient ochres and artefacts and, importantly, providing evidence for extended terrestrial and marine faunal assemblages from the north-west arid zone.

The archaeological evidence for animal depictions from the north-west arid zone reveals a long figurative tradition, which is though to start before the Last Glacial Maximum and continues through the Holocene. Species depicted include large-range fauna such as emu and plains kangaroo, smaller territorially focused marsupials such as wallabies and quolls and a wide variety of birds and reptiles. Species outside their current distributions or extinct include the bandicoot and thylacine. While depictions may have been executed to inform dietary, regenerative, totemic and mythological narratives, there is a precision in anatomical detail in all analysed classes (e.g. kangaroos, turtles and fish) which allows robust attribution to genus and species levels. Between 28% and 45% of all motifs from the coast, ranges and desert lowlands are of animals and tracks. The painting and engraving traditions of the north-west arid zone clearly have a significant naturalistic component which is of significance for studies of human and natural ecology. This first review of animal depictions in the rock art of the arid zone illustrates there are changes in species depictions across different habitats and through time. Localised case studies of kangaroo and turtle depictions show accurate depictions to species level, and importantly these match archaeo-faunas recovered from stratified deposits in the wider region. Extinctions and changes in range are noted at the local and regional levels and include clear depictions of the thylacine across the arid zone, bandicoot and possum in the Little Sandy Desert and the nail-tailed wallaby, a species with a more tropical distribution today. Emu, large kangaroos and a number of quadrupeds are also recorded in the early art of the Dampier Archipelago. Ongoing excavations of 50 ka sites from the Northwest Shelf and Canning Stock Route provide valuable faunal assemblages, which may be compared with, and linked to, zoomorphic rock art depictions.

While the rock art of the arid zone is often characterised as predominantly tracks and geometric motifs, in fact there is a long tradition of naturalistic, figurative animal depictions. Artists are clearly displaying familiarity with and detail of animal behaviour, tracks, body morphology and decoration to a level that allows accurate identification to family, genus and even species level. These understandings provide important data for cultural and natural ecology studies and ultimately more informed understandings of the values of the Australian deserts.

References

Clune G (2002) Abydos: an archaeological investigation of Holocene adaptations on the Pilbara Coast, Northwestern Australia. PhD thesis, University of Western Australia

David B (2017) Cave Art. Thames and Hudson, London

Davidson I (2018) Images of animals in rock art: Not just "good to think". In: David B, McNiven IJ (eds) Oxford handbook of the archaeology and anthropology of rock art. Oxford University Press, Oxford

de Koning S (2014) Thatharruga: a stylistic analysis of Turtle Engravings on the Dampier Archipelago, Western Australia. BA (Hons) thesis, University of Western Australia

Field E, McGowan HA, Moss PT, Marx SK (2017) A late quaternary record of monsoon variability in the northwest Kimberley, Australia. Quat Int 449:119–135

Harper S (2016) Outlining the Port Hedland style: a distinctive local signature within the broader shared iconographies of the Pilbara, northwest Australia. J Anthropol Soc S Aust 40:70–107

Lorblanchet M (1983) Chronology of the rock engravings of Gum Tree Valley and Skew Valley near Dampier, W.A. In: Smith M (ed) Archaeology at ANZAAS. Western Australian Museum, Perth, pp 39–59

Manne T, Veth P (2015) Late Pleistocene and early Holocene exploitation of estuarine communities in northwestern Australia. Quat Int 385:112–123

Maynard L (1979) The archaeology of Australian Aboriginal art. In: Mead SM (ed) Exploring the visual art of Oceania. University of Hawaii Press, Honolulu, pp 83–110

McCarthy FD (1962) The rock engravings of Port Hedland, northwestern Australia. Pap Kroeber Anthropol Soc 26:1–73

McDonald J (1993) The depiction of species in macropod track engravings at an Aboriginal art site in western New South Wales. Rec Aust Mus Suppl 17:105–115

McDonald J (2005) Archaic faces to headdresses the changing role of rock art across the arid zone. In: P Veth, M Smith, P Hiscock (eds) Desert peoples archaeological perspectives, pp. 116–141. Blackwell, Oxford

McDonald J (2015) I must go down to the seas again: Or, what happens when the sea comes to you? Murujuga rock art as an environmental indicator for Australia's north-west. Quat Int 385:124–135

McDonald J (2016) Discontinuities in arid zone rock art: Graphic indicators for changing social complexity across space and through time. J Anthropol Archaeol 46:53–67

McDonald J, Berry M (2016) Murujuga, northwestern Australia: When arid hunter-gatherers became coastal foragers. J Island Coast Archaeol 12:24–43

McDonald J, Veth P (2006a) A study of the distribution of rock art and stone structures on the Dampier Archipelago, WA. Department of Environment and Heritage, Canberra

McDonald J, Veth P (2006b) Rock art and social identity: a comparison of graphic systems operating in arid and fertile environments in the Holocene. In: Lilley I (ed) Archaeology of Oceania: Australia and the Pacific Islands. Blackwell Studies in Global Archaeology, Oxford, pp 96–115

McDonald J, Veth P (2009) Dampier archipelago petroglyphs: archaeology, scientific values and national heritage listing. Archaeol Ocean 44:49–69

McDonald J, Veth P (2010) L'iconographic du desert occidental d'Australie. In: Anderson J (ed) Diogène, pour une historie transcultuelle de l'art. Presses Universitaires de France, Paris, pp 9–27

McDonald J, Veth P (2012) The social dynamics of aggregation and dispersal in the Western Desert. In: McDonald J, Veth P (eds) Companion to rock art. Wiley-Blackwell, Oxford, pp 90–102

McDonald J, Veth P (2013a) Rock art in arid landscapes: Pilbara and Western Desert petroglyphs. Aust Archaeol 77:1–16

McDonald J, Veth P (2013b) The archaeology of memory: the recursive relationship of Martu rock art and place. Anthropol Forum 23:1–19

McDonald J, Steelman KL, Veth PM, Mackey J, Loewen J, Thurber CR, Guilderson TP (2014) Results from the first intensive dating program for pigment art in the Australian arid zone: Insights into recent social complexity. J Archaeol Sci 46:195–204

McDonald J, Reynen W, Petchey F, Ditchfield K, Byrne C, Vannieuwenhuyse D, Leopold M, Veth P (2018) Karnatukul (Serpent's Glen): a new chronology for the first occupation of the Australian deserts. PLoS One

Morse KH, Ryan IK (2009) Towards a Late Holocene archaeology of the Inland Pilbara. Archaeol Ocean Supplement 44:6–15

Mulvaney KJ (2010) *Murujuga Marni* – Dampier Petroglyphs: shadows in the landscape echoes across time. PhD thesis. University of New England, Armidale

Mulvaney KJ (2011) Dampier Archipelago: decades of development and destruction. Rock Art Res 28:17–25

Mulvaney KJ (2013) Iconic Imagery: Pleistocene rock art developed across northern Australia. Quat Int 285:99–110

Mulvaney KJ (2014) Murujuga Marni: the rock art of the Macropod Hunters and the Mollusc Harvesters. University of Western Australia Publishing, Perth

O'Connor S, Veth P, Campbell C (1998) Serpent's Glen: a Pleistocene archaeological sequence from the Western Desert. Aust Archaeol 46:12–22

Perrine D (2003) Sea turtles of the world. Voyageur Press, Stillwater

Pillans B, Fifield LK (2013) Erosion rates and weathering history of rock surfaces associated with Aboriginal rock art engravings (petroglyphs) on Burrup Peninsula, Western Australia, from cosmogenic nuclide measurements. Quat Sci Rev 69:98–106

Reeves JM, Barrows TT, Cohen TJ, Kiem AS, Bostock HC, Fitzsimmons KE, Jansen JD, Kemp J, Krause C, Petherick L, Phipps SJ (2013) Climate variability over the last 35,000 years recorded in marine and terrestrial archives in the Australian region: an OZ-INTIMATE compilation. Quat Sci Rev 74:21–34

Rosenfeld A (1993) A review of the evidence for the emergence of rock art in Australia. In: Smith M, Spriggs M, Frankhauser B (eds) Sahul in review: late pleistocene archaeology in Australia, New Guinea and Island Melanesia. The Australian National University, Canberra, pp 71–80

Slack M (2015) Archaeologists demonstrate 46,000 years of occupation in Australia's arid northwest. https://www.australianarchaeologicalassociation.com.au/media-releases/ice-age-living-in-the-pilbara/

Smith MA, Watchman A, Ross J (2008) Direct Dating Indicates a Mid-Holocene Age for Archaic Rock Engravings in Arid Central Australia. Geoarchaeology 24:191–203

Stewart R (2016) An approach with style: a stylistic analysis of Macropod Rock Art on Murujuga (Burrup Peninsula), Western Australia. BA(Hons) thesis, The University of Western Australia, Australia

Tindale N (1974) Aboriginal tribes of Australia. University of California Press, Berkeley

Veth P (1993) The Aboriginal occupation of the Montebello Islands, northwest Australia. Aust Aborig Stud 2:39–50

Veth P (2005) Cycles of aridity and human mobility: risk-minimization amongst late Pleistocene foragers of the Western Desert, Australia. In: Veth P, Smith MA, Hiscock P (eds) Desert peoples: archaeological perspectives. Blackwell, Oxford, pp 100–115

Veth P (2006) Social dynamism in the archaeology of the Western Desert. In: David B, McNiven IJ, Barker B (eds) The social archaeology of indigenous societies. Australian Aboriginal Studies Press, Canberra, pp 242–253

Veth P, Gara T, P K (1994) The aboriginal face of rock engravings on the Burrup Peninsula. In: Sullivan M, Brockwell S, Webb A (eds) Archaeology in the North: proceedings of the Australian Archaeological Association conference. North Australia Research Unit (ANU), Darwin, pp 213–226

Veth P, Aplin K, Wallis L, Manne T, Pulsford T, Chappel A (2007) Late quaternary foragers on arid coastlines: archaeology of the Montebello Islands, Northwest Australia. British Archaeological Reviews, International Series, Oxford

Veth P, Smith M, Bowler J, Fitzsimmons K, Williams A, Hiscock P (2009) Excavations at Parnkupirti, Lake Gregory, Great Sandy Desert: OSL ages for occupation before the Last Glacial maximum. Aust Archaeol 69:1–10

Veth P, Ditchfield K, Hook F (2014) Maritime deserts of the Australian northwest. Aust Archaeol 79:156–166

Veth P, Ward I, Ditchfield K (2016a) Reconceptualising Last Glacial Maximum discontinuities: A case study from the maritime deserts of north-western Australia. J Anthropol Archaeol 46:82–91

Veth P, Ward I, Manne T (2016b) Coastal feasts: a Pleistocene antiquity for resource abundance in the maritime deserts of North West Australia. J Island Coast Archaeol 12:8–23

Veth P, Myer C, Heane P, Ouzman S (2017a) Plants before farming: The deep history of plant-use and representation in the rock art of Australia's Kimberley region, 2016. Quat Int. https://doi.org/10.1016/j.quaint.2016.08.036

Veth P, Manne T, Ulm S, Ward I, Ditchfield K, Dortch J, Hook F, Petchey F, Hogg A, Questiaux D, Demuro M, Arnold L, Spooner N, Levchenko V, Skippington J, Byrne C, Basgall M, Zeanah D, Belton D, Helmholz P, Bajkan S, Bailey R, Merigot K, Palczek C, McInnes B, Kendrick (2017b) New evidence for the maritime competencies of modern humans outside of Africa from 50,000 years ago, Barrow Island, NW Australia. Quat Sci Rev 168:19–29

Ward I, Larcombe P, Mulvaney K, Fandry C (2013) The potential for discovery of new submerged archaeological sites near the Dampier Archipelago, Western Australia. Quat Int 308–309:216–229

Ward I, Larcombe P, Veth P (2015) A new model for coastal resource productivity and sea-level change: the role of physical sedimentary processes in assessing the archaeological potential of submerged landscapes from the Northwest Australian Continental Shelf. Geoarchaeology 30:19–31

Ward I, Salvemini F, Veth P (2016) 3D visualisation of a chert artefact from Barrow Island. J Archaeol Sci Rep 7:432–436

Williams AN, Veth P, Steffen W, Ulm S, Turney CSM, Phipps S, Smith M, Reeves J (2015) A Continental Narrative: Human Settlement Patterns and Australasian Climate Change over the last 35,000 Years. Quat Sci Rev 123:91–112

Wood R, Jacobs Z, Vannieuwenhuyse D, Balme J, O'Connor S, Whitau R (2016) Towards an accurate and precise chronology for the colonization of Australia: the example of Riwi, Kimberley, Western Australia. PLoS ONE 11:e0160123. https://doi.org/10.1371/journal.pone.0160123

Wright BJ (1968) Rock art of the Pilbara region, north-west Australia. In: Occasional papers in aboriginal studies 11. Australian Institute of Aboriginal Studies, Canberra

Weeds in Australian Arid Regions

John K. Scott, Margaret H. Friedel, A. C. Grice, and Bruce L. Webber

Introduction

Australia's arid interior spans some 3100 km in the east-west direction and 1400 km north-south covering a largely continuous 3.3 M km^2 area across four states and the Northern Territory (NT) (Slatyer and Perry 1969; Watterson et al. 2015) (Fig. 1a). Although arid relative to the rest of Australia, this region has considerable heterogeneity in climate (the proportion of summer rain declines from north to south, the south receives mostly winter rain), topography (from ranges to salt lakes) and, therefore, vegetation communities (from woodlands to grasslands) (Slatyer and Perry 1969; Jessop 1981; Watterson et al. 2015). These landscape characteristics have considerable overlap with other arid regions of the world. As such, it is not surprising that the inevitable introduction of alien plant species into these regions has made novel contributions to the local flora, some of which are now highly invasive and/or threatening.

Set in the arid interior of the NT, the award-winning children's story of rosy dock (Baker 1995) illustrates the introduction of the weed *Rumex vesicaria* by European settlers and its subsequent invasion of the surrounding native vegetation. The story's message is that, while the global redistribution of plants by early European settlers

---

J. K. Scott (✉) · B. L. Webber
School of Biological Sciences, The University of Western Australia,
Crawley (Perth), WA, Australia

CSIRO Land and Water, Private Bag 5, P.O. Wembley, WA, Australia
e-mail: john.k.scott@uwa.edu.au

M. H. Friedel
CSIRO Land and Water, 001 – Business Innovation Centre, Desert Knowledge Precinct,
Alice Springs, NT, Australia

A. C. Grice
College of Marine and Environmental Sciences, James Cook University,
Townsville, QLD, Australia

H. Lambers (ed.), *On the Ecology of Australia's Arid Zone*,
https://doi.org/10.1007/978-3-319-93943-8_12

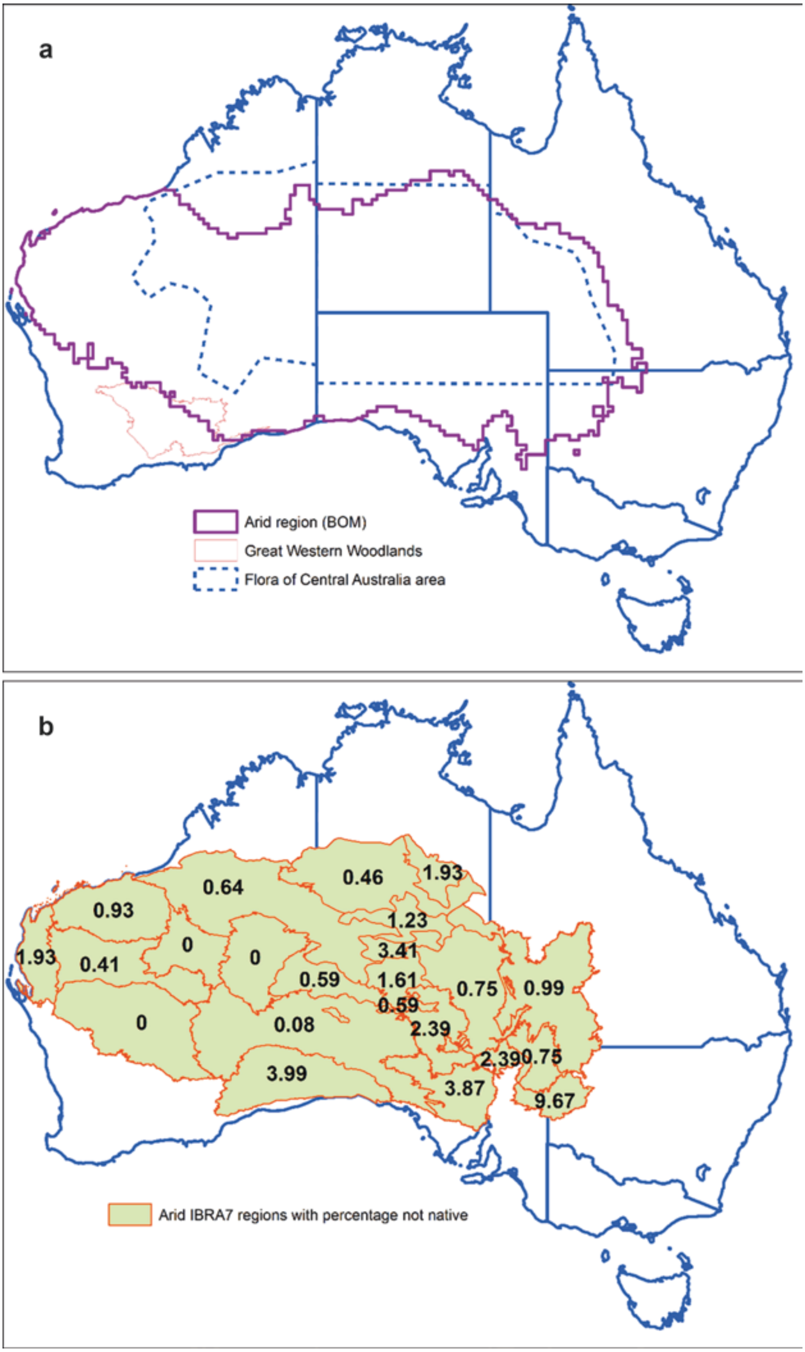


Fig. 1 (**a**) Arid region of Australia corresponding to areas with less than 350 mm annual rainfall (source: http://www.bom.gov.au/jsp/ncc/climate_averages/climate-classifications/index.jsp?maptype=seasb). Also indicated is the position of the Great Western Woodlands and the area covered by the Flora of Central Australia (Jessop 1981). (**b**) The IBRA7 regions are given in http://www.environment.gov.au/land/nrs/science/ibra), and the percentage alien are from the Atlas of Living Australia (http://www.ala.org.au/) for arid zone IBRA regions

was largely done with good intentions, the legacy of these actions continues in the form of invasive species such as the rosy dock. We are left wondering at the relative beauty of the massed invasive plant (the rosy dock) against the timeless appeal of the ancient native ecosystem it now occupies and what are the concerning threats that this weed now represents. Another legendary pathway for the introduction of weeds into arid Australia is via the vegetation-padded saddles of pioneering Afghan cameleers. Traversing the arid interior transporting goods, they discarded saddle stuffing and distributed seeds, including *Cenchrus ciliaris* (buffel grass) seed, at key waterholes, leaving them to establish and invade.

Understanding the historical context of plant introductions into the arid regions of Australia can be informative for guiding current and future management. In some cases we have greater certainty over the historical context of weed introductions. For example, the subsequent deliberate introduction of *Cenchrus ciliaris* seed can be traced to importations from Afghanistan following the First World War and the supply of seed for pasture production in both Western Australia (WA) and eastern Australia by the WA Department of Agriculture (Humphreys 1967). For many weeds, however, historical information about introductions is scattered through the literature and historical records, with no prior effort to synthesise information on introduction pathways for weeds in the arid zone of Australia.

For the majority of weeds in these Australian arid regions, the pathway of introduction of most weeds is probably more prosaic than that of *Cenchrus ciliaris*. Albrecht and Rogers (1999) conclude for the Tanami desert region (NT/WA) that introduction of alien plant species is associated with the movement of vehicles, machinery, animals and deliberate plantings. The rosy dock invasion is illustrated by Baker (1995) as originating from a garden plant introduction which is highly likely. Indeed some of the more prominent weeds of Australian arid regions are the result of deliberate introductions, either as pasture (*Cenchrus ciliaris*) or as shade trees (*Tamarix aphylla*). At least three *Prosopis* species, together with their hybrids, were introduced as shade and fodder trees and have naturalised in rangelands and arid regions of Australia. However, a significant proportion of weeds appear to have initially colonised elsewhere in Australia and secondarily dispersed into arid regions. The analysis of possible pathways included in Gosper et al. (2015) indicates that almost half (43%) of the 206 alien plant species found in the Great Western Woodlands of WA (Fig. 1a) are more geographically widespread in the neighbouring Mediterranean (winter rainfall) climate regions of southwest WA. An additional group of alien species also of Mediterranean climate origin (19%) appears to persist in the arid zone only due to being associated with watered urban environments (e.g. *Polygonum aviculare*). Smaller percentages of aliens in the Gosper et al. (2015) study originated as dry region adapted urban or horticultural plantings (6%; e.g. *Portulacaria afra*) or spread from summer-rainfall arid regions to the north (2%; e.g. *Argemone ochroleuca*).

While there are clear plant dispersal pathways between temperate and tropical Australia and comparable regions in other parts of the world, this is not the case with arid Australia. This paucity of pathways reduces the likelihood of accidental weed introductions. For example, there are few trade or cultural connections between Australia's arid regions and the Saharan or American deserts. In addition, trade in Australia's arid regions is largely one way, with massive amount of minerals and cattle being exported, but little being imported, especially without first transiting via another non-arid part of Australia (e.g. Perth WA, Darwin NT). Thus, the main ports of entry for arid weeds into Australia can act as bioclimatic filters to the immigration of plant species adapted to these landscapes.

The introduction and establishment of alien plants are just the beginning of their influence on their recipient landscape (as outlined by the invasion pathway sensu Blackburn et al. (2011)). In this chapter we provide the first review of weed species in arid regions of Australia and their management. We contextualise some of the "good intentions" – introductions such as *Cenchrus ciliaris* which are now widespread – and explore the often conflicting reasons behind the continued introduction of potential new weeds. In our focus on the impacts of these weeds, we also discuss the likely influence of anthropogenic global change, such as climate change, and the need to devise pragmatic yet robust management options for ecosystems that are now completely altered from their earlier states.

Characteristics of the Alien Flora of Australian Arid Regions

The characteristics of alien flora in the arid regions of Australia are best examined using the "weed status triplet" (Scott et al. 2014). That is, the properties of weeds (i.e. plants not wanted where they are found) can be best described based on (1) whether or not they are native or alien, (2) whether they are invasive or non-invasive (i.e. rapidly expanding their range) and (3) their level of impact (positive or negative) and the values associated with this impact. We follow the mapped definition of arid given by the Australian Bureau of Meteorology (Fig. 1a) corresponding to the region of western and central Australia where the average annual rainfall is below 350 mm, although some of the examples we mention (such as the Great Western Woodlands, Fig. 1a) are from the edge of the arid region. We define a weed as a plant not wanted where it is found, a somewhat subjective status; weeds may include both native and alien species (Scott et al. 2014). By alien we mean plant species occurring outside their natural past or present range and with dispersal potential in the timeframe under consideration (sensu Webber and Scott 2012).

Native or Alien

The percentage of alien species listed in Atlas of Living Australia for the 20 arid zone IBRA regions averages 1.77% and has a range of 0–9.67%, the latter being for the region that includes the town of Broken Hill (Fig. 1b; 438 alien species). The percentages given in Fig. 1b are most likely an underestimate for many of the IBRA regions. In an earlier assessment, the flora of central Australia (Fig. 1a) included 6%

species alien to Australia out of 1872 flowering plant species (Jessop 1981). The only field guide to weeds of arid regions includes 91 species out of 260 recorded from southern NT (Dhanji 2009). By comparison, overall the Australian flora of 17,590 species includes 11.1% species alien to Australia (Orchard 1999).

Up to 47 plant families are represented in the alien flora found in arid regions of Australia, the most common in terms of number of species being the Poaceae and Asteraceae (Jessop 1981). These two families are the third and fourth most species-rich families in the native Australian flora (Orchard 1999); only the Myrtaceae (with no alien species in arid regions) and Fabaceae (with few alien species in arid regions) have more species that are native to Australia.

One feature of the alien flora of Australia's arid regions is the relatively low numbers of naturalised and invasive succulent species from the families Aizoaceae, Crassulaceae and Euphorbiaceae, despite species from these families being introduced widely in Australia as garden plants. In contrast, Australia has already been subjected to invasion by members of the Cactaceae in southeast Queensland (QLD), where densities before management via biological control were so high that farms were abandoned (Hosking 2012). Some 27 Cactaceae species occur as established introductions to Australia, and of these, five are regarded as high risk in arid South Australia (SA) (Harvey 2009), and at least eight are naturalised outside urban areas in the NT (C. Brown, pers. comm. 27/7/2015). Cactaceae represent a serious threat to arid regions, and this is recognised in their status as Weeds of National Significance (WoNS) (Commonwealth of Australia and Australian Weeds Committee 2012) (Fig. 2a).

Native Weeds

Native weeds fall into two general categories. Firstly, plant species may be weedy (i.e. unwanted) in the area to which they are native. This includes "bush encroachment" (often also referred to as invasive natives) and plants that are poisonous to livestock. The second category is species that are considered to be native to Australia but have newly arrived in the area under consideration either accidentally or deliberately (e.g. as garden plants). Given that native status implicitly involves spatio-temporal context, and that Australia has a large area with considerable landscape heterogeneity, it is increasingly common for species to be moved within Australia to regions where they are not native. Moreover, there is likely to be an increasing incidence of this last category as the climate changes. Webber and Scott (2012) outline the issues required to determine if a species is native or alien. Importantly, this framework deliberately separates a pre-determined management option from native or alien status, facilitating a range of management options for native species that have become weedy.

Regarding the first category, encroachment of native vegetation is widely reported to be a result of poor rangeland management, although a wide range of factors (reduced fire frequency, climate change, removal of predators, increased CO_2

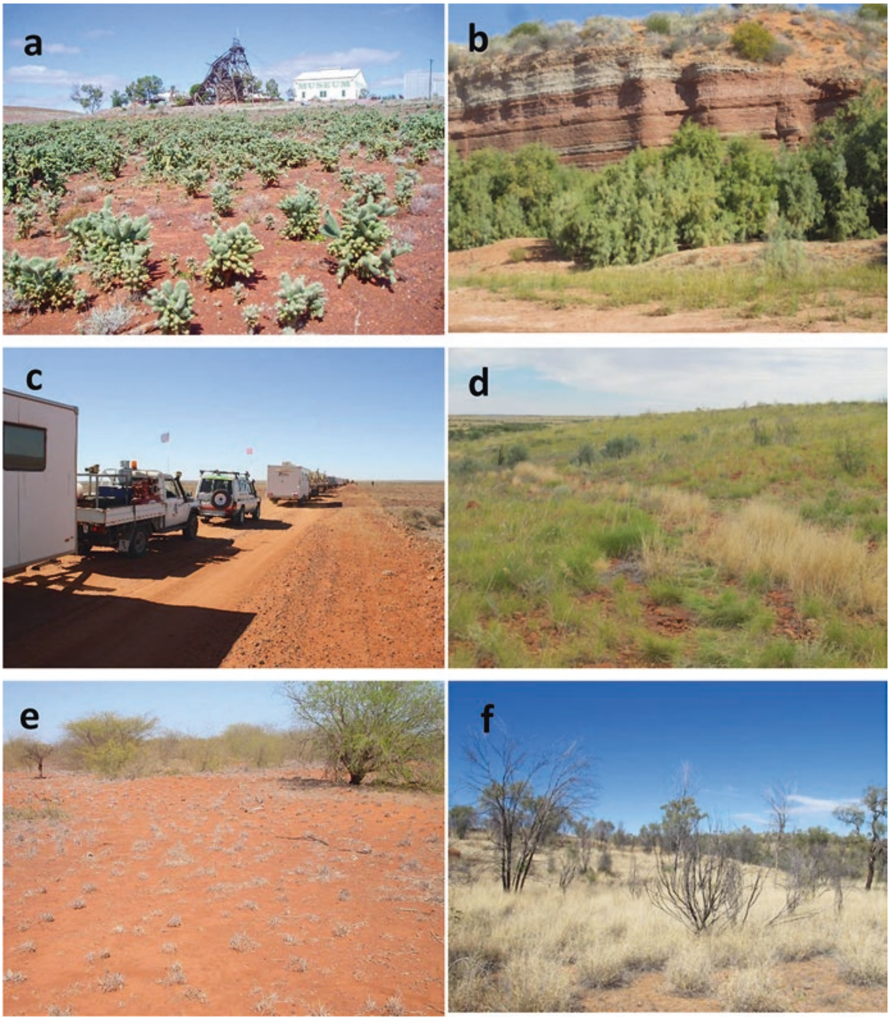


Fig. 2 Weeds invading arid regions of Australia (**a**) A. Invasion of *Cylindropuntia fulgida var. mamillata* at Gwalia, WA. Photo: M. Chuk). (**b**) Spread of *Tamarix aphylla* along the Finke River, NT. Photo: Rieks van Klinken, CSIRO. (**c**) Weeds can be spread to isolated areas by vehicles and equipment during exploration activities. Photo: Chris Brown, NT Weed Management Branch. (**d**) Spread of *Cenchrus ciliaris* (light coloured grass on camel pad traversing the photo) by feral camels, Nicker Creek, WA. Photo: Margaret Friedel, CSIRO. (**e**) Grazed *Cenchrus ciliaris* in foreground, *Prosopis* sp. in background at Mardie Station, WA. Photo: John K. Scott, CSIRO. (**f**) *Cenchrus ciliaris* in acacia woodlands at Simpsons Gap National Park, NT, following fire. Photo: Margaret Friedel, CSIRO

favouring C_3 shrubs) may be responsible (Eldridge et al. 2011). Thus, plant species increasing in abundance are often perceived as having a negative impact and are treated and classed as weeds, triggering changed management or control options. Some species in arid regions are treated as "weeds" because they are toxic to livestock. *Indigofera linnaei* (Birdsville indigo) and *Gastrolobium grandiflorum* (desert poison bush) in the NT and *Euphorbia boophthona* (Gascoyne spurge) and *Gastrolobium laytonii* (Breelya) in WA are four examples of native species that can kill livestock (Gardner and Bennetts 1956; Mitchell 1979). Management of these plants is impractical, so the threat is minimised by avoiding areas where they occur.

The second category of native weeds are species that have extended, or been introduced, beyond their original range. For example, *Heliotropium foliatum* is native to northern Australia including the Kimberley and the coastal part of the Great Sandy Desert (Craven 1996). However, it appears to have spread southwards to the Pilbara in recent times, where there are now a few occurrences in native vegetation and mining areas. The native windmill grass, *Chloris truncata,* appears to have extended its range from eastern Australia to SA and invaded WA in the 1900s (Michael et al. 2012). Lastly, the legume *Cullen graveolens* is native to the Pilbara rangelands and has spread southwards through livestock transport to the southwest of WA (Hussey et al. 2007). How these weed populations are categorised with respect to native or alien status depends on their natural dispersal ability, the distance dispersed and the time period under consideration (Webber and Scott 2012).

A minor additional category of weeds are those species for which it is not certain if they are native or alien. For example, *Phragmites australis* (common reed) is an invasive species of aquatic systems in arid regions (Hocking et al. 1998), where it encroaches into water up to 2 m deep, reducing flow and hindering access for people and livestock. Its native status in Australia is uncertain, because it has a cosmopolitan distribution (Hocking et al. 1998). However, this does not preclude the need for management (Webber and Scott 2012). The application of novel genetic methods may provide insight into the historical biogeographic context of species such as *Livistona mariae* palms and their possible introduction by humans into arid Australia (biocultural dispersal; Kondo et al. 2012; Trudgen et al. 2012).

Invasive Versus Non-invasive

The presence of an alien plant species in a region does not necessarily mean that it is invasive. By invasive we mean a subset of naturalised plants that are undergoing or have the potential for considerable and rapid expansion of their geographic range (Richardson et al. 2000; Scott et al. 2014). Given the vast size and climatic heterogeneity of Australia's arid region, it is not surprising that no alien species has colonised the entire arid region, although some are already very widespread (e.g. *Cenchrus ciliaris*, *Citrullus lanatus*, *Conyza bonariensis*, *Sonchus oleraceus*). There is evidence that some alien species have occupied their maximum potential range in Australia and are now not viewed as actively invading. For example, *Carrichtera annua* (Ward's weed) appears to have started its invasion of Australia from a single site in SA and then experienced a lag phase of about 30 years before rapid spread (i.e. invasion; 20 to over 100 km/year) since the 1960s to reach a range limit determined by the requirement for winter rainfall and calcareous soils (Cooke et al. 2011).

Tamarix aphylla exemplifies possibly the most rapid weed invasion in arid Australia. This species is commonly planted around outback station homesteads. Floods along the Finke River, NT in 1974 are thought to have led to a sequence of events (including rapid dispersal of seed, disturbance of the river bed and bank with uprooting of river bank trees and incursion of saline water) that resulted in the rapid colonisation of the riparian ecosystem by *Tamarix aphylla* (Griffin et al. 1989) (Fig. 2b). Subsequently, spread throughout the entire 600 km length of the river is attributed to vegetative reproduction through the dispersal of branch and root fragments during floods (Fuller 1993). *Tamarix aphylla* has the potential to colonise other river systems across inland Australia, and, as such, it represents a significant threat to riparian environments in these regions – the community with the highest diversity and production in arid Australia. In contrast, some invasions, for example, that of *Ziziphus mauritiana*, have been relatively slow, though inexorable (Grice 2002).

Flooding and wind dispersal are invoked in the story of the invasion of *Rumex vesicaria* (Baker 1995), while Griffin (1993) and Gosper et al. (2015) attribute the spread of *Cenchrus ciliaris* at Uluru National Park, NT and along the Goldfields Highway north of Kalgoorlie, WA, respectively, to the passage of vehicles. Favourable roadside microhabitats created by water run-off assist this spread. Pathways for weed invasion often depend on people: road maintenance (grading and slashing), road and rail corridor development and mining and exploration (sand mining in infested areas, transfer of weeds on vehicles (Fig. 2c); (Biosecurity South Australia 2012). In the NT, 1970s dust control measures on widely scattered Aboriginal communities included introduction of *Cenchrus ciliaris*. Feral animals, especially camels, continue to spread seed into areas remote from roads (Fig. 2d).

Invasion can also be measured in terms of increases in density. *Prosopis* sp. (mesquite) was planted in the 1930s on Mardie Station in northwest Australia (Fig. 2e). The historical pattern of invasion shows that the weed was widespread within only 35 years of planting, and subsequently it has infilled intervening area, indicating that cattle, and not flood events, were dispersing seed (Robinson et al. 2008). The weed increased its area of cover by about 1% per year, resulting in an infestation of some 150,000 ha, 30,000 of which is dense (Robinson et al. 2008).

Known Impacts and Their Value Judgement

The third element for assessing weeds is the level of impact they are having in their introduced range and the significance and implications of this impact. Impact is a measurable change in the region of invasion that can be attributed, either directly or indirectly, to the addition of an alien species (Scott et al. 2014), although the importance of the impact is always ultimately subjective. The most significant species in terms of impacts are called transformers; this is a subset of invasive plants that have impact to the extent that they change the character, condition, form or nature of ecosystems over a substantial area relative to the extent of that ecosystem (Richardson et al. 2000; Scott et al. 2014).

The most widespread and controversial alien plant in arid Australia is *Cenchrus ciliaris* (Fig. 2f). It is also the most-studied species, with reviews being published by Marshall et al. (2012) (as an environmental weed), Kharrat-Souissi et al. (2014) (role of polyploidy) and Grice et al. (2012) (the contentious nature of management as pasture or weed). *Cenchrus ciliaris* is widely and deliberately grown as a pasture plant in tropical and subtropical arid rangelands of the world, because of its high tolerance of drought and capacity to withstand heavy grazing (Fig. 2e). Consequently, it is an important economic species in Australian arid rangelands. It is, however, associated with significant negative environmental impacts, listed in Friedel et al. (2011) and Marshall et al. (2012), including increased fire frequency and intensity leading to the loss of trees, displacement of native grasses used by native herbivores and decline in richness of plant species and other organisms. Thus *Cenchrus ciliaris* can be viewed as both a negative and positive transformer species, depending on the value judgement of the assessing party.

Other weeds with known negative impacts in arid regions of Australia are not as controversial. The Weed of National Significance (WoNS) *Prosopis* spp. (mesquite) invasion of Mardie Station in the Pilbara is so dense that cattle are prevented from accessing water points (Dodd et al. 2012), and this is resulting in economic impact that is locally significant. The impacts associated with the invasion of the WoNS-listed weed *Tamarix aphylla* include increased salinity, reduction in plant and fauna species diversity, damage to infrastructure, reduced access to watering points for livestock and pasture losses (Griffin et al. 1989; Northern Territory Government of Australia 2016a).

Not all invasive species with impact are declared WoNS, although they may be declared significant under various state legislations. *Orbea variegata* (African carrion flower) was originally grown as a garden plant in arid regions and has established in the chenopod shrub lands of Whyalla, SA (Dunbar and Facelli 1999). It impacts native vegetation by reducing growth by restricting water availability to the dominant chenopod shrub *Atriplex vesicaria* and the annual plant community (Dunbar and Facelli 1999). Indeed Lenz and Facelli (2003) showed that the native chenopod facilitates establishment of the alien species by providing shade and reducing temperatures to enhance germination and growth for the weed.

It is important to recognise that being invasive does not necessarily mean that there is a significant negative impact. The annual species, *Rumex vesicaria*, is a major invader of mine sites that are being rehabilitated (Schatral et al. 2008) and other disturbed areas (Fig. 3a). *Rumex vesicaria* was previously used as a rehabilitation species (Schatral and Osborne 2002) and, being an annual species, would leave areas subject to seasonal erosion. Current practices avoid using alien weeds in restoration projects and aim to revegetate with native perennial species. However, the

Fig. 3 Weeds invading arid regions of Australia (**a**) A. *Rumex vesicaria* (with red fruiting heads in foreground). Stuart Highway verge, Henbury Station, NT. Photo: Margaret Friedel, CSIRO. (**b**) Ward's weed (*Carrichtera annua*) Coolgardie. Photo: John K Scott, CSIRO. (**c**) *Parkinsonia aculeata*. Photo: Bruce L. Webber, CSIRO. (**d**) Date Palm, *Phoenix dactylifera*, subject to containment at Millstream National Park, WA. Photo Bruce L. Webber, CSIRO. (**e**) *Passiflora foetida*, a target for biological control. Photo: Bruce L. Webber, CSIRO. (**f**) *Passiflora foetida* overtopping eucalyptus trees at Millstream National Park, WA. Photo: Bruce L. Webber, CSIRO

persistent seed bank of *Rumex vesicaria* makes it hard to control once established. *Asphodelus fistulosus* (onion weed) is a very widespread, highly visible weed of roadsides and can form dense populations in southern parts of the arid and semiarid regions. There has been public pressure for biological control of this weed (Cullen 2012). However, there is no clear evidence of economic or environmental impact in studies based in SA (Pitt et al. 2006), and it is likely that the abundance of the plant is a symptom of overgrazing. Another widespread species, *Carrichtera annua* (Ward's weed) (Cooke et al. 2011) (Fig. 3b), also requires further assessment to determine if there is any agricultural or environmental impact. While it is potentially toxic to livestock under drought conditions in NSW (Curran 2007), field experiments in SA by Harris and Facelli (2003) failed to show any competitive effects of *Carrichtera annua* on annual plant species. Further examples of widespread annual species without obvious impact are *Solanum nigrum* (Symon 1982) and *Sonchus oleraceus*. Both are strongly associated with human activity such as increased soil moisture and disturbance, and humans appear to be the most important dispersal vectors. Indeed, in Australia's rangelands, the 70–80% of alien species that are annuals probably have little, or more subtle, impacts that remain to be measured (Grice 2006). Further research on impact, in particular to see if there is a lag phase between invasion and impact starting, is needed especially given the widespread distribution of these and similar species.

Some weeds are more a social nuisance, rather than having an economic or environmental impact. *Tribulus terrestris* has spiny burrs that persist for years and are a constant nuisance in camping and town sites. *Argemone ochroleuca* (Mexican poppy) is also very spiny and likely to occur in ephemeral waterways in central Australia where people camp.

Weed Management

Weed management has to be strategic and carried out within an appropriate policy framework. At the national level, the Australian Weed Strategy with its identification of 32 Weeds of National Significance (http://weeds.ala.org.au/WoNS/) provides an overarching strategy that encompasses the arid regions. Each state has developed a weed strategy that complements the national approach. These strategies have been the major factor in the development of management approaches for the control of *Prosopis* spp., *Parkinsonia aculeata* (Fig. 3c), *Tamarix aphylla* and more recently cacti. Each of the Weeds of National Significance has a "Best Practice Manual", which guides management (these can be found on http://weeds.ala.org.au/). The only non-WONS weed of arid regions with comparably detailed management guidelines is *Cenchrus ciliaris* (Biosecurity South Australia 2012).

Australia's Natural Resource Management Regions and Local Government areas also impose responsibilities for weed control. A further government requirement is for the identification of weeds in environmental impact assessments of potential mining activities. This has led to many mining companies having their own Weed Management Plans. Individual properties or stations may also have documented Weed Management Plans.

Complementing the management strategies is the development in Australia of a Weed Risk Assessment System (Pheloung et al. 1999). This provides a framework for identifying the plant species that could threaten the target region. Numerous plant species have been assessed, usually with a focus on species relevant to a particular state (examples can be seen at http://weeds.ala.org.au/weedmanagement.htm). At a finer level, there is a need for risk assessment of cultivars of plants introduced to the region, such as if new cultivars of *Cenchrus ciliaris* are considered for importation.

One outcome of risk assessments is the identification of alert weeds (plants that currently have a restricted distribution but which could become important threats to biodiversity). Examples from the Alice Springs region are *Cenchrus setaceus* (fountain grass), *Prosopis* spp. (mesquite) and *Vachellia nilotica* (prickly acacia) (Northern Territory Government of Australia 2016b).

The different strategies of weed management can be grouped along the biosecurity continuum. First, there is the quarantine barrier and then management of incursions by eradication and/or containment, while well-established weeds are subject to control through, for example, herbicides, mechanical treatments, fire, grazing, integration of two or more of these and biological control.

Quarantine Barriers and Other Preventative Methods

It is well recognised that garden plants are the most likely source of new weed invasions. However, it is very rare (and often controversial) for this threat to be managed. The recent survey of 16 Pilbara towns for cactus species has led to the removal of garden plantings and discovery of three new populations that have "jumped the garden fence" (Rangelands N.R.M. Western Australia 2015). Likewise, cacti invasions have been detected in the NT (Batchelor Institute 2013). These preventative measures also educate the local population about the threat presented by cacti to arid regions. There are state-based quarantine barriers at borders and restrictions on the movement of plants within some states (e.g. WA), but there are no official quarantine barriers specifically in place to protect arid regions of Australia.

Eradication

Eradication means the removal of all individuals of a species, as well as possibilities for regeneration (i.e. seedbanks, vegetative parts) from an area into which there are limited possibilities of further immigration (Scott et al. 2014). Unfortunately, eradication programmes often fail, because the incursion is discovered a considerable time after it has begun (often more than 10 years); it is difficult to delimit the distribution of the species, and long-lived seed banks compromise control attempts (Panetta 2015). Despite this, there are examples of control efforts that could eventually achieve eradication in the arid regions of Australia.

Nerium oleander (common oleander) is a toxic species with potential to form monocultures with impacts on native vegetation and stream flow (Edmunds 2010). This alien species has invaded 13 km of a creek in SA's Flinders Ranges. Over 5 years, landholders, volunteers and contractors have co-operated to control and remove the plant with a longer-term objective of eradicating the weed from the area (Edmunds 2010).

A new infestation of the WoNS, *Parthenium hysterophorus* (parthenium weed) in the NT, is currently under containment with a view to eradication (Northern Territory Government of Australia 2016b). Also, *Parthenium hysterophorus* was detected in 2011 for the first time in the Pilbara, WA. When detected, the infested area with 48 plants was about one square metre and obviously at the initial invasion step. An eradication programme has started with monitoring assisted by the mine operating in the area (Penna and MacFarlane 2012). This eradication is likely to succeed as the biology of the weed is well known, and resources are available to survey and kill plants.

Containment

Containment is deliberate action to prevent range expansion within a predefined area (Scott et al. 2014; Fletcher et al. 2015). The management of an invasive palm and mesquite in the Pilbara, WA, are good examples of this strategy. The invasive date palm, *Phoenix dactylifera*, is being contained to the Millstream National Park (Department of Environment and Conservation Western Australia 2011) (Fig. 3d) by a range of methods. The male plants were left for aesthetic reasons in areas regularly accessed by tourists, whereas female plants were removed. This was done to maintain the cultural heritage (oasis) aspect of part of the National Park. When the male plants die, they will be replaced with native vegetation. Another unusual aspect of palm management at Millstream was the excavation of living specimens that were transported to Perth, where the palms are not invasive, for use in urban landscaping. The containment of *Phoenix dactylifera* in the Pilbara needs to be a long-term activity, because there is a seed bank that requires management (Department of Environment and Conservation Western Australia 2011).

The largest infestation of mesquite (*Prosopis* species and hybrids) in Australia is on Mardie Station, and it is subject to a range of weed management methods with containment as a strategic goal. Initially, the plan was to contain the infestation to Mardie Station by preventing spread to neighbouring properties. Subsequently, natural features in the landscape that are unfavourable to the weed such as rocky ridges and hills were exploited as containment barriers. Quarantining cattle into holding paddocks for a period before movement onto mesquite-free areas is important, because cattle eat mesquite pods and are a significant dispersal agent of the seed. In addition, all machinery leaving the property is cleaned to prevent seed dispersal (Osmond 2003; van Klinken and Campbell 2009).

Biological Control

Australian efforts in biological control across all ecosystems have targeted over 90 weed species with over 240 agents (arthropods and fungi) being released and resulting in significant economic and environmental benefit (Julien et al. 2012). Twelve alien weed species found in arid Australia have been considered or targeted.

Preliminary assessment of potential biological control agents has occurred for *Argemone mexicana* and *Argemone ochroleuca* (Heard and Segura 2012), *Asphodelus fistulosus* (Cullen 2012) and *Carthamus lanatus* (Morin and Sheppard 2012), but none have been introduced into Australia. In most cases the projects are suspended, because there has not been a sufficiently strong economic rationale for continuing the studies. The preliminary assessment of *Tribulus terrestris* (caltrop) found a diverse flora of native *Tribulus* species in the inland of Australia (Scott 2012) which makes it difficult (but not impossible) to find host-specific biological control agents. An additional three genera of weeds have been targeted for biological control, but their main distribution is outside the arid zone (Julien et al. 2012).

Biological control has been partially successful against *Prosopis* spp. in the Pilbara, WA (van Klinken 2012; van Klinken and Pichancourt 2015), the only case of some degree of success in arid Australia. Even so, management of this weed relies on a combination of biological control, mechanical and chemical control (van Klinken 2012), as well as quarantine and containment measures (as outlined above) and is an outstanding demonstration of integrated weed control. *Parkinsonia aculeata* (Fig. 3c) is also being targeted, including around Alice Springs, NT and the Pilbara region, WA (van Klinken and Heard 2012).

Biological control was considered as a solution to the problem of bush encroachment by native weeds in arid and semiarid regions of QLD and NSW during the 1970s and 1980s. Targeted species included *Eremophila mitchellii*, *Eremophila sturtii*, *Myoporum deserti*, *Dodonaea viscosa* subsp. *angustissima* (Julien and Sparks 2012) and *Cassinia* sp. (Holtkamp 2012). Not surprisingly, this did not work given that the problem was probably due to overgrazing of the understory. Moreover, the potential control organisms, being native, would have been expected to have already reached ecological equilibrium with the host plants.

In addition to the weed species already discussed, prospective targets for biological control of weeds in arid regions include *Passiflora foetida* (stinking passion flower, Fig. 3e, f), which is an invader of wetter microclimates (e.g. riparian ecosystems) in the Pilbara region of WA, and the WoNS, *Tamarix aphylla*, whose congeners have been successfully targeted by biocontrol in North America (Hudgeons et al. 2007). These potential targets, as well as the other mentioned above, where some research has occurred, all require better documentation of the impacts on the environment and economics, to decide whether the projects are justified and to allow any eventual benefits to be measured. Secondly, releases that have already been made into arid regions should be assessed, in particular to identify the environmental conditions for success or failure. Thirdly, many populations of target weeds occur in isolated populations, and redistribution of agents, perhaps on a regular basis, should be tried.

Chemical Control

Broad-scale application of herbicide does not occur in arid regions, being impractical across the large areas involved and given the low economic value of land. Instead, chemical control of plants in arid regions mostly involves highly targeted applications such as direct application to freshly cut stumps or control of weeds along water courses. Herbicide use is most appropriate when the infestations of shrubs or trees are sufficiently restricted and of sufficiently low density to warrant containment. Additional foliar sprays may be required as part of follow-up after larger plants have been sprayed, especially for regrowth from stumps, roots or stems. *Prosopis* spp., *Parkinsonia aculeata* and *Tamarix aphylla* are three invading tree species against which a range of chemical treatments have been applied (Osmond 2003; Queensland Department of Natural Resources Mines and Energy 2004; Northern Territory Government of Australia 2016a).

Herbicide resistance is the most important issue affecting weed control in Australian agriculture and occurs in annual weeds of cropping (e.g. *Chloris truncata, Conyza bonariensis*, *Sonchus oleraceus*) (Heap 2015) that are also weeds of arid regions. However, herbicide resistance has not been reported as originating from within the arid regions of Australia, probably because herbicide use is not intensive. Indeed, apart from herbicides for control of Weeds of National Significance, there are no herbicides specifically registered for general use in deserts or arid regions and only two for rangelands (Australian Pesticides and Veterinary Medicines Authority 2015). While *Cenchrus ciliaris* is listed as a pest of numerous crops (e.g. cotton), there are no herbicide registrations for weeds in *Cenchrus ciliaris* where it is grown as a pasture (Australian Pesticides and Veterinary Medicines Authority 2015).

Mechanical Control

Bulldozing, blade-ploughing and deep-ripping are used to open up dense infestations of *Tamarix aphylla* so that herbicides can be applied. This approach has been applied along over 400 km of the 600 km infestation on the Finke River, NT (Northern Territory Government of Australia 2016a). A range of large-scale mechanical treatments (e.g. chains, front-mounted blade plough) have been trialled for *Prosopis* control (van Klinken and Campbell 2009).

Fire, Grazing and Integrated Weed Management

Depending on the species concerned, weed impacts can be reduced or enhanced by fire. Fire was an integral part of arid Australian ecosystems for many thousands of years before European settlement. The introduction of livestock, combined with a reduction in fire frequency, contributed to the development of "woody weed" infestations in many susceptible areas (Noble 1997) including western NSW (see also "Native weeds" above). Provided that adequate fuel can be re-established, fire has the advantage of being far cheaper than chemical or mechanical treatments for combating woody weeds (Harland 1993; van Klinken and Campbell 2009). On the other hand, fire on its own may encourage the spread of *Cenchrus ciliaris* (Miller et al. 2010), but, if combined with follow-up herbicide while regrowth is green, it will aid control. Strategic grazing through fencing to soil type and stock water placement and management can reduce the growth and reproduction of *Cenchrus ciliaris*, as can integrate weed management involving various combinations of mechanical, herbicide, fire and grazing treatments at different spatial scales (Friedel et al. 2011).

Potential Uses

Some novel uses have been proposed for weedy species. For example, *Arundo donax* (giant reed), which presents a weed risk to riparian areas of arid and semiarid Australia, as well as much wetter regions, has been proposed as a source of biofuel and could be managed outside riparian areas with strict protocols which were required to prevent infestation of waterways (Virtue et al. 2010). "Woody weeds" could become a source of carbon credits through avoiding clearing of bush-encroached land, but questions regarding other values such as future pastoral productivity and biodiversity outcomes remain unresolved (Grant and Gavin 2015).

Climate Change

The future climate of Australia's arid regions (by 2090) is projected to be warmer, to have more frequent hot days and to have less frost (Watterson et al. 2015). There is likely to be less rainfall in winter (in the south) and in spring (throughout), but climatic changes in other seasons are unclear. The intensity of heavy rainfall events is projected to increase, but changes to drought frequency and intensity are less clear. Tropical cyclones are likely become less frequent, contrasting with an increase in the frequency of more intense storms.

More intense storms will likely increase the dispersal ability and invasion potential of weeds, many of which are associated with watercourses (e.g. *Tamarix aphylla*), and also provide suitable disturbed soil and open habitats for weed colonisation (e.g. many annual weeds and grasses). However, an increase in the number of hot days and less winter rainfall could make the arid regions less favourable for species originating in the Mediterranean and temperate climates of the south. It is not clear if there will be a lessened threat of weed invasion from the north, and responses to climate change are likely to be species-specific.

The assessment of climate change responses by arid-zone species has mostly focused on *Cenchrus ciliaris*. It acclimates to higher temperatures (Dwyer et al. 2007), increases growth in conditions of increased atmospheric CO_2 (Rudmann et al. 2001; Bhatt et al. 2007) and maintains competitiveness and response to fire under increased CO_2 (Tooth and Leishman 2014), conditions expected under global climate change. Higher temperatures may favour *Cenchrus ciliaris*, being a C_4 species, whereas increased CO_2 may favour C_3 shrubs over C_4 grasses, and declining rainfall may disadvantage all grasses (Friedel et al. 2014). *Cenchrus ciliaris* represents a major threat to the Great Western Woodlands (GWW), which are found on the southern boundary of the WA arid zone (Prober et al. 2012). Bare sandy areas characteristically separate vegetated areas, inhibiting extensive fires, but colonisation of these bare areas by *Cenchrus ciliaris* following climate change could lead to fire-induced transition from forest to grassland. Overall however, the ecological impact of climate change on weedy species in arid Australia is unclear.

Cacti are already a threat to Australia's arid rangelands under current climate. In addition, their CAM photosynthetic pathway preadapts them to the projected decreased rainfall under climate change. Because of the vast size of the arid zone, biological control will be the most likely solution to weed problems. However, the impact of the main biological control agent of cacti, *Cactoblastis cactorum*, may be compromised by increased CO_2 (Scott et al. 2014; Webber et al. 2014). The issue of climate change impacts on the sustained efficiency and effectiveness of existing biological control programmes is an urgent one, requiring research and monitoring to forewarn of future changes (Scott et al. 2014).

Change in climate may require new approaches to and philosophies for vegetation management. Significant shifts, expansions and contractions in species distributions, either tracking climate change naturally or via changes to landscape connectivity, will require rethinking of what it means to be native (Webber and Scott 2012). Secondly, our attitude to invasive alien trees may change due to their value in providing shade for thermal moderation. For over a century, the gardens around station homesteads in the arid region have generally been planted with alien shade trees. Some of these (e.g. mesquite, athel pine) have become major weed problems. However, there are many other alien trees that have not shown invasive tendencies, and perhaps these should be used in managed plantations as a refuge for animals under a climate of increasing temperature.

The occurrence of fire will also be affected by climate change. Bradstock (2010) argued that while weather suitable for fire might be somewhat predictable, vegetation responses to fire and lightning ignition rates are less so. Higher CO_2 may advantage shrubs over grasses, reducing available litter. On the other hand, it may change the carbon/nitrogen ratio and slow decomposition, so that litter remains as a fire intensifier in the landscape for longer. Less rain may mean less litter, whereas higher temperatures may lead to increases in litter production by some invasive grasses. The implications for flammable invaders or for control of bush encroachment will depend on local conditions including land use (Friedel et al. 2014).

Threats Posed by Australian Species to Arid Regions Elsewhere

Very few arid region species native to Australia have become weeds elsewhere in the world, and of those that have, it appears that all the global invaders of Australian origin belong to the family Chenopodiaceae. At least four species of *Atriplex* (*A. eardleyae*, *A. lindleyi*, *A. nummularia* and *A. semibaccata*) are established in karoo shrublands and other arid biomes in southern Africa (Mucina and Snijman 2011), while *Atriplex lindleyi* and *Atriplex nummularia* are naturalised in North America (Welsh 2015). *Maireana brevifolia*, a widespread arid region plant in Australia, has also been introduced to semi-desert regions of South Africa (Mucina and Snijman 2011) and is now recorded from Chile, the Middle East and the Canary Islands (Mucina and Snijman (2011) and references therein). Another chenopod species *Salsola australis* is a major invader of pasture in North America but was previously considered to be *Salsola tragus*, a Eurasian species (Borger et al. 2008). This species has been targeted for biological control in North America, with the search for agents being directed to Asia. A future management option for North America would be to search for biological control agents in Australia.

We contend that the number of weeds from Australian arid regions is low primarily because there are no crops and very few pasture species (e.g. *Atriplex lindleyi*) that originate from this region. The invasion risk of the recently developed Australian pasture legume, *Cullen* species (Dear et al. 2007), should be assessed. Additionally, there is almost no trade to similar climate regions (most trade is with colder regions (minerals) or tropical or Mediterranean regions (livestock)), and tourist activities are limited (few roads, limited and expensive accommodation), reducing the opportunity for export of species from the Australian arid regions.

Conclusions

Australia is a global leader in weed management research and implementation, in no small part due to the large number of invasive alien plants introduced into the country. Arid regions of Australia, however, are under-represented in both proportions of weed species for the continent and relative to native species, as well as the awareness of impacts and invasion dynamics for these weeds. While the former issue is good news for weed management, it does not remove the need for an improved understanding of the weeds that are already there and an awareness of the threats that weeds, both existing and novel ones, might represent in the future. This review represents the first overview of weeds of Australia's arid regions, and from it we can draw the following four insights. Firstly, weeds of arid regions are qualitatively different from those in other regions of Australia, with few species involved, mainly from the plant families Poaceae and Asteraceae. Secondly, while few species have spread and become invasive (*Tamarix aphylla*, *Prosopis* spp., *Opuntia* spp.), the impact of a few species can be significant, in particular the grass *Cenchrus ciliaris*, a species with the capacity to spread over most of the arid region (Lawson et al. 2004). Some native species are a threat both to arid regions in Australia and elsewhere in the world. Thirdly, management options come from across the biosecurity continuum, including the use of chemical and mechanical treatments, fire, grazing, combinations of these (integrated weed management) and biological control, and have been remarkably effective in some situations. Lastly, future climate change has the potential to exacerbate the threat from weeds, creating new opportunities for invasion, potentially compromising current control options, and requiring new research approaches. What this synthesis also highlights is the need for sustained and increased research for improving the management efficiency and effectiveness of weeds in arid regions to avoid another case of the rosy dock situation, "spreading like a red blanket further than the eye can see" (Baker 1995).

Acknowledgements We thank Hans Lambers and Rieks van Klinken for their comments on versions of the manuscript.

References

Albrecht D, Rogers L (1999) Weeds of the Tanami A field guide to the environmental weeds of the Tanami region, Central Australia. Normandy NFM Limited, Alice Springs

Australian Pesticides and Veterinary Medicines Authority (2015) Public chemical registration information system search. Available at https://portal.apvma.gov.au/pubcris. Accessed 7 Nov 2015

Baker J (1995) The story of rosy dock. Random House Australia, Milsons Point

Batchelor Institute (2013) New cactus weed found in Alice Springs. Available at http://www.batchelor.edu.au/portfolio/new-cactus-weed-found-in-alice-springs/. Accessed 23 Sept 2016

Bhatt RK, Baig MJ, Tiwari HS (2007) Growth, biomass production, and assimilatory characters in *Cenchrus ciliaris* L. under elevated CO_2 condition. Photosynthetica 45:296–298

Biosecurity South Australia (2012) South Australia buffel grass strategic plan: a plan to reduce the weed threat of buffel grass in South Australia. Government of South Australia. Available at http://www.pir.sa.gov.au/__data/assets/pdf_file/0005/177656/91806_SA_Buffel_Grass_Strat_Plan_FIN_WEB.pdf

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. Trends Ecol Evol 26:333–339

Borger CPD, Yan G, Scott JK, Walsh MJ, Powles SB (2008) *Salsola tragus* or *S. australis* (Chenopodiaceae) in Australia – untangling taxonomic confusion through molecular and cytological analyses. Aust J Bot 56:600–608

Bradstock RA (2010) A biogeographic model of fire regimes in Australia: current and future implications. Glob Ecol Biogeogr 19:145–158

Commonwealth of Australia, Australian Weeds Committee (2012) Weeds of national significance opuntioid cacti (*Austrocylindropuntia*, *Cylindropuntia*, *Opuntia* spp.) strategic plan. Australian Weeds Committee, Canberra

Cooke J, Groves RH, Ash J (2011) The distribution of *Carrichtera annua* in Australia: introduction, spread and probable limits. Rangel J 33:23–35

Craven LA (1996) A taxonomic revision of *Heliotropium* (Boraginaceae) in Australia. Aust Syst Bot 9:521–657

Cullen J (2012) Asphodelus fistulosus L. – onion weed. In: Julien M, McFadyen R, Cullen J (eds) Biological control of weeds in Australia. CSIRO, Canberra, pp 83–85

Curran G (2007) Possible ward's weed toxicity. New South Wales Animal Health Surveillance 2007/1, 4

Dear B, Li G, Hayes R, Hughes S, Charman N, Ballard R (2007) *Cullen australasicum* (syn. *Psoralea australasica*): a review and some preliminary studies related to its potential as a low rainfall perennial pasture legume. Rangel J 29:121–132

Department of Environment and Conservation Western Australia (2011) Millstream Chichester National Park and Mungaroona Range Nature Reserve Management Plan No. 69. Available at http://www.dpaw.wa.gov.au/images/documents/parks/management-plans/decarchive/millstream_mp_final_oct3.pdf

Dhanji S (2009) Weeds of central Australia a field guide. Greening Australia, Darwin

Dodd J, Reeves A, Watkins R, Anderson L (2012) Situation statement: the 'prickle bush' weeds (mesquite, parkinsonia and prickly acacia) in Western Australia. Department of Agriculture and Food, Western Australia Available at http://archive.agric.wa.gov.au/objtwr/imported_assets/content/pw/weed/decp/prickle_bush_weeds_situation.pdf

Dunbar KR, Facelli JM (1999) The impact of a novel invasive species, *Orbea variegata* (African carrion flower), on the chenopod shrublands of South Australia. J Arid Environ 41:37–48

Dwyer SA, Ghannoum O, Nicotra A, von Caemmerer S (2007) High temperature acclimation of C_4 photosynthesis is linked to changes in photosynthetic biochemistry. Plant Cell Environ 30:53–66

Edmunds LJ (2010) Good will and best practice – controlling oleander (*Nerium oleander*) in Parachilna Gorge, South Australia. In: Zydenbos SM (ed) 17th Australasian weeds conference Christchurch, New Zealand, 26–30 September, 2010, pp 91–94

Eldridge D, Bowker M, Maestre F, Roger E, Reynolds J, Whitford W (2011) Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. Ecol Lett 14:709–722

Fletcher CS, Westcott DA, Murphy HT, Grice AC, Clarkson JR (2015) Managing breaches of containment and eradication of invasive plant populations. J Appl Ecol 52:59–68

Friedel MH, Grice AC, Marshall NA, van Klinken RD (2011) Reducing contention amongst organisations dealing with commercially valuable but invasive plants: the case of buffel grass. Environ Sci Pol 14:1205–1218

Friedel M, Allan GE, Duguid A (2014) Do we know enough about vegetation dynamics to manage fire regimes in central Australia? Ecol Manag Restor 15:128–132

Fuller MR (1993) The invasion and control of *Tamarix aphylla* on the Finke River, central Australia. In: Wilson BJ, Swarbrick JT (eds) Proceedings II of the 10th Australian weeds conference and 14th Asian Pacific weed science society conference. Brisbane, Australia, 6–10 September, 1993, pp 44–46

Gardner CA, Bennetts HW (1956) The toxic plants of Western Australia. West Australian Newspapers Ltd, Perth

Gosper CR, Prober SM, Yates CJ, Scott JK (2015) Combining asset- and species-led alien plant management priorities in the world's most intact Mediterranean-climate landscape. Biodivers Conserv 24:2789–2807

Grant R, Gavin J (2015) How will the carbon economy impact southern Australian rangelands? Range Manag Newslett 15/3:4–5

Grice AC (2002) The biology of Australian weeds. 39. *Ziziphus mauritiana* Lam. Plant Protect Q 17:2–11

Grice AC (2006) The impacts of invasive plant species on the biodiversity of Australian rangelands. Rangel J 28:27–35

Grice AC, Friedel MH, Marshall NA, van Klinken RD (2012) Tackling contentious invasive plant species: a case study of buffel grass in Australia. Environ Manag 49:285–294

Griffin GF (1993) The spread of buffel grass in inland Australia: land use conflicts. In: Proceedings I of the 10th Australian weeds conference and 14th Asian Pacific weed science society conference. Brisbane, 6–10 September, 1993, Queensland Weed Society, Queensland Australia, pp 501–504

Griffin GF, Smith DMS, Morton SR, Allan GE, Masters KA, Preece N (1989) Status and implications of the invasion of tamarisk (*Tamarix aphylla*) on the Finke River, Northern Territory, Australia. J Environ Manag 29:297–315

Harland R (1993) Managing for woody weed control in western NSW. Woody Weeds Task Force, NSW Agriculture, Dubbo

Harris MR, Facelli JM (2003) Competition and resource availability in an annual plant community dominated by an invasive species, *Carrichtera annua* (L. Aschers.), in South Australia. Plant Ecol 167:19–29

Harvey A (2009) State Opuntioid Cacti Management Plan December 2009 for Biosecurity SA NRM Biosecurity. Available at http://www.pir.sa.gov.au/__data/assets/pdf_file/0007/237337/A809089_-_Opuntioid_cacti_Management_Plan_Attach.pdf. Accessed 8 Aug 2016

Heap I (2015) The international survey of herbicide resistant weeds. Available at www.weedscience.com. Accessed 6 Nov 2015

Heard TA, Segura R (2012) *Argemone mexicana* L. and *Argemone ochroleuca* Sweet – Mexican poppy. In: Julien M, McFadyen RE, Cullen J (eds) Biological control of weeds in Australia. CSIRO Publishing, Collingwood, pp 65–72

Hocking PJ, Finlayson CM, Chick AJ (1998) *Phragmites australis* (Cav.) Trin. ex Steud. In: Panetta FD, Groves RH, Shepherd RCH (eds) The biology of Australian weeds, vol 2. R.G. and F.J. Richardson, Melbourne, pp 177–206

Holtkamp RH (2012) *Cassinia* spp. – cassinia. In: Julien M, McFadyen RE, Cullen J (eds) Biological control of weeds in Australia. CSIRO Publishing, Collingwood, pp 146–149

Hosking JR (2012) *Opuntia* spp. In: Julien M, McFadyen RE, Cullen J (eds) Biological control of weeds in Australia. CSIRO Publishing, Collingwood, pp 431–436

Hudgeons JL, Knutson AE, Heinz KM, DeLoach J, Dudley TL, Pattison RR, Kiniry JR (2007) Defoliation by introduced *Diorhabda elongata* leaf beetles (Coleoptera: Chrysomelidae) reduces carbohydrate reserves and regrowth of *Tamarix* (Tamaricaceae). Biol Control 43:213–221

Humphreys LR (1967) Buffel grass (*Cenchrus ciliaris*) in Australia. Trop Grasslands 1:123–134

Hussey BMJ, Keighery GJ, Dodd J, Lloyd SG, Cousens RD (2007) Western Weeds a guide to the weeds of Western Australia, 2nd edn. Weed Society of WA Inc, Victoria Park

Jessop J (1981) Flora of Central Australia. A.H. & A.W. Reed Pty Ltd, Sydney

Julien M, Sparks D (2012) *Eremophila michellii* Benth. – budda *Eremophila sturtii* R.Br. – turpentine bush *Dodonaea viscosa* subsp. *angustissima* (DC.) JGWest – narrow-leaf hopbush *Myoporum deserti* (A.Cunn. ex Benth.) Chinnock – poison-bush. In: Julien M, McFadyen RE, Cullen J (eds) Biological control of weeds in Australia. CSIRO Publishing, Collingwood, pp 256–258

Julien M, McFadyen R, Cullen J (2012) Biological control of weeds in Australia. CSIRO Publishing, Collingwood

Kharrat-Souissi A, Siljak-Yakovlev S, Brown SC, Baumel A, Torre F, Chaieb M (2014) The polyploid nature of *Cenchrus ciliaris* L. (Poaceae) has been overlooked: new insights for the conservation and invasion biology of this species – a review. Rangel J 36:11–23

Kondo T, Crisp MD, Linde C, Bowman DMJS, Kawamura K, Kaneko S, Isagi Y (2012) Not an ancient relic: the endemic *Livistona* palms of arid central Australia could have been introduced by humans. Proc R Soc B 279:2652–2661

Lawson BE, Bryant MJ, Franks AJ (2004) Assessing the potential distribution of buffel grass (*Cenchrus ciliaris* L.) in Australia using a climate-soil model. Plant Protect Q 19:155–163

Lenz TI, Facelli JM (2003) Shade facilitates an invasive stem succulent in a chenopod shrubland in South Australia. Austral Ecol 28:480–490

Marshall VM, Lewis MM, Ostendorf B (2012) Buffel grass (*Cenchrus ciliaris*) as an invader and threat to biodiversity in arid environments: a review. J Arid Environ 78:1–12

Michael PJ, Yeoh PB, Scott JK (2012) Potential distribution of the Australian native *Chloris truncata* based on modelling both the successful and failed global introductions. PLOS One 7:e42140

Miller G, Friedel M, Adam P, Chewings V (2010) Ecological impacts of buffel grass (*Cenchrus ciliaris* L.) invasion in central Australia – does field evidence support a fire-invasion feedback? Rangel J 32:353–365

Mitchell AA (1979) Poisonous plants in Northern Territory rangelands. Aust Rangel J 1:239–243

Morin L, Sheppard AW (2012) *Carthamus lanatus* L. – saffron thistle. In: Julien M, McFadyen RE, Cullen J (eds) Biological control of weeds in Australia. CSIRO Publishing, Collingwood, pp 139–145

Mucina L, Snijman DA (2011) *Maireana brevifolia* (Chenopodiaceae: Camphorosmeae), a new naturalized alien plant species in South Africa. Bothalia 41:235–238

Noble JC (1997) The delicate and noxious scrub: CSIRO studies on native tree and shrub proliferation in the semi-arid woodlands of Eastern Australia. CSIRO Wildlife and Ecology, Lyneham

Northern Territory Government of Australia (2016a) Athel pine. Available at https://nt.gov.au/environment/weeds/list-of-declared-weeds-in-the-nt/athel-pine. Accessed 8 Aug 2016

Northern Territory Government of Australia (2016b) Weed management plans. Available at https://landresources.nt.gov.au/rangelands/guidelines-and-management-plans/weed-management-plans. Accessed 8 Aug 2016

Orchard AE (1999) Introduction. In: Flora of Australia, vol 1, 2nd edn. CSIRO Publishing, Melbourne, pp 1–9

Osmond R (2003) Mesquite best practice manual: control and management options for mesquite (*Prosopis* spp.) in Australia. Queensland Government Department of Natural Resources and Mines, Brisbane

Panetta FD (2015) Weed eradication feasibility: lessons of the 21st century. Weed Res 55:226–238

Penna A-M, MacFarlane M (2012) Parthenium incident in the Pilbara, Western Australia: how is this 'a good news story'? In: Eldershaw V (ed) Proceedings of the 18th Australian weeds conference. Melbourne, Victoria, Australia, 8–11 October 2012. Weed Society of Victoria Inc., Melbourne, pp 13–16

Pheloung PC, Williams PA, Halloy SR (1999) A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. J Environ Manag 57:239–251

Pitt JL, Virtue JG, Feuerherdt LJ (2006) Onion weed: pest or perception? In: Preston C, Watts JH, Crossman ND (eds) Proceedings of the 15th Australian weeds conference, Adelaide, South Australia, 24–28 September 2006, pp 454–457

Prober SM, Thiele KR, Rundel PW, Byrne M, Christidis L, Gosper CR, O'Connor MH, Grierson PF, Macfarlane C, Recher HF, Scott JK, Standish RJ, Stock WD, van Etten EJB, Wardell-Johnson GW, Watson A, Yates CJ (2012) Climate adaptation in intact landscapes: a framework for managing change and resilience applied to the world's largest Mediterranean-climate woodland. Clim Chang 110:227–248

Queensland Department of Natural Resources Mines and Energy (2004) Parkinsonia. Approaches to the management of parkinsonia (*Parkinsonia aculeata*) in Australia. Queensland Department of Natural Resources, Mines and Energy, Brisbane

Rangelands N.R.M. Western Australia (2015) Keeping a watch on cacti in the Pilbara. Available at http://www.rangelandswa.com.au/994/keeping-a-watch-on-cacti-in-the-pilbara. Accessed 23 Sept 2016

Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. Divers Distrib 6:93–107

Robinson TP, van Klinken RD, Metternicht G (2008) Spatial and temporal rates and patterns of mesquite (*Prosopis* species) invasion in Western Australia. J Arid Environ 72:175–188

Rudmann SG, Milham PJ, Conroy JP (2001) Influence of high CO_2 partial pressure on nitrogen use efficiency of the C_4 grasses *Panicum coloratum* and *Cenchrus ciliaris*. Ann Bot 88:571–577

Schatral A, Osborne JM (2002) Weeds threatening rehabilitation efforts on mine sites in the gold fields of Western Australia and the Northern Territory: competition between *Rumex vesicarius* (Polygonaceae) and Australian native plant species and seedbank studies. In: Proceedings of the 13th Australian weeds conference. Perth, Western Australia, 8–13 September 2002. Plant Protection Society of WA, Perth, p 569

Schatral A, Short N, Osborne JM, Andreoli E, Hansen M (2008) Studies on the soil seed bank of the environmental weed *Rumex vesicarius* (Fam.: Polygonaceae) at a rehabilitated mine site in semi-arid Western Australia. J Arid Environ 72:2075–2081

Scott JK (2012) *Tribulus terrestris* L. – caltrop. In: Julien M, McFadyen RE, Cullen J (eds) Biological control of weeds in Australia. CSIRO Publishing, Collingwood, pp 576–580

Scott JK, Webber BL, Murphy H, Ota N, Kriticos DJ, Loechel B (2014) AdaptNRM Weeds and climate change: supporting weed management adaptation. Available at http://adaptnrm.csiro.au/invasive-plants-climate-change/. Accessed 16 Dec 2014

Slatyer RO, Perry RA (1969) Arid lands of Australia. Australian National University Press, Canberra

Symon DE (1982) *Solanum* (Solanaceae) in arid Australia. In: Barker WR, Greenslade PJM (eds) Evolution of the flora and fauna of arid Australia. Peacock Publications, Frewville, pp 335–339

Tooth IM, Leishman MR (2014) Elevated carbon dioxide and fire reduce biomass of native grass species when grown in competition with invasive exotic grasses in a savanna experimental system. Biol Invasions 16:257–268

Trudgen MS, Webber BL, Scott JK (2012) Human-mediated introduction of *Livistona* palms into central Australia: conservation and management implications. Proc R Soc B Biol Sci 279:4115–4117

van Klinken RD (2012) *Prosopis* spp. – mesquite. In: Julien M, McFadyen RE, Cullen J (eds) Biological control of weeds in Australia. CSIRO Publishing, Collingwood, pp 477–485

van Klinken RD, Campbell SD (2009) The biology of Australian weeds: 54. *Prosopis* species. In: Panetta FD (ed) The biology of Australian weeds, vol 3. R.G. and F.J. Richardson, Melbourne, pp 238–273

van Klinken RD, Heard TA (2012) *Parkinsonia aculeata* L. – parkinsonia. In: Julien M, McFadyen RE, Cullen J (eds) Biological control of weeds in Australia. CSIRO Publishing, Collingwood, pp 437–447

van Klinken RD, Pichancourt J-B (2015) Population-level consequences of herbivory, changing climate, and source-sink dynamics on a long-lived invasive shrub. Ecol Appl 25:2255–2270

Virtue JG, Reynolds T, Malone J, Preston C, Williams C (2010) Managing the weed risk of cultivated *Arundo donax* L. In: Zydenbos SM (ed) 17th Australasian weeds conference Christchurch, 26–30 September, 2010, pp 176–179

Watterson I, Abbs D, Bhend J, Chiew F, Church J, Ekström M, Kirono D, Lenton A, Lucas C, McInnes K, Moise A, Monselesan D, Mpelasoka F, Webb L, Whetton P (2015) Rangelands cluster report, climate change in Australia projections for Australia's natural resource management regions: cluster reports. CSIRO and Australian Government Bureau of Meteorology, Australia. Available at http://www.climatechangeinaustralia.gov.au/media/ccia/2.1.4/cms_page_media/172/RANGELANDS_CLUSTER_REPORT.pdf. Accessed 17 Feb 2015

Webber BL, Scott JK (2012) Rapid global change: implications for defining natives and aliens. Glob Ecol Biogeogr 21:305–311

Webber BL, van Klinken RD, Scott JK (2014) Invasive plants in a rapidly changing climate: an Australian perspective. In: Ziska LH, Dukes JS (eds) Invasive species and global climate change. CABI Publishing, Wallingford, pp 169–197

Welsh SL (2015) Atriplex Linnaeus. *Flora of North America* 4, http://www.efloras.org/florataxon.aspx?flora_id=1&taxon_id=103110. Accessed 16 Nov 2015

Feral Animals in the Semi-arid and Arid Regions of Australia: Origins, Impacts and Control

Neil D. Burrows

Introduction

For millions of years, Australia's terrestrial fauna and flora, driven by climatic oscillations and geomorphological processes, co-evolved in isolation. The result was a rich diversity of unusual wildlife, high levels of endemism and, prior to the arrival of humans, a pristine wilderness existing in a dynamic equilibrium. Following the arrival of Aborigines some 40–60 ka, Australia ceased to exist as a wilderness. Largely through hunting and burning the vegetation, Aborigines changed the structure and composition of the biota (Roberts et al. 1994; Bowman 1998; Flannery 2002; Gammage 2011; Jurskis 2014). This was further exacerbated by the introduction of the first feral animal to the Australian continent, the dingo (*Canis lupus dingo)*, some 3500–4000 years ago from neighbouring Indonesia or New Guinea (Gollan 1984; Clarkson et al. 2015). The dingo established across the entire mainland, including the arid zone, and asserted itself as a top-order predator (Glen and Dickman 2005; Moseby et al. 2012). It is thought to have caused the extinction of at least three vertebrates on the mainland: the thylacine (*Thylacinus cynocephalus*), the Tasmanian devil (*Sarcophilus harrisii*) and the Tasmanian native hen (*Gallinula mortierii*) (Corbett 1995; Johnson and Wroe 2003).

European settlement in 1788 saw the beginning of an unprecedented level of human-caused disruption to the Australian environment and its biota which included the introduction of exotic plants and animals, of which 23 species of mammals and 26 species of birds successfully established in the wild (Bomford 1991; Forsythe et al. 2004). Native wildlife has had to compete with a range of introduced and feral animals for habitat, and native fauna has been subjected to highly efficient predators such as the European red fox (*Vulpes vulpes*) and the feral cat (*Catus felis*), predators against which they have poorly evolved defences. Many feral animals adapted

---

N. D. Burrows (✉)
Department of Biodiversity, Conservation and Attractions, Kensington, WA, Australia
e-mail: Neil.Burrows@dbca.wa.gov.au

H. Lambers (ed.), *On the Ecology of Australia's Arid Zone*,
https://doi.org/10.1007/978-3-319-93943-8_13

well to the Australian environment, and without factors that normally control populations in their natural environment such as climate, food, habitat availability, predation and disease, the feral animals quickly populated, spread and occupied suitable habitats across the continent, often displacing native wildlife. Feral animals have had and continue to have significant ecological, environmental, economic and cultural impacts on Australia. For example, the economic impact on agriculture alone is estimated to be in excess of $285 million dollars per annum (Gong et al. 2009) in addition to the largely immeasurable damage to other less tangible environmental values. Feral animals impact on native wildlife by predation, competition for food and shelter, destroying habitat and spreading diseases. Feral cats and foxes have contributed to the decline and local extinction of native birds, reptiles and mammals (Clarke 2001; Kinnear et al. 2002; Denny and Dickman 2010); herbivores such as rabbits, feral goats, horses, donkeys and camels have caused irreversible damage to vegetation, habitat, soils and waterways (Mckenzie et al. 2006). The annual environmental cost of vertebrate pest animal damage, as difficult as it is to value, is estimated to about $350 million (McLeod 2004), and the combined annual environmental, biodiversity and agricultural cost has been estimated at close to $1 billion (Saunders et al. 2010).

Introduced and feral animals carry a variety of diseases that can impact domestic stock, pets and native animals. Hendersen (2009) reviewed diseases and pathogens in feral pigs, foxes, wild dogs, feral cats, feral goats, rabbits, cane toads, rodents and European carp and reported this group of animals hosted a range of serious bacterial, viral, fungal and helminth diseases and protozoan pathogens capable of affecting a wide range of native species. Feral animals can also carry and spread diseases commonly found in domestic stock, providing a reservoir for diseases and parasites that is not readily controllable.

The extent of impact of feral animals on environmental, economic, social and cultural values is a function of the species of feral animal, its distribution and density, there being thresholds below which negative impacts are negligible or immeasurable (Hone 2007). Cost-effective control measures, therefore, will aim to reduce impacts to values to acceptable levels, rather than to eradicate the pest animal per se. However, in the absence of good data on the density – damage level relationship, setting appropriate control objectives and expenditure is problematic. Given this context, this chapter provides an overview of the feral and introduced pest mammals that are of most concern to environmental and economic values in the arid and semi-arid regions of Australia. An introduced animal is any exotic animal introduced to Australia, whereas a feral animal is a species that was originally brought to Australia as a domestic animal (as a companion animal or as livestock) but which has escaped domestication and become wild. Species such as the European red fox that were not domesticated but were introduced into the wild for hunting are technically not feral animals but introduced pests; however, for simplicity exotic mammals that have adapted to the wild will be referred to here as feral animals.

Following their introduction, many species of feral animals dispersed into the harsh climatic environment of semi-arid and arid Australia. For many species, such as deer, climate and vegetation were barriers to their establishment, preferring more mesic forests and woodlands (Hall 2005), but other species were able to persist and thrive because of artificial watering points (James et al. 1999) or because they were well adapted to arid environments. Of the feral mammals found in Australia, 11 inhabit various parts of the arid and semi-arid regions of the continent, being cattle (*Bos taurus*), goat (*Capra bircus*), camel (*Camelus dromedaries*), donkey (*Equus asinus*), horse (*Equus caballus*), fox (*Vulpes vulpes*), cat (*Felis catus*), rabbit (*Oryctolagus cuniculus*), house mouse (*Mus musculus*), black rat (*Rattus rattus*) and pig (*Sus scrofa*). Of these, cattle, goat, camel, horse, donkey, rabbit, cat and fox are of most concern with regard to economic and environmental impacts in the semi-arid and arid region. Black rats are of conservation concern where they occur on arid offshore islands, and there have been some successful eradication programs. The origin, basic ecology, impacts and control methods for each of these will be considered in the following pages.

Cattle (*Bos taurus*)

Origin

Six cattle were among livestock that arrived from England with the First Fleet, and within months of arrival, they had wandered off and became feral – possibly the second species to do so (after the dingo). Over the ensuing years, cattle numbers increased with breeding of local herds and further imports. With the expansion of pastoralism, herds spread across the continent, including the semi-arid and arid region, where the establishment of artificial watering points enabled a beef industry to be established. Invariably, cattle escaped from pastoral properties, or evaded muster, and lived in a wild state. Cattle need regular access to water, so water availability has limited their spread. Today, most feral herds in the semi-arid and arid regions can be found in the rugged Pilbara and Kimberley regions of Western Australia in national parks and unfenced pastoral properties where they have access to artificial watering points or to pools in river systems and wetlands (Low 2008) (Fig. 1, Plate 1).

Impacts

As with almost all feral animals, the extent of environmental and economic impact depends on their population density and the resilience of the ecosystems they inhabit. If numbers are sufficiently high, feral cattle can interfere with the running of pastoral properties by increasing grazing pressure, contaminating the genetic quality of domestic herds, and hosting diseases. As with domestic stock, feral cattle feed on a range of native grasses, herbs and shrubs. While there are few detailed

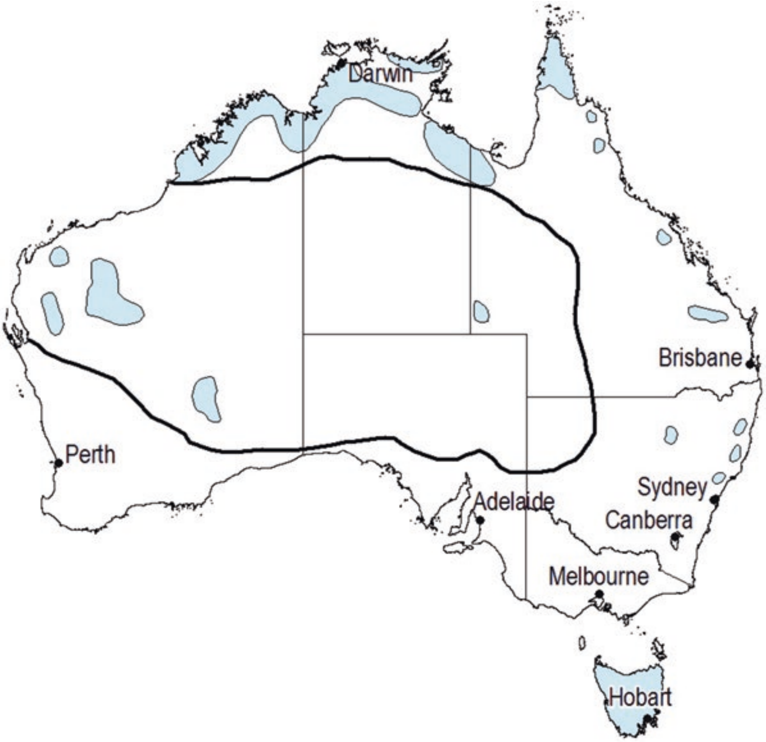


Fig. 1 Feral cattle can occur in any areas of past or present cattle grazing but are most prominent in the areas shown (blue) (Adapted from Van Dyk and Strahan 2008). The black line circumscribes the arid zone

studies on the ecological impacts of feral cattle specifically, it is known from observation that excessive cattle grazing and trampling is particularly damaging to soils, riparian zones and wetlands including mound springs, many of which are of high conservation significance. Damage to soil and vegetation structure by cattle in central Australia can degrade the habitat of reptiles and small mammals, including the rare bronzeback snake lizard (*Ophidiocephalus taeniatus*), the critically endangered central rock rat (*Zyzomys pedunculatus*) and the vulnerable crest-tailed mulgara (*Dasycercus cristicauda*) (Cogger et al. 1993; Cole 1999; Masters et al. 2003; Crowley 2010; Read and Cunningham 2010).

Control

Maintaining boundary fencing in good condition will reduce the number of stock becoming feral. Feral cattle may also be trapped at watering points or caught during general mustering operations. If resources are available, feral cattle can be fenced

Plate 1 (Photo Neil Burrows)

out of sensitive habitats such as mound springs and riparian zones. In inaccessible terrain, aerial shooting is the most effective form of control.

Goat (*Capra hircus*)

Origin

As with cattle, feral goats arrived with the First Fleet to provide a source of fresh meat and milk, and in the 1800s, angora and cashmere goats were imported to South Australia from Asia to start a goat fibre industry. With the collapse of the industry in the 1920s, herds were set free and became feral. Being 'hardy' and a source of fresh meat and milk, goats accompanied settlers, miners and railway- and telegraph-construction camps throughout Australia's arid and semi-arid regions in particular (Parkes et al. 1996). Today, feral goat populations are largest in the semi-arid and arid regions, with about 2.6 million feral goats occurring in a wide range of habitats across about 1.21 million km^2 (Parkes et al. 1996). The main concentrations are in western New South Wales, Midwestern Queensland, central eastern South Australia and Midwestern Western Australia (Parkes et al. 1996). These areas are mostly arid or semi-arid lands used for pastoralism, primarily for wool sheep. The distribution of feral goats in arid and semi-arid rangelands is limited by availability of water. Populations can be sustained where there are artificial watering points or permanent natural waters in river systems and mound springs.

During an era when sheep wool was in high demand, feral goats competed with the more valued sheep for food, causing an estimated annual loss to sheep production of about $17.8 million (Parkes et al. 1996). Because of their damaging impacts on the pastoral industry and the environment, feral goats are declared pests in several states. Consistent with the legislative requirements for landholders to manage pest animals, and because they competed with the more valuable sheep, goat numbers in the pastoral regions were controlled to relatively low levels by commercial mustering, trapping at watering points or shooting. However, during the 1990s the demand for wool, hence its price, fell, resulting in many pastoralists selling their sheep flocks and turning to 'farming' feral goats as a source of income; some jurisdictions now refer to feral goats not as declared pests, but as 'rangeland stock', causing confusion about their legal status (Forsythe and Parkes 2004). Consequently, their numbers nationally increased rapidly from about 1.4 million in 1997 to 4.1 million in 2008 (Pople and Froese 2012). Aerial surveys in 1987 and 1990 of 1.2 million km^2 in the Gascoyne-Murchison region of Western Australia estimated the feral goat population at about 363,000 and 596,000, respectively, an 18% per annum rate of increase (Southwell and Pickles 1993). Aerial surveys in South Australia estimated the feral goat population in 1990 at 200,000 (Pople et al. 1996). In good seasons, feral goats can increase by 40–75% per annum (Mahood 1985; Henzell 2008), highlighting their fast reproductive rate in suitable conditions (water and food). However, in 2010 the national feral goat population had declined to about 3.3 million (Pople and Froese 2012), and recent anecdotal evidence suggests that numbers may have declined even further as a result of the fickle market for goat meat and an increase in the density and distribution of wild dogs (Fig. 2, Plate 2).

Impacts

As mentioned, feral goats compete with livestock for food, often a scarce resource in the semi-arid and arid regions of the country. Where they occur at relatively high densities, feral goats are the most destructive pest animal in the semi-arid and arid regions. They are highly efficient generalist herbivores, able to eat almost any vegetation including foliage, bark, twigs, flowers, fruits, roots, plant litter and seeds on the ground (Parkes et al. 1996). Grazing by feral goats can prevent seedling regeneration and significantly alter the floristic composition of plant communities (Harrington 1986). There are few plants in the semi-arid and arid pastoral regions of Australia that goats can't and don't eat. Unlike sheep or cattle, goats are sufficiently nimble to stand on their hind legs, or partially climb trees to browse. In addition they are able to access vegetation in rugged gorges, breakaways and stony ranges, habitats usually inaccessible by other stock but which often support rare assemblages of plants and animals (lizards) (Gibson et al. 2012). They are particularly destructive

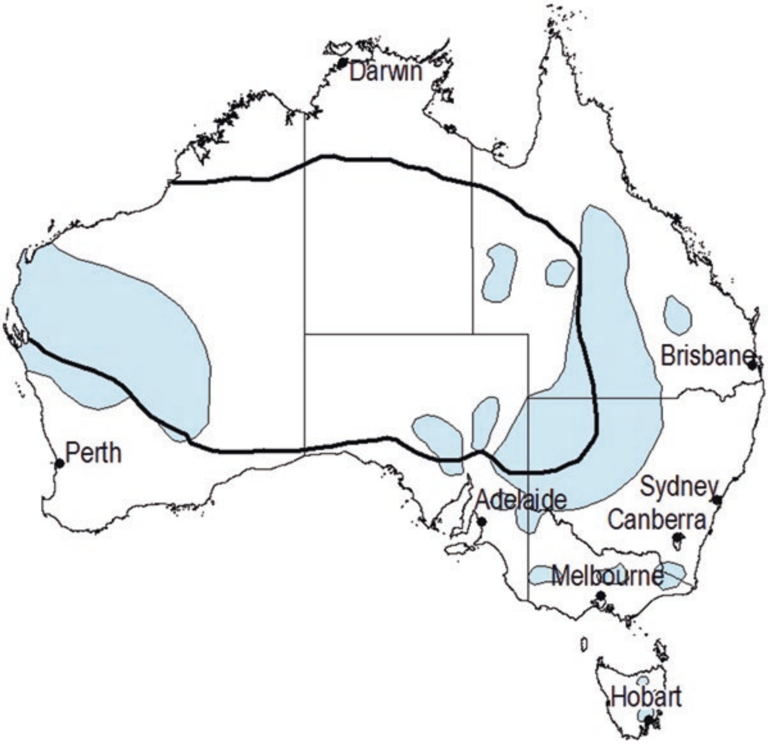


Fig. 2 The distribution of feral goats (blue) (Adapted from Van Dyk and Strahan 2008). Black line circumscribes the arid zone

to vegetation that has not evolved with herbivores such as island vegetation (Parkes 1990). Unlike other stock and most native herbivores, feral goats can persist during drought conditions, provided they have access to water, because they are able to survive on low-nutrient fibrous vegetation (Doyle et al. 1984). Unprecedented levels of herbivory during droughts can cause irreversible changes to plant communities. A number of studies report that removal of vegetation by feral goats, together with trampling, increases soil erosion (Henzell 1993; Elderidge 1998; Bayne et al. 2003). For example, Green et al. (1998) found that high-intensity grazing by goats near Cobar in New South Wales rapidly removed grass, killed most shrubs and damaged the soil structure making it highly susceptible to wind erosion. They concluded that this would lead to an increase in unpalatable shrubs, a decrease in perennial grasses and a reduction in the productivity of these semi-arid lands.

There are few studies quantifying the extent to which feral goats impact on the habitat of native fauna, but given their damaging impact on vegetation and soil, it is likely severe where grazing pressure is high. The Department of the Environment, Water and Heritage (DEWHA) (2008a) lists 57 threatened taxa that could be adversely affected by unmanaged goats, including 8 species of birds, 45 plant

Plate 2 (Photo Department of Agriculture and Food Western Australia)

species, 1 insect and 3 mammal species, being the yellow-footed rock-wallaby (*Petrogale xanthopus*), the brush-tailed rock-wallaby (*P. penicillata*) and the black-footed rock-wallaby (*P. lateralis*) (Gordon et al. 1993; Sharman et al. 1995; Menkhorst and Hynes 2010; Pearson 2013). The New South Wales Scientific Committee also identifies six threatened reptile species and two ecological communities that are likely threatened by feral goats. There is considerable anecdotal evidence of the damaging impact of high levels of grazing by feral goats. For example, following the removal of almost 30,000 introduced herbivores, including about 15,000 feral goats, from the Peron National Park in the Shark Bay World Heritage Area in Western Australia, over a 10-year period, there was an increase in the recovery of the vegetation and sightings of the threatened thick-billed grasswren (*Amytornis modestus*) (Brown 2001). The build-up of feral goat droppings around water holes and springs can degrade and damage habitat through eutrophication, thereby affecting freshwater biodiversity (Parkes et al. 1996).

Because of their potential to severely and permanently degrade native vegetation and damage soils, competition and land degradation by feral goats are listed in the Commonwealth Endangered Species Protection Act 1992 as a ‘Key Threatening Process’ to the survival of native species.

Control

As mentioned, in most Australian states, feral goats are classed as pest animals, and there is a legal requirement to control and, in some cases, to eradicate them. However this is contradicted by economic incentives to retain feral goat herds as an alternative source of revenue, especially following the decline in wool prices (e.g. Norris and Low 2005; Agnew et al. 2010), so the provisions of the law pertaining to the pest status of feral goats are rarely enforced.

Notwithstanding this, the most cost-effective feral goat control measures depend on a number of factors such as the density of goats, remoteness, accessibility, commercial opportunities and nature of the terrain and whether they are watering on artificial or natural watering points (Campbell and Donlan 2005; Agnew et al. 2010). Goats have been successfully trapped on artificial watering points during dry periods when there is no surface water, the preferred option when there is a market for the goats (Russell et al. 2011). Where trapping is not feasible or desirable such as in rugged or inaccessible terrain, aerial shooting has been successful (Pople et al. 1998), although Bayne et al. (2000) reported that aerial culling is relatively expensive (average $61 per goat) and that success is variable depending on whether the herd was naïve to aerial culling, in which case culling success was 40% (of the herd), or whether the herd had previously experienced aerial culling, when success rate fell to 21% as animals exhibited evasive behaviour. Other techniques that have been employed with limited success include ground shooting and poisoning of water holes with 1080 poison (Brown 2001). Agnew et al. (2010) provide an integrated framework for feral goat control, the elements of which include mustering, aerial culling and trapping at water points, with the sale of goats for meat off-setting the cost of the control program. Because of the potential for rapid reinvasion, it is essential that goat control measures are regionally coordinated across a number of adjoining landholders (Pople et al. 1998).

Camel (*Camelus dromedaries*)

Origin

One-humped camels were first introduced into Australia from Pakistan around 1840 as a means of transport, both as riding camels and in harnessed teams for hauling heavy loads. Their physical and physiological attributes made them ideally suited to arid and semi-arid conditions. They were used in preference to horses for exploring the dry interior, for hauling heavy loads associated with major infrastructure projects of the day including the construction of railways, roads, telegraph lines and barrier fences, and they were used for hauling agricultural products and mining equipment (McKnight 1969). Because of the cost of purchasing and shipping camels to Australia from Pakistan, the largest, strongest animals with good temperament

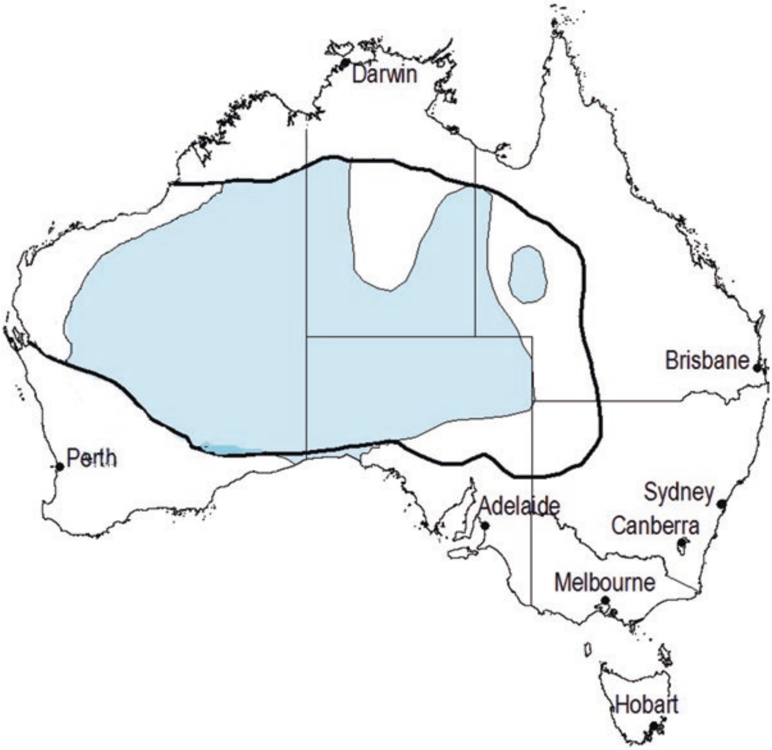


Fig. 3 The distribution of feral camels (blue) (Adapted from Van Dyk and Strahan 2008). Black line circumscribes the arid zone

were chosen, establishing something of a superior gene pool in the Australian camel population, which peaked just prior to the rise of motorised transport in the 1920s at about 20,000 (McKnight 1969).

Following the introduction of motorised transport, thousands of camels were released into the bush to become feral. Today, feral camels are widely distributed throughout arid Australia, occupying some 3.3 million km^2 of arid Western Australia, South Australia, the Northern Territory and Western Queensland (Saalfeld and Edwards 2010) (Fig. 3). Short et al. (1988) estimated the national camel population to be 43,000 in the late 1980s, and Edwards et al. (2004a) estimated a minimum population of 300,000 by 2001 and suggested the population was growing at about 10% per annum. By 2008 following increased aerial survey effort across a number of jurisdictions, the population was estimated at about 1 million (Saalfeld and Edwards 2010), of which about 50% occur in Western Australia, 27% in the Northern Territory and the remainder in South Australia and Queensland. The variability in population estimates is not only due to the different times the estimates were made but also to the different sampling techniques and assumptions made when extrapolating sample data to the continental scale. Notwithstanding this, the population of

Plate 3 Feral camel with satellite tracking collar (Photo Neil Burrows)

feral camels in arid Australia is probably in the vicinity of 750,000 animals, making Australia the only country in the world with a significant wild dromedary camel population.

Camel population density in the arid zone is highly variable but averages about 0.3 animals km^2 (Ward et al. 2005; Saalfeld and Edwards 2010). There is no indication that the feral camel population size has stabilised, and in the absence of natural predators, disease or coordinated control programs, the population will likely continue to grow at about 10% per annum for the foreseeable future (Edwards et al. 2004a) (Plates 3 and 4).

Impacts

Camels are well adapted to the semi-arid and arid regions of Australia. Primarily browsers, they can feed on a wide range of plants, go for long periods without drinking water and travel large distances in search for food and water, and their physiology is such that they can tolerate the often extreme climatic conditions of the arid zone (McLeod and Saunders 2001; Dorge and Heuck 2003; Lethbridge et al. 2010). While there are limited detailed studies on the ecological impacts of feral camels, there is mounting evidence that they are having significant negative impacts on a

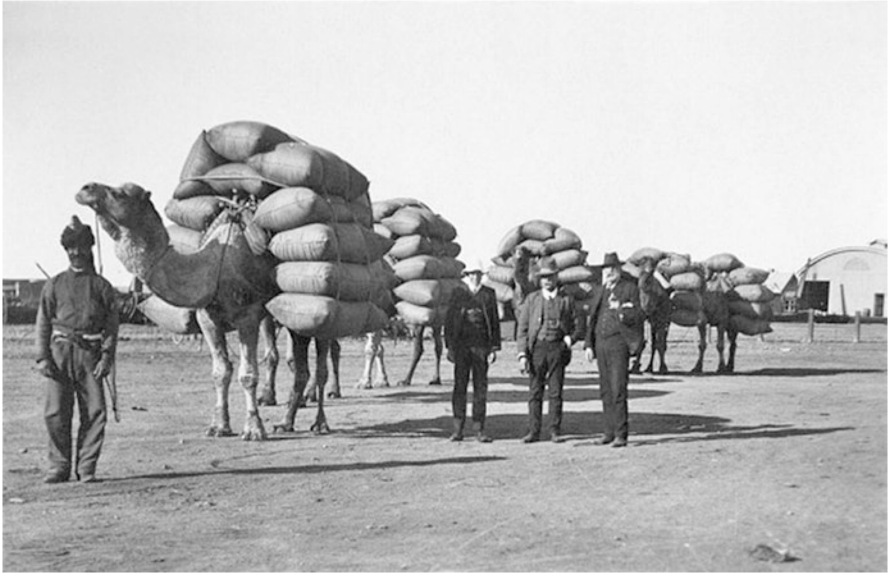


Plate 4 (Photo State Library of South Australia)

range of environmental, economic, infrastructure, social and cultural values throughout arid Australia. These impacts have been detailed by Edwards et al. (2010) and include damage to vegetation by browsing, trampling and suppression of recruitment; competition with native animals for food, shelter and water; degradation of wetlands and rock holes important to local Aboriginal people through fouling, trampling and sedimentation; damage to remote community infrastructure particularly during drought periods when camels tend to congregate around communities; and damage to infrastructure on pastoral properties including fences and watering points. Edwards et al. (2010) estimated the cost of damage by feral camels on assets that could be commercially valued at $10.7 million per annum.

Diet studies have shown that camels will eat a broad range of plants, feeding on about 80% of available species (Dorge and Heuck 2003). They will selectively and heavily browse some species including uncommon plants such as *Santalum acuminatum*, *Acacia sessiliceps* and *Erythrina vespertilio*, which is a concern for the conservation of these species in landscapes occupied by camels. Other preferred species include *Santalum lanceolatum*, *Ventilago viminalis*, *Atalaya hemiglauca* and *Eremophila longifolia*, but these species recover following good rainfall (Dorge and Heuck 2003). Edwards et al. (2010) list 43 central Australian plant species that are vulnerable to local extinction or depletion as a result of camel browsing. The list also includes species that are culturally important to Aboriginal people. Dorge and Heuck (2003) reported that in central Australia, significant damage to vegetation occurred when camel density exceeded two animals per km^2. This is an average figure for a particular land system, and it is likely that in some drier habitats such as near Lake Eyre, or around water points and rock holes, or for preferred browse species, serious damage could occur at lower densities (Lethbridge and Pitt 2009; Edwards et al. 2010). The impact of feral camels on fauna habitat is largely unknown, although reducing camel density is a recommended action to protect the habitat of a number of endangered arid zone mammals including the crest-tailed mulgara (*Dasycercus cristicauda*) (Maxwell et al. (eds.) 1996).

Control

Aside from human intervention, there are no constraints to the population growth of camels in the Australian arid zone into the foreseeable future. Outside the pastoral zone, non-commercial control efforts have been spasmodic and largely ineffective in significantly reducing overall population growth. In the absence of any foreseeable natural controls to the continued growth of the feral camel population and commensurate increase in negative impacts, it will be the responsibility of landholders and managers to reduce the negative impacts of camels to arid zone values. Camels are large animals living in an open, exposed landscape, so theoretically could be eradicated by aerial shooting. However, given the vast area occupied by camels, this is probably unachievable and unnecessary, so targeted control to protect local assets is a more feasible strategy. Having knowledge of where the primary assets are in relation to the distribution of feral camels, and some knowledge about the relationship between camel density and impacts on assets, enables cost-effective local or landscape-scale control programs to be planned and implemented. As a rule of thumb, Edwards et al. (2010) recommend that feral camels should be managed to a density of 0.1–0.2 animals per km^2 or less in order to lessen broad-scale negative environmental, economic, cultural and social impacts. In some circumstance, as mentioned above, this density threshold may be less. Localised control of camel densities to protect identified, local values will require an ongoing control program, as camels will continue to reinvade from beyond control zones.

Culling (commercial and non-commercial) is currently the only effective means of controlling feral camel populations. Commercial operations are preferable because it is ‘self-funding control’, there are some economic benefits to participants and the culled animals are utilised. Virtue et al. (2016) reported that 16.5% (27,000) of feral camels removed under the Australian Feral Camel Management Program were commercial operations where camel meat was utilised, mostly for pet meat. Modelling by Zeng and Gerritsen (2013) concluded that in the short to medium term, commercial harvesting at these levels would not reduce the feral camel population, although they noted there were some social and economic benefits. They concluded that initially large-scale culling is necessary to reduce the camel population to a level where a growing commercial harvesting industry could provide effective population control. There are many challenges to commercial culling of feral camels including remoteness, the clumped distribution and mobility of feral camels, transport costs and the relatively low value of camel meat as pet food (Virtue et al. 2016). Other commercial opportunities such as harvesting feral camel meat for human consumption and exporting live camels are small markets and, under current cost structures, will not enable the establishment of a significant industry in the foreseeable future.

Non-commercial culling, or culling to waste, is carried out from the air or on the ground. Local or landscape-scale aerial culling programs can be very effective, although costly, ranging from $60 to $100 per camel culled. These programs will not reduce the overall feral camel population in the long term, but if repeated at sufficiently regular intervals, they can significantly reduce the local density of camels. Historically, culling operations have been paid for by governments, so there is uncertainty about the level of ongoing funding necessary for regular culling operations. Occasional ad hoc culling operations that do not have clear asset protection objectives, including setting threshold levels of camel densities needed to protect assets, or which expend money and effort on operations where camel densities are below the ‘threat’ threshold anyway, are ineffective and wasteful. In order to determine whether a culling operation is warranted, that is, whether animal density exceeds the threshold, it is important to carry out a pre-cull aerial survey. Post-cull surveys are necessary to enable the success or otherwise of the culling operation to be measured in terms of proportion of animals removed and remaining density. The measure of successful feral camel management is not the number of animals killed, but the number remaining, and the likely impact these will have on valued assets. Opportunistic, regular culling from the ground, such as is undertaken by many pastoralists, can be effective at maintaining low camel densities (Gee and Greenfield 2007).

Appropriately robust fencing including electric fencing can be an effective barrier to feral camels. Construction and maintenance of long distances of fencing will be cost prohibitive in most situations, but it may be a viable option for relatively short distances to protect high-value assets such as cultural values (e.g. rock holes) and conservation assets.

There is a need for either controlled studies or the establishment of long-term monitoring sites to better quantify the environmental and ecological impacts of feral camels in various locations and at various densities. This will help land managers make decisions about cost-effective, targeted control strategies.

European Rabbit (*Oryctolagus cuniculus*)

Origin

Domestic rabbits for eating arrived from England with the First Fleet in 1788. The first feral populations, numbering in their thousands, were reported in south-east Tasmania in 1827 (Williams et al. 1995). In addition to domestic rabbits becoming feral, rabbits were deliberately introduced into the wild near Geelong, Victoria, in 1858 for hunting and spread rapidly across the continent. By the 1890s they were

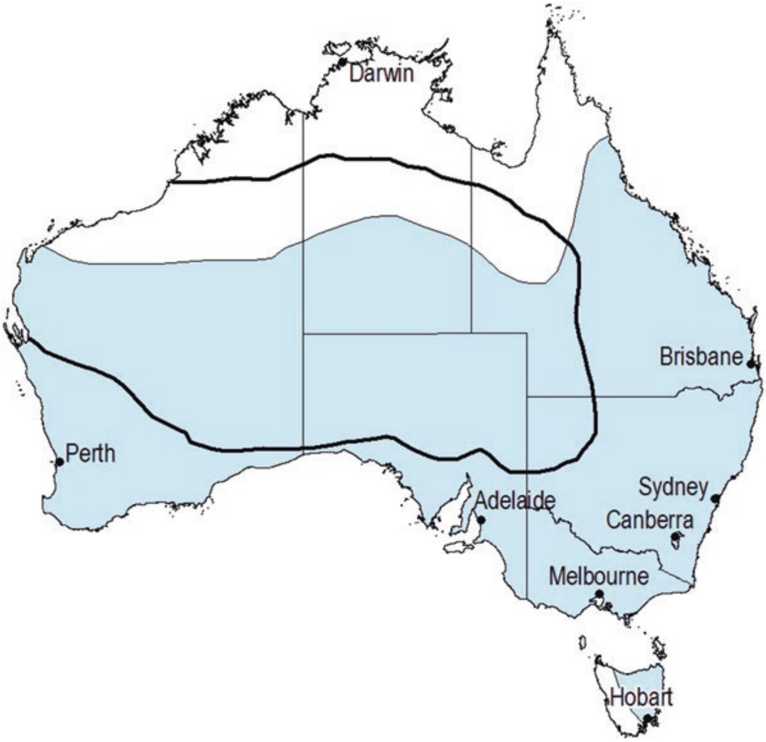


Fig. 4 Distribution of rabbits (blue) (Adapted from Van Dyk and Strahan 2008). The black line circumscribes the arid zone

well into South Australia and Queensland, by 1900 they had penetrated the deserts into central Australia, and by 1910 they had crossed the Nullarbor into Western Australia (Williams et al. 1995). Colonisation of Australia by rabbits has been reported as the fastest rate of colonisation by an introduced mammal anywhere in the world; the fox followed close behind the rabbit (Caughley 1977). Today, rabbits are one of the most abundant and widely distributed wild animals in Australia, occurring in almost all habitats south of the Tropic of Capricorn, above which their distribution is patchy. Either high temperatures, periods of moisture imbalance, shallow soils or poor quality browse limits or prevents rabbits from establishing in the north. They are widespread but patchy throughout the semi-arid and arid regions of the continent south of the Tropic of Capricorn, favouring more fertile soils on run-on areas, by-washes, drainage lines, breakaways and lakes systems. In arid environments, their distribution and abundance fluctuates, depending on the seasons (rainfall) (Fig. 4, Plate 5).

Plate 5 (Photo Department of Agriculture and Food Western Australia)

Impacts

Rabbits have had a massive adverse impact on the Australian environment, probably more than any other introduced animal. Before the introduction of myxomatosis and rabbit calicivirus disease (RCD), they caused significant and, in places, irreversible damage to native vegetation, habitat and soils as well as profoundly impacting agricultural production. Prior to the introduction of RCD, annual production losses in the agricultural industry attributable to rabbits have been estimated at $600 million (McLeod 2004; ACIL 1996). In the arid and semi-arid zone, economic losses due to rabbits include decreased livestock carrying capacity as a result of competition, soil and pasture degradation and crop losses due to grazing, digging and burrowing. For example, on a pastoral property in South Australia, stock carrying capacity increased by 40% following rabbit control (Williams et al. 1995).

As well as economic impacts, rabbits have had severe environmental impacts in the semi-arid and arid zones. In the absence of controlled experiments, it is difficult to isolate the impacts of rabbits on the environment from the combined, cumulative impacts of all herbivores including livestock and native animals. However, there is well-documented evidence of rabbits competing with native fauna for browse and, in some cases, wiping out native plants (Croft et al. 2002). The rabbit '*Threat Abatement Plan*' (DEWHA 2008d) lists 19 endangered bird species, 13 endangered mammal species and more than 100 endangered plant species, many of which occur in the arid zone, as threatened by rabbits. Of particular concern is that rabbits can destroy seedling regeneration, preventing recruitment and leading to localised extirpation of native plant species (Auld 1990; Henzell 1991). In the semi-arid and arid regions, there are many relatively long-lived arborescent keystone plant species such as a mulga (*Acacia aneura*), the rare Murchison snakewood (*A. burrowsiana)* and cypress pine (*Callitris columellaris*) that only recruit episodically, usually following exceptional rainfall seasons. Infrequent but otherwise successful germination of these plants can be destroyed by rabbits and other feral animals such as goats, and in the absence of recruitment, these populations eventually senesce and die (Lacey 1972; Lang and Graham 1983; Henzell 1991; Cooke 2011). During drought, rabbits ringbark shrubs and small trees and completely strip leaves and twigs from shrubs, often killing the plants (Williams et al. 1995 citing Hall et al. 1964). Rabbits have severely damaged chenopod vegetation and caused the extirpation of several chenopod species in western New South Wales (Beadle 1948). As well as severely altering the structure and floristic composition of plant communities, grazing by rabbits can denude the vegetation, exposing soil to severe erosion (Myers et al. 1994; Eldridge and Simpson 2001). Competition for browse by rabbits has been implicated in the multifactorial causes of decline and extinction of medium-sized mammals in the semi-arid and arid zones (Burbidge and McKenzie 1989), and there is evidence that rabbits displaced native burrowing mammals such as the boodie (*Bettongia lesueur*), rufous hare-wallaby (*Lagorchestes hirsutus*) and bilby (*Macrotis lagotis*) (Williams et al. 1995). In addition to having direct effects on native species through competition, rabbits contribute to the impact of introduced predators on native fauna by maintaining higher densities of these predators. Possibly the only ecological benefit afforded by rabbits, particularly in the context of a declined native mammal fauna in the arid zone, is that they are a significant food source for large raptors such as the wedge-tailed eagle (*Aquila audax*) (Olsen 1995).

Control

Prior to the release of myxomatosis in 1950, attempts at controlling rabbits such as shooting, trapping, fencing, poisoning, introduction of exotic predators (such as ferrets and cats) and ripping burrows had little long-term impact on the spread, density and impact of rabbits (Williams et al. 1995). However, within 6 months of its release, the rabbit-specific myxoma virus was reported to have killed 99% of rabbits as the virus spread through the temperate regions of Australia (Kerr and Best 1998). Within a relatively short time though, the mortality rate reduced to 30–80%, as exposed populations developed resistance (Deeker 1992; Best and Kerr 2000). In an arid region of South Australia, the introduction of myxoma virus has no effect on the local rabbit population, but rabbit haemorrhagic disease (RHD) had a significant and lasting impact on the population (Bowen and Read 1998). Mosquitoes and fleas transmit the myxoma virus, but because these vectors prefer moist, temperate climates, the virus has had little impact on rabbit populations in the arid region. Consequently, myxomatosis has been effective only when mosquito numbers are high following erratic summer rainfall (Bowen and Read 1998).

The other important biological control is the rabbit calicivirus disease which, following its escape from quarantine facilities on Wardang Island in 1995, has proved to be more effective in dry climates than myxomatosis (Bowen and Read

1998), particularly when rabbits are at medium to high densities; it is less effective when rabbits are at low densities (Sharp et al. 2001). Australia currently has only one strain of calicivirus, which is relatively stable, and rabbits are developing genetic resistance to infection; research is being undertaken to identify new field strains to release. Other more traditional methods can be effective at the localised level, or when used in conjunction with biocontrol, including poisoning with 1080, fumigation of warrens, mechanical destruction of warrens and above-ground shelters, trapping and shooting.

Horse (*Equus caballus*) and Donkey (*Equus asinus*)

Origin

Prior to motorised transport, horses were the primary form of transport; they arrived in Australia with the First Fleet in 1788 (Dobbie et al. 1993). Further shipments of working horses from Europe and other parts of the world followed, and settlers soon began to breed local herds for personal transport and as work horses, including to haul coaches, sulkies and drays and to work on farms and in the bush hauling ploughs and timber. Horses were vital to the expansion of farming and pastoralism into the arid and semi-arid zones, being used to transport people and equipment and for mustering stock. Horses were also crucial for transport and as beasts of burden in times of war, and tens of thousands were bred for war service, including the iconic 'Walers', specially bred horses used by Australian light horse regiments in the Middle East campaign during World War I (Yarwood 1989). It is estimated that 8 million horses died on the Western front alone during World War I (Trueman 2015). At the end of the war and with the increased use of motorised transport, many 'Walers' were released into the bush, adding to the existing feral population. Even after the advent of motorised transport, horses continued to be used for mustering stock on outback pastoral properties until recent times. Today, most mustering is done using helicopters, motorbikes and 'buggies', although some pastoralists still prefer to use horses in combination with machines. As machines replaced horses, thousands of horses were released into the bush or were simply left in the bush and established feral herds.

Unlike camels, horses need to drink regularly, so the distribution of feral horses throughout the arid and semi-arid regions is limited by availability of either artificial watering points or permanent water in river pools, gorges and wetlands. Today, there are about 400,000 feral horses in Australia, making it the largest feral horse population in the world (Dawson et al. 2006). Most of these occur in the semi-arid and arid regions (Fig. 5, Plates 6 and 7).

Donkeys first arrived in Australia as early as 1793 for use as pack and haulage animals, but it wasn't until after the 1860s that they became more widely used as pack animals in the arid and semi-arid regions of South Australia and Western

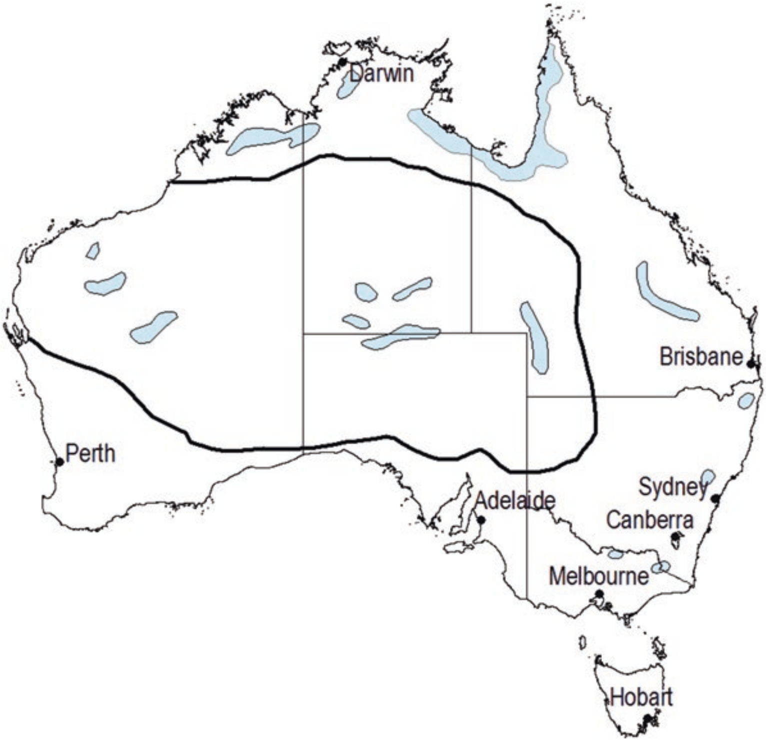


Fig. 5 Feral horses can occur in any areas of past or present pastoralism but are most prominent in the areas shown (blue) (Adapted from Van Dyk and Strahan 2008). The black line circumscribes the arid zone

Australia (Bough 2006). They were imported from a number of countries including Spain, Mexico and parts of Asia, but most came from India (Walker 1973). In arid environments, donkeys were considered to be superior to horses and bullocks, because, being smaller, they ate less, were strong and hardy and could survive better on the natural vegetation (Kennedy 1992). They were particularly useful in the Kimberley in Western Australia and in the Victoria River region in the Northern Territory, where a toxic native plant (*Crotalaria crispata*) killed and sickened horses, but did not affect donkeys (McKnight 1976). In the late nineteenth century, during the Western Australian gold rush and the opening up of the arid rangelands for pastoralism, donkeys proved invaluable, with large teams used to haul stores, wool and other materials (Bough 2006 citing Long 2003). As with horses, donkeys were used as transport, haulage and pack animals in war including World Wars I and II. The feats of the Australian stretcher bearer Private John Simpson Kirkpatrick and his donkey during the Gallipoli Campaign in World War I are legendary (Cochrane 1992).

As with camels and horses, motorised transport replaced donkeys throughout the early 1900s, and donkeys were released into the bush. Provided they had access to

Plate 6 (Source: Ecological Society of Australia, Dale Nimmo – photo by Claire Owen)

Plate 7 (Photo Australian War Memorial)

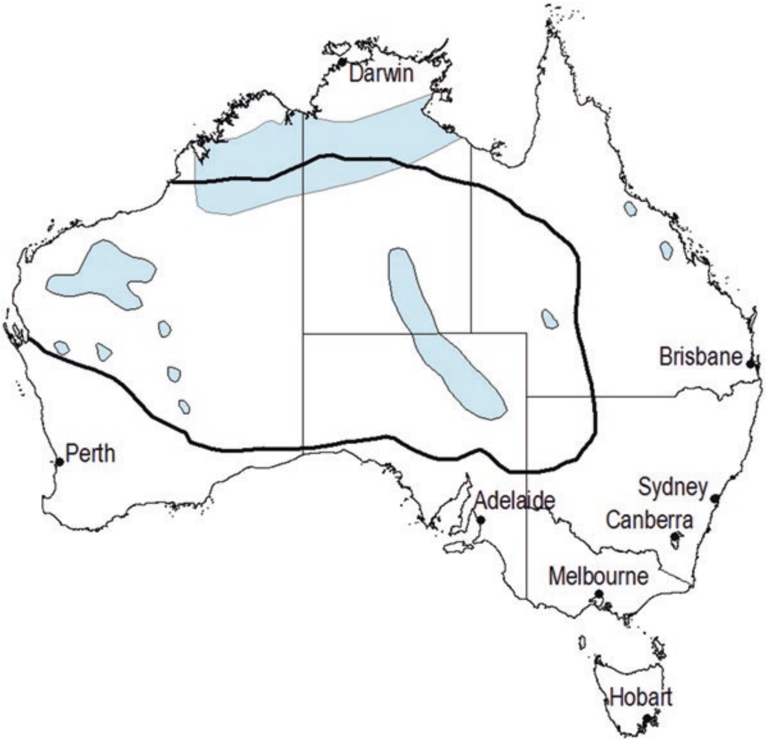


Fig. 6 Distribution of feral donkeys (blue) (Adapted from Van Dyk and Strahan 2008). The black line circumscribes the arid zone

water such as artificial watering points, river pools or wetlands, they not only thrived in the wild but quickly multiplied. Bough (2006) provides an example of where a team of 60 donkeys was released in the McArthur River area of the Northern Territory in 1936 and increased to about 1500 within 6 decades. Choquenot (1990) reports that a feral donkey population in the Northern Territory increased by 23–25% annually. Significant numbers of feral herds were first reported in the 1920s, and by 1949, the donkey, an animal once highly valued, was officially declared a pest animal in Western Australia. It is estimated that today there are between 2 million and 5 million feral donkeys in Australia (Department of the Environment and Heritage 2004; Choquenot 2008), but there have been few systematic, nationwide surveys, so such estimates are unreliable. In 1964 the Western Australian government estimated that at least 100,000 roamed the eastern half of the Kimberley (Bough 2006). Relatively recent aerial surveys in the Northern territory estimate feral horse and donkey populations of 265,000 and 165,000, respectively (Edwards et al. 2004a, b), and given that a significant but unknown proportion of these animals are in the Northern Territory, an estimated population of 5 million donkeys would seem very high (Fig. 6, Plates 8 and 9).

Plate 8 (Photo Department of Agriculture and Food Western Australia)

Impacts

Provided they have access to water, feral horses and donkeys can inhabit a variety of land forms and vegetation types throughout the semi-arid and arid zones, although their distribution is patchy (Dobbie et al. 1993; Choquenot 1990). They are capable of interfering with farming and pastoral operations by competing with stock for food, fouling water holes, damaging fences, interfering with mustering operations and potentially carrying exotic diseases. A review by Nimmo and Miller (2007) found that the documented environmental effects of feral horses include soil loss, compaction and erosion; trampling of vegetation; reducing plant species richness; inducing mortality of native trees through bark chewing; damage to bog habitat; damage to water bodies; facilitation of weed invasion; and altering community composition of birds, fish, crabs, small mammals and reptiles. Despite these observations, the specific ecological effects of feral horses at various densities are poorly known (Dobbie et al. 1993; Nimmo and Miller 2007). Similarly, the extent of damage caused by feral donkeys has not been well documented (Bough 2006), although, given the somewhat similar ecology of the species, the impacts could be expected to be similar. It is likely that feral donkeys and horses per se are no more or less damaging to the environment than domestic stock, but their added numbers on pastoral properties add to total grazing pressure and associated impacts. In the conservation

Plate 9 (Photo Historical Society Ravensthorpe Western Australia)

estate where the aim is to protect wildlife values by excluding exotic herbivores, they could become serious environmental pests capable of degrading soils, vegetation and habitat and introducing weeds. Because of a dearth of studies, the relationship between the density of feral horses and donkeys and potential environmental damage they may inflict in particular land systems has not been well established. In one of the few published accounts of the impact of feral horses on native fauna, Matthews et al. (2001) reported that a population of black-footed rock-wallabies in the Finke George National Park near Alice Springs increased significantly after feral horses were removed.

Control

In the arid and semi-arid regions away from artificial watering points, drought has a significant impact on populations of feral horses and donkeys. Where they have access to water, trapping, mustering and aerial shooting from helicopter are the most effective methods for humanely controlling them over large areas (Dobbie et al. 1993). Research into fertility control has been underway for several decades (Turner et al. 2001), and despite some promising results (Killian et al. 2004), there is no proven cost-effective method, so aerial shooting remains the preferred option.

For example, over the period 1978–1987, 180,000 donkeys were shot in the Kimberley region, and between 1981 and 1984, 83,000 were shot in the Victoria River area (Choquenot 2008). However, in the absence of ongoing control, numbers can quickly return to previous levels (Freeland and Choquenot 1990).

Given the long economic, cultural and social association between humans and animals such as horses and donkeys, it is not surprising that the culling of these animals is highly contentious and can arouse deep emotions. There is the added concern by some that in jurisdictions where these animals have been declared pests, they are not protected by the same animal welfare legislation that is afforded other non-pest animals (Bough 2006; Nimmo and Miller 2007).

Wild Canids: Fox (*Vulpes vulpes*) and Wild Dog (Dingo, *Canis lupus dingo* and Feral Domestic Dog, *C. l. familiaris*)

Origins

Dingoes (*C. l. dingo*) were transported to Australia by indigenous people around 3500–4000 years ago, most likely from New Guinea or Indonesia (Gollan 1984; Corbett 1995; McNiven and Hitchcock 2005). While they were initially a companion and hunting animal, feral packs quickly developed and spread across the Australian mainland, occurring in a wide diversity of habitats. Domestic dogs (*C. l. familiaris*) arrived with the First Fleet in 1788 and feral domestic dogs and hybrids with dingoes have been present since this time (Fleming et al. 2001; Corbett 1995). Dingoes, feral domestic dogs and hybrids are collectively referred to here as 'wild dogs' on the basis that their ecology in the wild, including their impacts on economic and environmental values, and their control, is undifferentiated. Hybridisation has resulted in a lower proportion of pure dingoes, especially in south-western and south-eastern Australia, where wild dogs are mostly hybrids or feral domestic dogs (Newsome and Corbett 1982; Jones 2009; Stephens et al. 2015). However, in the semi-arid and arid regions of the continent, and away from human settlements, there remains a high proportion of pure dingoes in the wild dog population (Newsome and Corbett 1985).

Wild dogs are widely distributed throughout the country and are present in most environments. They are mostly nocturnal, highly mobile and elusive, making it difficult to estimate their actual numbers. For this reason, indirect measures such as track counting, measuring frequency of visits to bait stations or trail cameras and aerial sightings are used to estimate relative population density and changes in population such as before and after control measures (Allen et al. 1996; Fleming et al. 2001; Burrows et al. 2003). Estimates of population density in New South Wales, for example, range from 0.1 to 0.3 wild dogs per square kilometre (Fleming et al. 2001), but this will vary greatly across the continent depending on control programs and prey availability (Fig. 7, Plate 10).

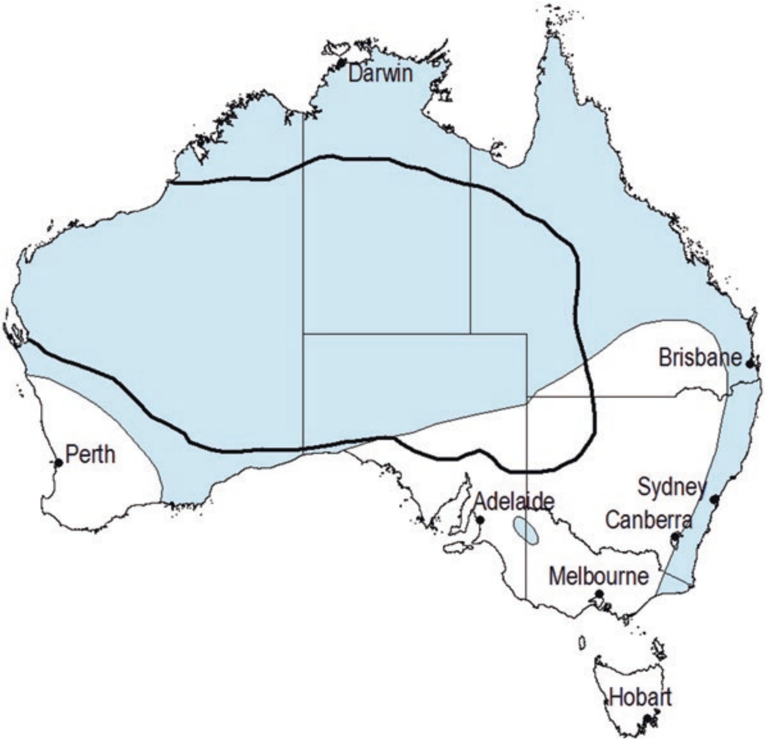


Fig. 7 The distribution of dingoes and wild dogs (hybrids) (blue) (Adapted from Van Dyk and Strahan 2008). The black line circumscribes the arid zone

The European red fox was introduced to Victoria from England for recreational hunting in the 1860s and 1870s (Saunders et al. 1995). It spread rapidly, and by the turn of the century, it was so widespread and common that some shires in Victoria and South Australia declared it a pest and were offering bounties. The fox was in New South Wales by 1893, South Australia by 1901, Southern Queensland by 1907 and Western Australia by 1912 (Saunders et al. 1995). This rapid spread, including across the Nullarbor, was aided by human dispersal and the spread of rabbits, a primary prey item. Today, foxes occur across most of Australia except the tropical north and some offshore islands (Long 1988; Saunders et al. 1995). Until recently, Tasmania was thought to be free of foxes but in response to some evidence of a low density of foxes, detection and eradication efforts began there in 2002 (Saunders et al. 2006). However, the presence of foxes in Tasmania is controversial with some suggesting that the evidence may have been an elaborate hoax.

The fox is a highly successful coloniser, an opportunistic predator and scavenger and is able to survive in a wide range of habitats including arid and semi-arid Australia (Corbet and Harris 1991; Catling and Coman 2008). Its northern distribution is similar to the distribution of rabbits, although there is some evidence that its distribution and density may be affected by the presence of dingoes (Saunders et al.

Plate 10 (Photo Neil Burrows)

1995). As with many predators, it is difficult to determine the actual population of foxes, because they are mostly nocturnal and elusive, so the actual number of foxes in the semi-arid and arid regions is unknown. The author is familiar with an eradication program on the Peron Peninsula in the semi-arid Sharp Bay region of Western Australia conducted in the mid-1990s which removed an estimated 1000 foxes from an area of 1000 km^2, equivalent to a fox density of one animal per km^2. This was thought to be a high density for this environment, but the area also supports a high density of rabbits, and it has been well established that rabbits are the staple diet of foxes in semi-arid pastoral and farming regions (Brooker 1977). Clearly, in the absence of control measures, fox density will depend on food availability and competition from other meso-predators. The limited data available suggest fox densities of 1–2 animals km^{-2} in the more productive regions of the semi-arid pastoral and farming region (Newsome and Catling 1992). In arid central Australia, fox density is generally low but is temporally and spatially variable. Following good seasons, fox density increases as prey increases, and density is usually higher around playa lakes, riparian zones, breakaways and other more productive systems in the landscape that provide refugial habitat for rabbits and other prey species. In a prolonged drought, foxes were absent or at undetectably low levels in the Gibson Desert in Western Australia, suggesting their presence or absence in the arid interior beyond the pastoral zone depends on rainfall, which drives prey abundance (Burrows et al.

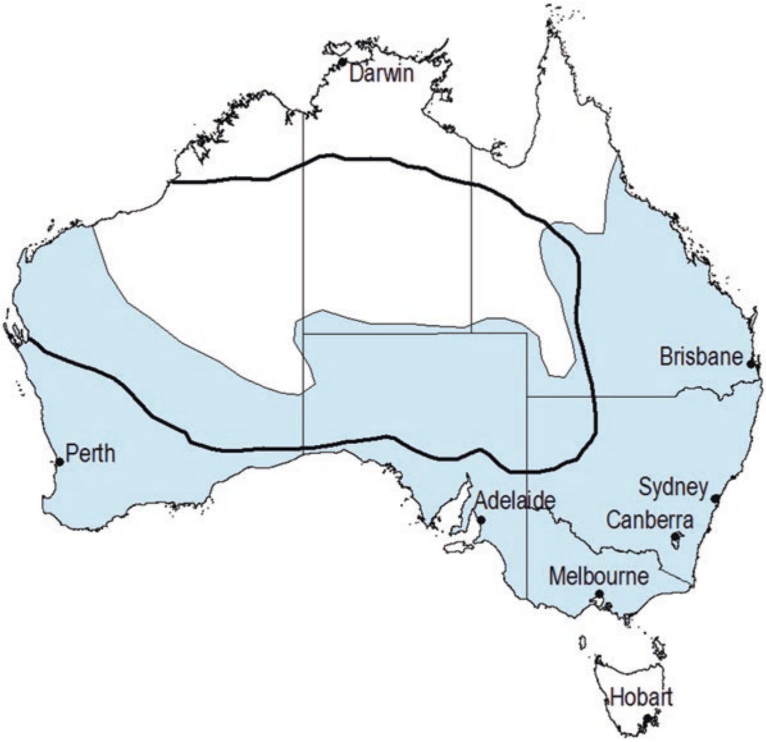


Fig. 8 The distribution of foxes (blue) (Adapted from Van Dyk and Strahan 2008). The black line circumscribes the arid zone

2003). A crude estimate based on limited density data suggests the Australian fox population is about 7.2 million (McLeod 2004) (Fig. 8).

Impacts

Wild dogs have harassed and killed stock including sheep, goats, cattle and other stocks since European settlement. Today, they continue to do so, having a significant economic impact on farming and pastoralism, including in the semi-arid and arid regions of Australia (Fleming et al. 2001; Allen and West 2013). Table 1 summarises estimated annual costs to sheep and cattle producers being $66.3 million per annum (McLeod 2004). This is an underestimate of the total economic cost, because it does not consider other agricultural industries. For example, there is anecdotal evidence that wild dogs have significantly impacted rangeland goat operations in the Gascoyne and Murchison regions of Western Australia.

In terms of environmental impact, the dingo is suspected of causing the extinction of at least three native species on the mainland, being the thylacine (*Thylacinus*

Table 1 Annual cost of wild dogs to sheep and cattle production in Australia

Cost component	Control cost ($million)	Loss cost ($million)	Total cost ($million)
Sheep production	–	15.9	15.9
Cattle production	–	32.4	32.4
Management cost (baiting, etc.)	6.50	–	6.5
Fencing cost	10.0	–	10.0
Research cost	1.5	–	1.5
Total	18.0	48.3	66.3

After McLeod (2004)

cynocephalus), the Tasmanian devil (*Sarcophilus harrisii*) and the Tasmanian native hen (*Gallinula mortierii*) (Corbett 1995), although this has been questioned (Johnson and Wroe 2003). While it is known that wild dogs prey on a range of native wildlife, including the large macropods, it is unclear to what extent this impacts on the sustainability of populations of native species today. Unlike other introduced species, dingoes arrived a very long time ago and became a 'natural' part of the ecology of semi-arid and arid Australia. However, together with the more recent arrival of other introduced predators (foxes and cats), the cumulative effect of predation and other perturbations may be taking a toll on wildlife, especially remnant or isolated populations of endangered fauna (e.g. Robertshaw and Harden 1986).

There is currently debate about whether the negative impacts of wild dogs on native fauna are offset by their suppressive effect on the other introduced predators, the fox and feral cat. It has been argued that, consistent with meso-predator release theory, controlling or eradicating wild dogs results in an increase in populations of foxes and feral cats, therefore an increase in predation pressure on native species (Johnson 2006; Dickman et al. 2009). However, there is little scientific evidence to support this proposition (Allen et al. 2014). On the other hand, there is evidence that wild dogs can reduce populations of other pests including feral goats, rabbits and introduced rodents, especially during drought periods (Corbett and Newsome 1987).

After the wild dog, the fox is the largest terrestrial predator in mainland Australia, and predation by foxes has significant economic and environmental impacts. The main economic impact is on sheep farming where lambing losses due to foxes are estimated at about 2%, but in some areas it is as high as 30% (Lugton 1993), amounting to an estimated economic loss of $17.5 million per annum (McLeod 2004). Since its introduction, the fox has long been implicated in the decline of native fauna (e.g. Christensen 1980). Australia's semi-arid and arid zones have the highest rate of modern declines and extinctions in native fauna in the world, and predation by foxes and feral cats is implicated in the decline and extinction of about 33% of all arid zone mammals and about 90% of medium-sized mammals (Burbidge and McKenzie 1989; McKenzie et al. 2006). The fox is also a threat to many native ground-nesting birds such as the mallee fowl and night parrot and reptiles such as the green turtle (Saunders et al. 1995) and a serious impediment to native fauna reintroductions (Kinnear et al. 2002). Consequently, it is listed as a key threatening process under the Commonwealth Environment Protection and Biodiversity Conservation Act 1999 (the EPBC Act). Under the EPBC Act, the Australian government, in consultation with the states and territories, has developed the *Threat Abatement Plan for Predation by the European Red Fox* (DEWHA 2008b). Of the threatened species listed under the EPBC Act, foxes are considered a threat to 14 species of birds, 48 mammals, 12 reptiles and 2 amphibians, with the orange-bellied parrot (*Neophema chrysogaster*), spotted quail-thrush (*Cinclosoma punctatum*), herald petrel (*Pterodroma heraldica*), Gilbert's potoroo (*Potorous gilbertii*) and western swamp tortoise (*Pseudemydura umbrina*) listed as critically endangered (DEWHA 2008b).

There are a number of well-documented cases where fox removal in various locations in Western Australia has resulted in population increases of endangered native mammals, many of which once occupied the arid zone. These include rock-wallabies (*Petrogale lateralis and P. rothschildi*), woylie (*Bettongia penicillata*), tammar (*Macrotis eugenii*), numbat (*Myrmecobius fasciatus*), brushtail possum (*Trichosurus vulpecula*) and quenda (*Isoodon obesulus*) (Christensen 1980; Kinnear et al. 1988; Kinnear et al. 2002; Friend 1990; Burrows and Christensen 2002; Possingham et al. 2004). In New South Wales, fox control increased survival of the endangered and iconic semi-arid bird zone the mallee fowl (*Leipoa ocellata*) (Priddel and Wheeler 1990).

The fox could also act as a carrier of rabies, should the disease be accidentally introduced into Australia. Rabies mostly affects members of the dog family but can also be passed on to humans, livestock and native mammals (Saunders et al. 1995).

Control

Given their distribution over such a vast area of Australia, and limited resources of landholders and land managers, eradication of wild dogs and foxes from the continent is not feasible, although localised eradication is. Neither bounties nor hunting have had a broad-scale, lasting impact on these canids, although there is anecdotal evidence that intense localised hunting and trapping can have an impact. However, such methods are expensive and labour-intensive, require ongoing effort and are only effective in limited areas (Saunders and McLeod 2007). Barrier fencing has long been a means of controlling the insurgence of pest animals into agricultural areas in Australia. The earliest substantial barrier fence, the No. 1 rabbit-proof fence, was constructed through Western Australia's arid zone in 1907 to prevent the rabbit invasion from the east. Since then more than 10,000 km of barrier fencing have been constructed in various parts of the country, including to prevent incursions by wild dogs (Broomhall 1991). From anecdotal evidence and surveys of pastoralists, there is general agreement that barrier fencing, in combination with other control measures such as trapping and poisoning, can have economic benefits.

However, the construction and maintenance of barrier fencing is costly, and fences can interrupt the migration of native fauna including kangaroos and emus.

Well-constructed predator-proof fenced exclosures can be effective for protecting conservation values such as threatened fauna, and a number of these have been built in the semi-arid and arid zones in recent times. They are also expensive but could be justified to protect high conservation values (Bode et al. 2012). In some regions, poison baiting of canids has been successful in reducing predation pressure on native fauna. In south-western Australia, ongoing regular broad-area aerial baiting with 1080 poison baits targeting foxes (Western Shield) has resulted in the successful recovery of a number of native mammal species (Kinnear et al. 2002; Armstrong 2004). Burrows et al. (2003) reported virtual eradication of foxes and wild dogs for up to 15 months following aerial baiting with 1080 poison baits of a 1600 km^2 area of the Gibson Desert during a drought period. The effectiveness of broad-area aerial baiting to control wild dogs is variable and depends on availability of alternative food sources but is generally regarded as cost-effective (Thomson 1986).

The appeal of 1080 as a pesticide is that, in regions of Australia such as South West Australia, it is a naturally occurring chemical in a number of native plant species ('poison' plants), particularly *Gastrolobium* spp. and *Oxylobium* spp. Native fauna that have co-evolved with these plants show a high resistance to the toxin compared with animals that have not, such as dogs, foxes and cats (King et al. 1978; Twigg et al. 2003). However, caution must be used because there are regions of arid Australia where native fauna have not co-evolved with these plants, and consequently, their resistance to 1080 is relatively low (Twigg and King 1991; Twigg et al. 2003; Twigg 2014). Risk to nontarget animals, including small mammals and birds, can be minimised by using a bait medium that is non-palatable to nontargets, reducing the level of toxin in the baits, reducing baiting density or placing the baits away from habitats used by susceptible animals (McIlroy et al. 1968). The animal welfare impacts of 1080 poisoning is of concern, but because the toxin acts by interrupting neurological function, it is difficult to know the extent to which animals actually feel pain (Twigg and Parker 2010). To mitigate potential suffering, there has been some experimentation using analgesics such as diazepam in 1080 baits. This reduced the level of anxiety in foxes that had taken baits but extended the time to death (Marks et al. 2009). Further research to better understand the effect of 1080 on target and nontarget animals and to improve the humaneness of 1080 baiting is warranted, especially in those regions where native fauna has not co-evolved with 'poison' plants.

Preventing the introduction of foxes to new areas, such as islands, is a high priority. Islands are often refuges for native animals no longer found on the mainland. Fertility control through immunocontraception has been investigated as means of fox control (Bradley 1994; Bradley et al. 1998), as has chemical fertility control (Marks et al. 1996), but neither technique is sufficiently developed to be safely used as a routine control measure.

Despite adverse impact on the livestock industry, there are growing efforts to preserve pure dingoes. Under some state and territory legislations, dingoes are conserved and protected as a native species in areas where they pose no threat to livestock. The greatest threat to dingoes is hybridisation with feral domestic dogs, and it has been suggested that pure dingoes may become extinct by 2100 (Fleming et al. 2001).

Cat (*Felis catus*)

Origin

Cats first arrived in Australia with European settlers from about 1824 to 1886, and being companion animals, they were present wherever Europeans settled. Cats were feral on Macquarie Island by 1820, only 10 years after the island was discovered by sealers (Brothers et al. 1985). There was likely almost immediate 'leakage' of pet cats from settlements into the wild, establishing feral populations that spread further into the bush. As well as being kept as pets, large numbers of cats were used as a biological control agent and released into the wild in Victoria and South Australia in the 1880s and in Western Australia on the Nullarbor Plain near Eucla in 1898 to control rabbits (Rolls 1969; Abbott 2008). By about 1900, the continent was entirely colonised by feral cats (Abbott 2002; Abbott et al. 2014). While it is difficult to reliably census feral cats, it is estimated that today there are about 18 million in Australia distributed through all habitats (except some of the wettest rainforests) in mainland Australia and Tasmania and on many offshore islands (Pimental et al. 2001; DEWHA 2008c citing McLeod 2004).

Being well adapted to arid environments, cats thrive in the semi-arid and arid regions of Australia. Their success as an invasive carnivore is due to their size, physiology, athleticism and fecundity. They are highly efficient hunters, being able to take prey species almost up to their own body weight; they prey on ground-dwelling species as well as arboreal animals; they eat a wide range of prey including insects, reptiles, birds and mammals (Jones and Coman 1981; Paltridge et al. 1997); and they do not need to drink water, obtaining sufficient moisture from their prey. Females can breed as early as 8-month-old and in good seasons and can have two litters per year, allowing rapid increases in population (Jones and Coman 1982). In the arid and semi-arid regions, based on limited data, cat density estimates vary depending on seasonal fluctuations of food supply (prey availability). For example, during prolonged drought, densities in the Gibson Desert were about 0.05 animals per km^2, but following good seasons (rainfall), this increased to 0.13 per km^2 (Christensen and Burrows 1995). On the other hand, in the Shark Bay area of Western Australia with a high density of rabbits, Short and Turner (2005) reported a cat density of 2.8 animals per km^2 (Fig. 9, Plate 11).

Fig. 9 The distribution of feral cats (Adapted from Van Dyk and Strahan 2008). The black line circumscribes the arid zone

Impacts

The main impact of feral cats is on wildlife conservation rather than agricultural economic values. Cats have direct impacts on native fauna through predation but can have an indirect effect by carrying and transmitting diseases such as toxoplasmosis (Dickman 1996). The predatory impact of cats on native wildlife was raised as a concern by early naturalists, including McKeown, who in 1922, observed, 'that cats do not appear to be having an impact on rabbits, but together with the fox, they were "exterminating" ground-birds and other species'.

The extent to which the feral cat has been the primary cause of declines of native fauna after European settlement is poorly documented and controversial (Dickman 1996; Abbot et al. 2014), largely because of confounding influences of other factors such as foxes, altered fire regimes and disease. However, feral cats have been strongly implicated in the extinction of up to seven species of mainland mammals as well as regional and island extinctions of native mammals and birds (Denny and Dickman 2010; Abbot et al. 2014). It is well documented that feral cats have caused the failure of many endangered fauna reintroduction attempts in the semi-arid and

Plate 11 (Photo Neil Burrows)

arid zones (Short 2016), and they are recognised as the main barrier to reconstructing and protecting faunal assemblages in these environments (Christensen and Burrows 1995). If there is doubt about the impact of feral cats as agents of decline and extinction of native fauna, then rather than wait for definitive proof, the prudent response is to assume the cat is guilty until proven innocent.

Today, 35 vulnerable and endangered bird species, 36 mammal species, 7 reptile species and 3 amphibian species are thought to be adversely affected by feral cats (Denny and Dickman 2010). While there is debate about the role of cats in faunal extinctions, there is no doubt they are proficient hunters of Australian wildlife. For this reason, legislation has been introduced to many jurisdictions that aims to restrict the breeding and predation potential of domestic cats and to restrict the number of domestic cats becoming feral cats in peri-urban areas. Predation by feral cats was listed as a key threatening process under the Federal Endangered Species Protection Act 1992 (incorporated in the Environment Protection and Biodiversity Conservation Act 1999). A Threat Abatement Plan for Predation by Feral Cats was produced in 1999 and amended in 2008 to promote the recovery of vulnerable and endangered native species and threatened ecological communities (Environment Australia 1999; DEWHA 2008c). It should be noted that in the absence of traditional prey species that have declined or become extinct since European settlement, desert Aboriginal people hunt feral cats (and rabbits) as a food source, so do not necessarily see them as a harmful pest.

Control

Feral cats have colonised the vast and remote semi-arid and arid regions of Australia. This, together with their evasive and largely nocturnal behaviour, and their popularity as a companion animal, makes eradication of this harmful pest unachievable on the mainland. There have been successful eradication programs on a number of offshore islands, where the area is relatively small, and there is no ability for reinvasion (Algar et al. 2002). However, on the mainland, the focus of conservation and land management agencies is to mitigate the harmful impacts of feral cats in and around targeted high-priority, high conservation values. Most common control or 'predation-mitigation' methods include trapping, shooting, poisoning and fenced exclosures. Biological control including immunocontraception, gene drive technology and the introduction of infectious diseases is technically, operationally and ethically not feasible at the moment (Bradley 1994). Trapping can be very effective for removing animals from a relatively confined area but is not feasible as a broad-area control measure. Not only is it labour-intensive, trapping risks harming nontarget species, especially if traps are set on the ground. Shooting is equally ineffective, because of the relatively low density of feral cats in arid environments and because of their evasive nature. Well-designed cat-proof fenced exclosures can be very effective at protecting native animals from predation, essentially creating 'inland islands', or refugia (Somers and Hayward (eds.) 2012; Dickman 2012). Construction and maintenance costs limit the number and size of enclosures that can be built, but where they exist in the arid zone, they have been very successful. There is likely to be an increase in the use of enclosures to provide refugia for threatened arid zone fauna into the future.

Baiting using 1080 poison has shown most promise as a method for broad-area control of feral cats (and other introduced predators) (Algar and Burrows 2004). Following the development of a novel cat bait medium, broad-area aerial baiting using the toxin 1080 is now routinely used in targeted areas of the semi-arid and arid regions of Western Australia where there are high conservation values at risk of predation (Algar and Burrows 2004). Feral cats are reluctant to scavenge, preferring live prey. However, there are periods when live prey abundance is low, increasing famine pressure on feral cats. Shortage of prey usually coincides with cold, dry weather, and operational trials in Western Australian deserts have demonstrated that this is the optimal time to deliver cat baits (Algar and Burrows 2004; Algar et al. 2007). The window of opportunity for effective control by baiting is relatively narrow, and the effectiveness of baiting has been variable. Based on a track count index (Burrows et al. 2003) and occasional radio tagging of animals before and after baiting, baiting efficacy (knock-down of the pre-bait population) can range from about 25% to almost 80% (Algar and Burrows 2004). Trials in arid Western Australia using biomarkers have shown that there are a few native species including reptiles that will consume cat baits. These species have a high resistance to 1080 (Twigg et al. 2003; Twigg 2014). Carnivorous marsupials such as mulgara (*Dasycercus* *cristicauda*) consume the cat baits, but the benefit of reduced cat predation due to baiting has resulted in a net increase in their numbers (Hamilton et al. 2010).

Conclusion

Following European settlement, Australia experienced an invasion of exotic animals deliberately introduced for transport, livestock, as companion animals or for recreational hunting. Many of these became feral pests and quickly spread across the continent, occupying a diversity of habitats including the semi-arid and arid regions. In an environment naïve to their ecology, they have caused and continue to cause substantial adverse economic and environmental damage. For the most part, total eradication of feral animals is not feasible, so landholders should aim to manage populations at various spatial and temporal scales to reduce the damage they cause to values. The extent of damage is largely a function of the density of the offending feral animal species, and control measures are usually expensive. In order to manage feral animals in a cost-effective manner that reduces impact on values, it is necessary to understand and quantify the relationships between densities of feral animals and the damage they cause – simply killing feral animals will be expensive but will not necessarily deliver a beneficial economic or environmental outcome.

There are a number of control methods available for feral animals including conventional control techniques and, since the 1950s, biological control (Saunders et al. 2010). Many of these pest feral animals were at one time, highly valuable to humans, and in today's society, there still exist strong bonds and cultural associations with these animals, especially those that were used for transport such as horses, donkeys and camels (e.g. Decker et al. 2001; Nimmo and Miller 2007). This sentiment is summed up by Walker (1973) who wrote:

> It seems a tragic reflection on Man and his sense of values that animals that were once invaluable – who played such a vital part in the opening up of this great country – should, in a generation or two, be thought of as vermin and hunted down in their thousands to be killed for the bounty paid on their ears or as pet meat.

As well as being sensitive to these cultural associations with what are now pest feral animals, control programs must comply with the animal welfare standards enshrined in legislation in all states. Aside from legal obligations, there is a community expectation that all animals, including pests, are to be treated humanely. Therefore, animal welfare issues must be an important consideration when planning feral animal control programs. However, there is often tension between conservation ecology, which focusses on the survival and persistence of populations, species and ecological communities and animal welfare, which focusses on the welfare of individual animals. In the words of environmental philosopher Mark Sagoff (1984); 'Environmentalists cannot be animal liberationists. Animal liberationists cannot be environmentalists. The environmentalist would sacrifice the lives of individual creatures to preserve the authenticity, integrity and complexity of ecological systems.

The liberationist - if the reduction of animal misery is taken seriously as a goal - must be willing, in principle, to sacrifice the authenticity, integrity and complexity of ecosystems to protect the rights, or guard the lives, of individual animals'. The control of pest animals to achieve environmental and biodiversity benefits brings this philosophical conflict into sharp focus. The role of science is to inform the debate; ultimately, societies and their governments will determine the outcome.

Acknowledgements I thank John Dunn GIS Branch Department of Parks and Wildlife for preparing distribution maps based on those of Van Dyk and Strahan (2008).

References

Abbot I (2002) Origin and spread of the cat, *Felis catus*, on mainland Australia, with a discussion of the magnitude of its early impact on native fauna. Wildl Res 29:51–74

Abbot I (2008) The spread of the cat *felis catus*, in Australia: re-examination of the current conceptual model with additional information. Conserv Sci West Aust 7:1–17

Abbot I, Peacock D, Short J (2014) The new guard: the arrival and impacts of cats and foxes. In: Glen A, Dickman C (eds) Carnivores of Australia: past, present and future. CSIRO Publishing, Melbourne, pp 69–104

ACIL (1996) The economic importance of wild rabbits to rural production in Australia. Report to the International Wool Secretariat. ACIL Economics and Policy Pty Ltd., Canberra

Agnew DC, Patrick GPJ, Arnold BK (2010) A framework for the management of feral goats in semi-arid South Australia. In: Elderidge D, Waters DJ (eds) Proceedings of the 16th Biennial conference of the Australian Rangeland Society Bourke, NSW. Australian Rangelands Society, Perth

Algar DA, Burrows ND (2004) Feral cat control research: western shield review- February 2003. Conserv Sci West Aust 5:131–163

Algar DA, Burbidge AA, Angus GJ (2002) Cat eradication on Hermite Island, Montebello Islands, Western Australia. In: Veitch CR, Clout MN (eds) Turning the tide: the eradication of invasive species: proceedings of the international conference on eradication of island invasives. World Conservation Union, Gland, pp 14–18

Algar DA, Angus GJ, Williams MR, Mellican AE (2007) Influence of bait type, weather and prey abundance on bait uptake by feral cats on Peron peninsula, Western Australia. Conserv Sci West Aust 6:109–149

Allen BL, West P (2013) Influence of dingoes on sheep distribution in Australia. J Aust Vet Assoc 91:261–267

Allen BL, Engeman RM, Krupa HA (1996) Evolution of three relative abundance indices for assessing dingo populations. Wildl Res 23:197–205

Allen BL, Lundie-Jenkins G, Burrows ND, Engeman RM, Fleming PJS, Leung LKP. (2014) Does lethal control of top-predators release mesopredators? A re-evaluation of three Australian case studies. USDA National Wildlife Research Center – Staff Publications. Paper 1438

Armstrong R (2004) Baiting operations; western shield. Conserv Sci 5:31–50

Auld TD (1990) Regeneration in populations of arid zone plants *Acacia carnei* and *A. oswaldii*. Proc Ecol Soc Aust 16:267–272

Bayne P, Harden B, Pines K, Taylor U (2000) Controlling feral goats by shooting from a helicopter with and without the assistance of ground-based spotters. Wildl Res 27:517–523

Bayne P, Harden R, Davies I (2003) Feral goats (*Capra hircus* L.) in the Macleay River gorge system, north-eastern New South Wales, Australia. I. Impacts on soil erosion. Wildl Res 31:519–525

Beadle NCW (1948) The vegetation and pastures of New South Wales. Government Printer, Sydney

Best SM, Kerr PJ (2000) Coevolution of host and virus: the pathogenesis of virulent and attenuated strains of Myxoma virus in resistant and susceptible European rabbits. Virology 276:36–48

Bode M, Brennan KEC, Morris K, Burrows N, Hague N (2012) Choosing cost-effective locations for conservation fences in the local landscape. Wildl Res 39:192–201

Bomford M (1991) Importing and keeping exotic vertebrates in Australia. Bureau of Rural Resources, Canberra

Bough J (2006) From value to vermin: a history of the donkey in Australia. Aust Zool 33:388–397

Bowen Z, Read J (1998) Population and demographic patterns of rabbits (*Oryctolagus cuniculus*) at Roxby Downs in arid South Australia and the influence of rabbit haemorrhagic disease. Wildl Res 25:655–662

Bowman DMJS (1998) The impact of aboriginal landscape burning on the Australian biota. New Phytol 140:385–410

Bradley M (1994) Experimental strategies for the development of an immunocontraceptive vaccine for the European red fox, *Vulpes vulpes*. Reprod Fertil Dev 6:307–317

Bradley MP, Hinds LA, Bird PH (1998) Oral delivery of immunocontraceptive antigens for foxes in Australia. 11th Australian vertebrate pest conference programme and proceedings, Bunbury, Western Australia, pp 197–203

Brooker MG (1977) Some notes on the mammalian fauna of the western Nullarbor plain, Western Australia. West Aust Nat 14:2–15

Broomhall FH (1991) The longest fence in the world. Hesperian Press, Fremantle

Brothers NP, Skira IJ, Copson GR (1985) Biology of the Feral Cat, *Felis catus* (L.), on Macquarie Island. Aust Wildl Res 12:425–436

Brown PH (2001) Eradication of domestic stock and feral goats on Peron Peninsula, Shark Bay: 10 years on (1990–2000). Report to the Department of Conservation and Land Management, Perth, Western Australia, 31pp

Burbidge AA, McKenzie NL (1989) Patterns in the decline of Western Australia's vertebrate fauna: causes and conservation implications. Biol Conserv 50:143–198

Burrows ND, Christensen PES (2002) Long-term trends in native mammal capture rates in a jarrah forest in South-Western Australia. Aust For 65:211–219

Burrows N, Algar D, Sinagra J, Ward B, Robinson A, Liddelow G (2003) Controlling introduced predators in the Gibson Desert of Western Australia. J Arid Environ 55:691–713

Campbell K, Donlan JC (2005) Feral goat eradications on islands. Conserv Biol 19:1362–1374

Catling P, Coman BJ (2008) Fox. In: Van Dycke S, Strahan R (eds) The mammals of Australia: Third Edition. Reed New Holland, Sydney, pp 740–741

Caughley GC (1977) Analysis of vertebrate populations. Wiley, London

Choquenot D (1990) Rate of increase for populations of feral donkeys in northern Australia. J Mammal 71:151–155

Choquenot D (2008) Donkeys. In: Van Dycke S, Strahan R (eds) The mammals of Australia, 3rd edn. Reed New Holland, Sydney, pp 751–752

Christensen PES (1980) A sad day for native fauna. For Focus 23:3–12

Christensen PES, Burrows N (1995) Project desert dreaming: the reintroduction of native mammals to the Gibson Desert. In: Serena M (ed) Reintroduction biology of Australian and New Zealand Fauna. Surrey Beatty, Chipping Norton, pp 199–208

Clarke GM (2001) Environmental pest species in Australia. Australian Government, Environment Australia, Canberra

Clarkson CM, Smith B, Marwick R, Fullagar LA, Wallis P, Faulkner T, Manne E, Hayes RG, Roberts Z, Jacobs X, Carah KM, Lowe J, Matthews J, Florin SA (2015) The archaeology, chronology and stratigraphy of Madjedbebe (Malakunanja). II: a site in northern Australia with early occupation. J Hum Evol 83:46–64

Cochrane P (1992) Simpson and the donkey; making of a legend. Melbourne University Press, Melbourne

Cogger H, Cameron E, Sadlier R, Eggler P (1993) The action plan for Australian reptiles. Australian Nature Conservation Agency, Canberra

Cole J (1999) A recovery plan for the central rock rat (*Zyzomys pedunculatus*). Report to the endangered species program, National Heritage Trust, Canberra

Cooke BD (2011) The ecological impact of wild European rabbits *Oryctolagus cuniculus* (L.) in Mediterranean-like and arid climatic regions of Australia. Report to the Invasive Animals Cooperative Research Centre, Canberra

Corbet GB, Harris S (1991) The handbook of British mammals, 3rd edn. Blackwell, Oxford

Corbett LK (1995) The dingo in Australia and Asia. University of New South Wales Press, Sydney

Corbett LK, Newsome AE (1987) The feeding ecology of the dingo. III. Dietary relationships with widely fluctuating prey populations in arid Australia: an hypothesis of alternation of predation. Oecologia 74:215–227

Croft JD, Fleming PJS, van de Ven R (2002) The impact of rabbits on a grazing system in eastern New South Wales.1. Ground cover and pastures. Aust J Exp Agric 42:909–916

Crowley G (2010) Managing pest animals for wildlife conservation. http://www.landmanager.org.au/managing-pest-animals-wildlife-conservation-feral-cattle-bos-taurus-and-bos-indicus

Dawson MJ, Lane C, Saunders G (eds) (2006) Proceedings of the national feral horse management workshop, Invasive Animals Cooperative Research Centre, Canberra

Decker DJ, Brown TL, Siemer WF (2001) Human dimensions of wildlife management in North America. The Wildlife Society, Bethesda

Deeker W (1992) New rabbit biological control strategies for the 90s in Australia. Vertebrate Biocontrol Centre Paper No. 1. CSIRO, Canberra, Australia

Denny EA, Dickman CR (2010) Review of cat ecology and management strategies in Australia. Invasive Animals Cooperative Research Centre, Canberra

Department of the Environment and Heritage (2004) Feral horse (Equus caballus) and feral donkey (Equus asinus). Natural Heritage Trust, Canberra

Department of the Environment, Water, Heritage and the Arts (DEWHA) (2008a) Threat abatement plan for competition and land degradation by unmanaged goats. DEWHA, Canberra

Department of the Environment, Water, Heritage and the Arts (DEWHA) (2008b) Background document for the threat abatement plan for predation by the European red fox. DEWHA, Canberra

Department of the Environment, Water, Heritage and the Arts (DEWHA) (2008c) Threat abatement plan for predation by feral cats. DEWHA, Canberra

Department of the Environment, Water, Heritage and the Arts (DEWHA) (2008d) Threat abatement plan for competition and land degradation by rabbits. DEWHA, Canberra

Dickman C (1996) An overview of the impact of feral cats on Australian native fauna. Australian Nature Conservancy Agency, Canberra

Dickman C (2012) Fences or ferals? Benefits and costs of conservation fencing in Australia. In: Somers J, Hayward MW (eds) Fencing for conservation: restriction of evolutionary potential or a riposte to threatening processes? Springer, New York, pp 43–63

Dickman C, Glen A, Letnic M (2009) Reintroducing the dingo: can Australia's conservation wastelands be restored? In: Hayward MW, Somers MJ (eds) Reintroduction of top-order predators. Wiley-Blackwell, Oxford, pp 238–269

Dobbie WR, Berman DM, Braysher ML (1993) Managing vertebrate pests: feral horse. Australian Government Publishing Service, Canberra

Dorge B, Heuck J (2003) Demonstration of ecologically sustainable management of camels on aboriginal pastoral land. National Heritage Trust final report on project Number 200046

Doyle PT, Egan JK, Thalen AJ (1984) Intake, digestion and nitrogen and sulfur retention in angora goats and merino sheep fed herbage diets. Aust J Exp Husb 24:165–169

Edwards GP, Saalfeld K, Clifford B (2004a) Population trend of feral camels in the Northern Territory, Australia. Wildl Res 32:509–517

Edwards GP, Pople AR, Saalfeld K, Caley P (2004b) Introduced mammals in Australian rangelands: future threats and the role of monitoring programmes in management strategies. Austral Ecol 29:40–50

Edwards GP, Zeng B, Saalfeld WK, Vaarzon-Morel P (2010) Evaluation of the impacts of feral camels. Rangel J 32:43–54

Elderidge DJ (1998) Trampling of microphytic crusts on calcareous soils and its impact on erosion under rain-impacted flow. Catena 33:221–239

Eldridge DJ, Simpson R (2001) Rabbit (*Oryctolagus cuniculus* L.) impacts on vegetation and soils, and implications for management of wooded rangelands. Basic Appl Ecol 2:4–8

Environment Australia (1999) Threat abatement plan for predation by feral cats. Environment Australia, Canberra

Flannery T (2002) The future eaters: the ecological history of the Australasian lands and people. Grove Press, New York

Fleming P, Corbett L, Harden R, Thomson P (2001) Managing the impacts of dingoes and other wild dogs. Bureau of Rural Science, Canberra

Forsythe DM, Parkes JP (2004) Maximising the conservation benefits of the commercial goat industry in Australia. Final report for the Australian Government Department of the Environment and Heritage, Canberra

Forsythe DM, Duncan RP, Bomford M, Moore G (2004) Climatic suitability, life history traits, introduction effort, and the establishment and spread of introduced mammals in Australia. Conserv Biol 18:557–569

Freeland WJ, Choquenot D (1990) Determinants of herbivore carrying capacity: plants, nutrients, and *Equus Asinus* in northern Australia. Ecology 71:589–597

Friend JA (1990) The numbat *Myrmecobius fasciatus*: history of decline and potential recovery. Proc Ecol Soc Aust 16:369–377

Gammage B (2011) The biggest estate on Earth*;* how aborigines made Australia. Allen and Unwin, Sydney

Gee P, Greenfield B (2007) South Australian arid lands feral camel management plan. South Australian Arid Lands Natural Resources Management Board

Gibson N, Meissner R, Markey AS, Thompson WA (2012) Patterns of plant diversity in ironstone ranges in arid south western Australia. J Arid Environ 77:25–31

Glen AS, Dickman CR (2005) Complex interactions among mammalian carnivores in Australia and their implications for wildlife management. Biol Rev Camb Philos Soc 80:387–401

Gollan K (1984) The Australian dingo: in the shadow of man. In: Archer M, Clayton G (eds) Vertebrate zoogeography and evolution in Australia. Hesperian Press, Fremantle, pp 921–927

Gong W, Sinden J, Braysher M, Jones R (2009) The economic impacts of vertebrate pests in Australia. Invasive Animals Cooperative Research Centre, Canberra

Gordon G, McCrae P, Lim L, Reimer D, Porter G (1993) The conservation status of the yellow-footed rock wallaby in Queensland. Oryx 27:159–168

Green RSB, Nettleton WB, Chartres CJ, Leys JF, Cunningham RB (1998) Runoff and micromorphological properties of a grazed haplargid near Cobar, NSW, Australia. Aust J Soil Res 36:87–108

Hall G (2005) Management of wild deer in Australia. J Wildl Manag 69:837–844

Hamilton N, Onus M, Forrest K (2010) Fighting back; mulgaras return. Landscope 26:6–9

Harrington GN (1986) Herbivore diet in a semi-arid *Eucalyptus populnea* woodland. 2. Feral goats. Aust J Exp Agric 26:423–429

Henderson WR (2009) Pathogens in invasive animals of Australia. Invasive Animals Cooperative Research Centre, Canberra

Henzell R (1991) Rabbits, feral goats, Mulga and rangelands stability. In: Working papers of the 9th Australian vertebrate pest control conference, Adelaide, South Australia, pp 18–21

Henzell R (1993) The ecology of feral goats. In: Freudenberger D (ed) Proceedings of the National Workshop on feral goat management: planning for action. Bureau of Resource Science, Canberra, pp 9–16

Henzell R (2008) Goat *Capra hircus* Linnaeus 1758. In: Van Dyck S, Strahan R (eds) The mammals of Australia, 3rd edn. Reed New Holland, Sydney, pp 768–769

Hone J (2007) Wildlife damage control. CSIRO Publishing, Collingwood

James CD, Landsberg J, Morton SR (1999) Provision of watering points in the Australian arid zone: a review of effects on biota. J Arid Environ 41:87–121

Johnson C (2006) Australia's mammal extinctions: a 50000 year history. Cambridge University Press, Cambridge

Johnson CN, Wroe S (2003) Causes of extinction of vertebrates during the Holocene of mainland Australia: arrival of the dingo, or human impact? The Holocene 13:941–948

Jones E (2009) Hybridisation between the dingo, *Canis lupus dingo*, and the domestic dog, *Canis lupus familiaris*, in Victoria: a critical review. Aust Mammal 32:1–7

Jones E, Coman BJ (1981) Ecology of the feral cat, *Felis catus* (L.), in south-eastern Australia I. Diet Aust Wildl Res 8:537–547

Jones E, Coman BJ (1982) Ecology of the feral cat *Felis catus* (L.) in South-Eastern Australia 11. reproduction. Aust Wildl Res 9:111–119

Jurskis V (2014) Firestick ecology: Fairdinkum science in plain English. Connor Court Publishing, Ballarat

Kennedy MJ (1992) Hauling the loads: a history of Australia's working horses and bullocks. Melbourne University Press, Melbourne

Kerr PJ, Best SM (1998) Myxoma virus in rabbits. Rev Sci Tech 17:256–268

Killian GLA, Miller NK, Diehl J, Rhyan J, Thain D (2004) Evaluation of three contraceptive approaches for population control of wild horses. In: Timm RM, Gorenzel WP (eds) Proceedings of the 21st Vertebrate pest conference. Visalia California, USDA National Wildlife Research Center – Staff Publications. Paper 370, pp 263–268

King DR, Oliver AJ, Mead RJ (1978) The adaptation of some western Australian mammals top food plants containing fluroacetate. Aust J Zool 26:699–712

Kinnear JE, Onus ML, Bromilow RN (1988) Fox control and rock wallaby population dynamics. Aust Wildl Res 15:435–450

Kinnear JE, Sumner NR, Onus ML (2002) The red fox in Australia – an exotic predator turned biocontrol agent. Biol Conserv 108:335–359

Lacey CJ (1972) Factors influencing occurrence of cypress pine regeneration in New South Wales. Forestry Commission of New South Wales technical paper no. 21

Lang RT, Graham CR (1983) Rabbits and the failure of regeneration in Australian arid zone acacia. Aust J Ecol 8:377–381

Lethbridge M, Pitt J (2009) Feral camel surveys in the Nullarbor region June 2009. A discussion of survey outcomes and methods to inform land management for protection of environmental assets. Alinytjara Wilurara Natural Resources Management Board, South Australia

Lethbridge MR, Anderson N, Harper ML, Gee P (2010) Movements and landscape use of camels in central Australia revealed by GPS satellite. Rangel J 32(1):33

Long JL (1988) Introduced birds and mammals in Western Australia. Technical series No. 1, Agriculture Protection Board of WA, Perth

Long J (2003) Introduced mammals of the world: their history, distribution and influence. CSIRO, Victoria

Low T (2008) Cattle. In: Van Dyk S, Strahan R (eds) The mammals of Australia, 3rd edn. Reed New Holland, Sydney, pp 766–767

Lugton IW (1993) Diet of red foxes in south-west New South Wales with relevance to lamb predation. Rangel J 15:39–47

Mahood IT (1985) Some aspects of ecology and the control of feral goats (*Capra hircus*) in western NSW. MSc thesis, Macquarie University, Sydney

Marks CA, Nijk M, Gigliotti F, Busana F, Short RV (1996) Preliminary field assessment of a cabergoline baiting campaign for reproductive control of the red fox (*Vulpes vulpes*). Wildl Res 23:161–168

Marks CA, Gigliotti F, Busana F (2009) Assuring that 1080 toxicosis in the red fox (*Vulpes vulpes*) is humane II. Analgesic drugs produce better welfare outcomes. Wildl Res 36:498–505

Masters P, Dickman CR, Crowther M (2003) Effects of cover reduction on mulgara *Dasycercus cristicauda*, (Marsupialia: Dasyuridae), rodent and invertebrate populations in Central Australia: implications for land management. Austral Ecol 28:658–665

Matthews D, Bryan R, Edwards G (2001) Recovery of the black-footed rock-wallaby following horse removal on Finke Gorge National Park, Northern Territory. In Proceedings of the 12th Australasian Vertebrate pest conference. 21–25 May 2001, Melbourne, Victoria, Australia. Natural Resources and Environment, Melbourne, p 204

Maxwell S, Burbidge AA, Morrris K (eds) (1996). Action plan for Australian marsupials and Monotremes. Australasian Marsupial and Monotreme Specialist Group, IUCN Species Survival Commission

McIlroy JC, Gifford EJ, Cooper RJ (1968) Effects on non-target animal populations of wild dog baiting campaigns with 1080 poison. Aust Wildl Res 13:447–453

McKenzie NL, Burbidge AA, Baynes A, Brereton RN, Dickman CR, Gordon G, Gibson LA, Menkhorst PW, Robinson AC, Williams MR, Woinarski JCZ (2006) Analysis of factors in the recent decline of Australia's mammal fauna. J Biogeogr 34:597–611

McKnight TL (1969) The camel in Australia. Melbourne University Press, Melbourne

McKnight TL (1976) Friendly vermin: a survey of feral livestock in Australia. University of California Press, Berkeley

McLeod R (2004) Counting the cost: impact of invasive animals in Australia 2004. Cooperative Research Centre for Pest Animal Control, Canberra

McLeod JC, Saunders GR (2001) Improving management strategies for the red fox by using projection matrix analysis. Wildl Res 28:333–340

McNiven I, Hitchcock GJ (2005) Torres Strait islander marine subsistence specialisation and terrestrial animal translocation. Mem Queensland Mus Cult Heritage Ser 3:105–162

Menkhorst P, Hynes E (2010) National Recovery Plan for the brush-tailed rock-wallaby *Petrogale penicillata*. Department of Sustainability and Environment, East Melbourne

Moseby KE, Neilly H, Read JL, Crisp HA (2012) Interactions between a top order predator and exotic mesopredators in the Australian Rangelands. Int J Ecol 2012:250352 15 pages. https://doi.org/10.1155/2012/250352

Myers K, Parer I, Wood D, Cooke BD (1994) The rabbit in Australia. In: Thompson HV, King CM (eds) The European rabbit: the history and biology of a successful colonizer. Oxford Science Publications, London, pp 108–157

Newsome AE, Catling PC (1992) Host range and its implication for wildlife rabies in Australia. In: P O'Brien, G Berry (eds) Wildlife rabies contingency planning in Australia. Bureau of rural resources proceedings no. 11. Australian Government Printing Service, Canberra, pp 23–32

Newsome AE, Corbett LA (1982) The identity of the dingo II. Hybridization with domestic dogs in captivity and in the wild. Aust J Zool 30:365–374

Newsome AE, Corbett LA (1985) The identity of the dingo III. The incidence of dingoes, dogs and hybrids and their coat colours in remote and settled regions of Australia. Aust J Zool 33:363–375

Nimmo DG, Miller KK (2007) Ecological and human dimensions of management of feral horses in Australia: a review. Wildl Res 34:409–417

Norris A, Low T (2005) Review of the management of feral animals and their impact on biodiversity in the rangelands; a resource to aid NRM planning, Pest Animal Control CRC Report 2005, Pest Animal Control CRC, Canberra

Olsen PD (1995) Australian birds of prey: the biology and conservation of raptors. University of New South Wales Press, Sydney

Paltridge R, Gibson D, Edwards G (1997) Diet of the feral cat (*Felis catus*) in Central Australia. Wildl Res 24:67–76

Parkes J (1990) Eradication of feral goats on islands and habitat islands. J R Soc N Z 20:297–304

Parkes J, Henzel R, Pickles G (1996) In:) Managing vertebrate pests; feral goats (ed) Bureau of Resource Sciences and the Australian Nature Conservancy. Australian Government Publishing Service, Canberra

Pearson DJ (2013) Recovery plan for five species of rock wallabies: Black-footed rock wallaby (*Petrogale lateralis*), Rothschild rock wallaby (*Petrogale rothschildi*), Short-eared rock wallaby (*Petrogale brachyotis*), Monjon (*Petrogale burbidgei*) and Nabarlek (*Petrogale concinna*) 2012–2022. Department of Parks and Wildlife, Perth, WA

Pimentel D, McNair S, Janecka J, Wightman J, Simmonds C, O'Connell C, Wong E, Russel L, Zern T, Acquino T, Tsomondo T (2001) Economic and environmental threats of alien plant, animal and microbe invasions. Agric Ecosyst Environ 84:1–20

Pople T, Froese J (2012) Distribution, abundance and harvesting of feral goats in the Australian rangelands 1984–2011. Final report to ACRIS Management Committee, Queensland Government

Pople AR, Grigg GC, Cairns SC, Alexander P, Beard LA, Henzell RP (1996) Trends in numbers and changes in the distribution of feral goats (*Capra hircus*) in the south Australian pastoral zone. Wildl Res 23:687–696

Pople AR, Clancy TF, Thompson JA, Boyd-Law S (1998) Aerial survey methodology and the cost of control for feral goats in Western Queensland. Wildl Res 25:393–407

Possingham H, Jarman P, Kearns A (2004) Independent review of western shield – February 2003. Conserv Sci West Aust 5:2–18

Priddel D, Wheeler R (1990) Survival of mallee fowl *Leipoa ocellata* chicks in the absence of ground-dwelling predators. Emu 90:81–87

Read J, Cunningham R (2010) Relative impacts of cattle grazing and feral animals on an arid zone reptile and small mammal assemblage. Austral Ecol 35:314–324

Roberts R, Rhys Jones G, Spooner NA, Head MJ, Murray AS, Smith MA (1994) The human colonisation of Australia: Optical dates of 53,000 and 60,000 years bracket human arrival at Deaf Adder Gorge, Northern Territory. Quat Sci Rev 13:575–583

Robertshaw JD, Harden RH (1986) The ecology of the dingo in north-eastern New South Wales.4. Prey selection by dingoes, and its effect on the major prey species, the swamp wallaby, Wallabia-Bicolor (Desmarest). Aust Wildl Res 13:141–163

Rolls EC (1969) They all ran wild. The story of pests in the land of Australia. Angus and Robertson, Sydney

Russell BJ, Lentic M, Fleming JS (2011) Managing feral goat impacts by manipulating their access to water in the rangelands. Rangel J 33:143–152

Saalfeld WK, Edwards GP (2010) Distribution and abundance of feral camels (*Camelus dromedarius*) in Australia. Rangel J 32:1–9

Sagoff M (1984) Animal liberation and environmental ethics: bad marriage, quick divorce. Osgoode Hall Law J 22:297–307

Saunders G, McLeod L (2007) Improving fox management strategies in Australia. Bureau of Rural Science, Canberra

Saunders G, Coman B, Kinnear J, Braysher M (1995) Managing Vertebrate pests: foxes. Australian Government Printing Service, Canberra

Saunders G, Lane C, Harris S, Dickman C (2006) Foxes in Tasmania: a report on an incursion of an invasive species. Invasive Animals Cooperative Research Centre

Saunders G, Cooke B, McColl K, Shine R, Peacock T (2010) Modern approaches for the biological control of vertebrate: an Australian perspective. Biol Control 52:288–295

Sharman GB, Maynes GM, Eldridge MDB, Close RL (1995) Yellow-footed rock – wallaby (*Petrogale xanthopus*). In: Strahan R (ed) The mammals of Australia. The Australian Museum Trust, Sydney, pp 156–157

Sharp A, Holmes K, Norton M, Marks A (2001) Observations on the effects of rabbit calicivirus disease on low and medium density rabbit populations in western New South Wales. Rangel J 23:194–203

Short J (2016) Predation by feral cats key to the failure of a long-term reintroduction of the western barred bandicoot (Perameles bougainville). Wildl Res 43(1):38
Short J, Turner B (2005) Control of feral cats for nature conservation. IV. Population dynamics and morphological attributes of feral cats at Shark Bay, Western Australia. Wildl Res 32:489–501
Short G, Caughley G, Grice D, Brown B (1988) The distribution and relative abundance of camels in Australia. J Arid Environ 15:91–97
Somers MJ, Hayward M (eds) (2012) Fencing for conservation: restriction of evolutionary potential or a riposte to threatening processes? Springer, New York
Southwell CJ, Pickles GS (1993) Abundance, distribution, and rate of increase of feral goats in Western Australia. Rangel J 15:334–348
Hall EAA, Specht RL, Eardley CM (1964) Regeneration of the vegetation on Koonamore Vegetation Reserve, 1926–1962. Aust J Bot 12:205–264
Stephens D, Wilton AN, Fleming PJS, Berry O (2015) Death by sex in an Australian icon: a continent-wide survey reveals extensive hybridization between dingoes and domestic dogs. Mol Ecol 24:5643–5656
Thomson PC (1986) The effectiveness of aerial baiting for the control of dingoes in North-Western Australia. Aust Wildl Resh 13:165–176
Trueman CN (2015) Horses in world war one. http://www.historylearningsite.co.uk/world-war-one/the-western-front-in-world-war-one/animals-in-world-war-one/horses-in-world-war-one/
Turner JW, Liu IKM, Flanagan DR, Rutberg AT, Kirkpatrick JF (2001) Immunocontraception in feral horses: one inoculation provides one year of infertility. J Wildl Manag 65:235–241
Twigg LE (2014) Fluoroacetate, plants, animals and a biological arms race. In: Lambers H (ed) Plant life on the sandplains in Southwest Australia, a global biodiversity hotspot. UWA Publishing, Crawley, pp 225–240
Twigg LE, King DR (1991) The impact of fluoroacetate-bearing vegetation on native Australian fauna; a review. Oikos 61:412–430
Twigg LE, Parker R (2010) Is sodium fluoroacetate (1080) a humane poison? The influence of mode of action, physiological effects, and target specificity. Anim Welf 19:249–263
Twigg LE, Martin GR, Eastman AF, King DR, Kirkpatrick WE (2003) Sensitivity of some Australian animals to sodium fluoroacetate (1080); additional species and populations and some ecological considerations. Aust J Zool 51:515–531
Van Dyk S, Strahan R (eds) (2008) The mammals of Australia, 3rd edn. Reed New Holland, Sydney
Virtue GJ, Gee PD, Secomb NM, O'Leary PR, Grear BP (2016) Facilitating feral camel removal in Australia through commercial use. Rangel J 38:143–151
Walker A (1973) Australian donkeys. Humphrey & Formula Press, Victoria
Ward BG, Ward CG, Liddelow GL (2005) Camel populations in Central Western Australia determined from aerial surveys. Conserv Sci West Aust 12:21–26
Williams CK, Parer I, Coman BJ, Burley J, Braysher ML (1995) Managing vertebrate pests: rabbits. Bureau of Resources Science/CSIRO. Australian Government Publishing Services, Canberra
Yarwood AT (1989) Walers: Australian horses abroad. Miegunyah Press, Carlton
Zeng B, Gerritsen R (2013) Inadequate contribution of commercial harvest to feral camel control in Australia. J Environ Plan Manag 56:1212–1224

Climate Change

Ian Foster

Introduction

On the broadest scale, Australia's climate can be divided into four classifications:

- Summer rain dominant. This covers the tropical north of the continent where most rain comes from warm season weather and climate systems such as the Australian Monsoon and tropical cyclones.
- Winter rain dominant. This covers much of southern, and especially south-western, Australia. Weather and climate systems are mostly midlatitude in origin and defined by the interplay between midlatitude low-pressure systems and the intervening high-pressure cells of the subtropical ridge.
- Even rain distribution through the year – on average at least. This covers much of eastern Australia, where rainfall can be significant in both winter and summer. Interannual rainfall variability can be high, driven largely by El Niño/Southern Oscillation events in the Pacific Ocean. Smaller-scale analogous events in the tropical Indian Ocean (Indian Ocean Dipole) can be significant rain sources as well.
- Arid zone, where rainfall is low on average and where significant rain events are often few and far apart. This covers most of the inland and represents approximately half the land area of Australia. Many of the major rain events in this region usually originate in tropical weather systems, such as northwest cloud bands or tropical cyclones.

For the first three classifications, seasonal and annual rainfall totals increase with proximity to the coast. Each of these classifications can be subdivided further, but the broad zones are evident, as shown in Fig. 1.

I. Foster (✉)
Department of Primary Industry and Regional Development, South Perth, WA, Australia
e-mail: Ian.Foster@dpird.wa.gov.au

H. Lambers (ed.), *On the Ecology of Australia's Arid Zone*,
https://doi.org/10.1007/978-3-319-93943-8_14

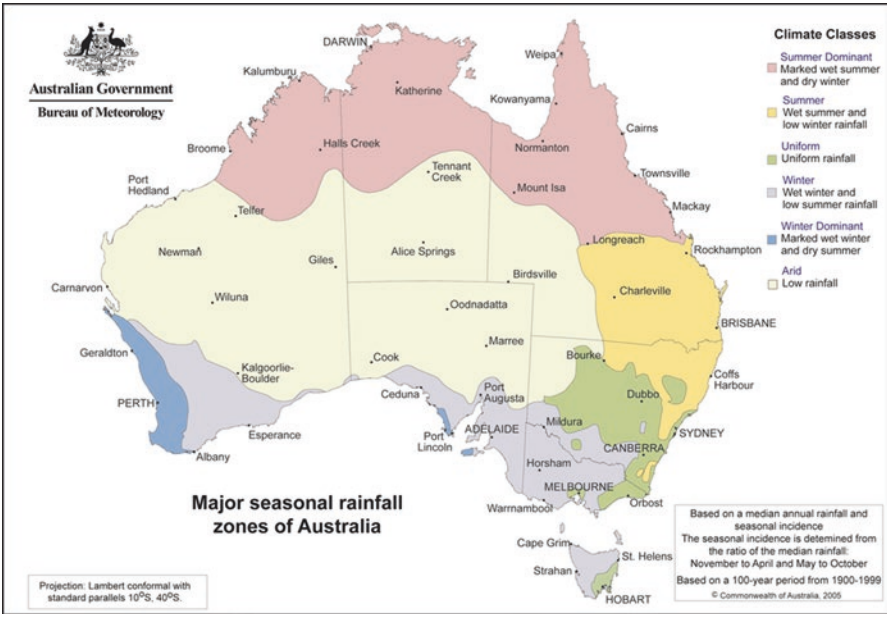


Fig. 1 Major climate zones as defined by seasonal rainfall patterns. (Source: Bureau of Meteorology, http://www.bom.gov.au/jsp/ncc/climate_averages/climate-classifications)

The Australian continent is surrounded by three major oceans – Pacific, Indian and Southern – and each basin influences Australian climate in its own way. These are variously described as climate influences, climate phenomena or climate drivers and reflect typical or recurring modes of variability in the climate dynamics of these basins. Each driver affects climate variability by amplifying or supressing the frequency of occurrence of weather systems as they change through the annual cycle.

The annual cycle represents the shift in seasons arising from the tilt in the Earth's axis and the resulting movement of regions' maximum solar heating. The first manifestation is a progression of temperatures from winter through summer and back again. Weather systems associated with the annual shift in heating therefore also occur seasonally. As Australia occupies a range of latitudes from approximately 10°S to 40°S, its climate is split between two major centres of action. Northern Australia is dominated by tropical weather systems, brought seasonally in summer via the Australian monsoon (Bureau of Meteorology 2008a). Southern Australia's climate is dominated by midlatitude low-pressure systems as they extend northwards in winter. The south also sits under the prevailing subtropical ridge, whose strength and latitude strongly affect rainfall opportunities (Bureau of Meteorology 2008b). While seasonal rainfall distribution is opposite (i.e. winter-dominant rain vs summer-dominant rain), the centres of action share a common attribute of relatively low interannual rainfall variability. In contrast, most of inland Australia, located between these centres, has very high interannual rainfall variability (Fig. 2).

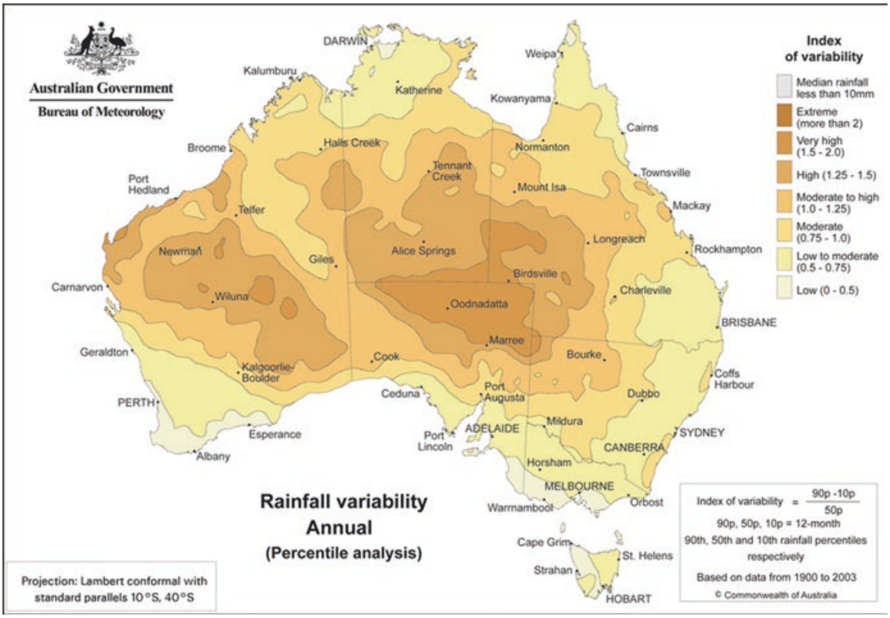


Fig. 2 Variability of annual rainfall as defined by percentiles. (Source: Bureau of Meteorology, http://www.bom.gov.au/jsp/ncc/climate_averages/rainfall-variability)

Mean annual rainfall is generally low (less than 300 mm), because the subtropical ridge is the dominant weather system over inland Australia, and the region is far from sources of moisture. Heaviest rain events tend to occur in summer, because tropical incursions are usually the only mechanism to transport a large amount of water vapour into the inland. Periods of low or no rainfall can extend for many months. The subtropical ridge is an extensive band of high pressure that encircles the globe at middle latitudes (Bureau of Meteorology 2008b). The position of the ridge varies with the seasons, allowing cold fronts to pass over southern Australia in winter but pushing them south of the continent in summer. Conditions along the ridge tend to be stable and dry. Consequently, southern Australia is characterised by dry, hot summers, and winter rainfall occurs mostly with frontal systems (Bureau of Meteorology 2007).

In summer, southward movement of solar heating promotes persistent low pressure over northern Australia. This draws moisture from nearby tropical oceans into the Australian summer monsoon. The monsoon can be in either an 'active phase', characterised by stronger winds and rain, or an 'inactive phase', characterised by lighter winds and less rain. These intra-seasonal phases are associated with passage of Madden-Julian Oscillation (MJO) events (Bureau of Meteorology 2012). Tropical cyclones and monsoon depressions (essentially the same type of system, though differing in intensity) usually form during active phases. Southward tracking of these weather systems and movement of the monsoon trough itself are major sources of significant rain events over inland Australia. As potential evaporation is very high over arid Australia in summer, rainfall events must be heavy to be effective in accumulating soil water and consequently promoting plant growth. Continuous periods of stored soil water are vital and are often a better indication of plant growth than monthly or seasonal rainfall totals.

Climate influences are themselves modulated by even larger-scale climate events occurring in the ocean basins around the continent. The most prominent impact comes from El Niño/Southern Oscillation (ENSO) events. These occur basin-wide across the Pacific Ocean at approximately 3–8-year intervals. ENSO events are usually a coupled phenomenon, where spatial changes in ocean temperatures (El Niño and its opposite phase La Niña) interact with tropical winds and clouds to induce large changes in atmospheric pressure across the basin (Southern Oscillation). There is also a neutral phase of ENSO, when neither El Niño nor La Niña is occurring. Spatial patterns of sea surface temperature and atmospheric pressure anomalies are often weak in this phase. Extensive literature exists on ENSO, and readers are referred to Bureau of Meteorology (2008c) for an overview.

In general, El Niño events suppress the onset and intensity of the Australian monsoon and also of tropical cyclone activity. Tropical cyclones tend to occur further away from the coast in El Niño years, and the number of coastal crossings is usually less. Opportunities for significant rain over the inland are therefore reduced. While the duration of El Niño events can vary, there is a typical cycle over an approximately 18-month period. A common pattern is for the event to develop during the austral winter, reach a peak over spring and summer and decay in the austral autumn of the following year. This breakdown can bring heavy rain and floods over much of eastern Australia. Many major Australian droughts or periods of prolonged dry conditions are associated with El Niño events (Bureau of Meteorology 2014).

La Niña events tend to do the opposite; commonly enhancing the summer monsoon, which in turn usually spawns more tropical cyclones than normal. The timescale of occurrence is similar, with events developing in the austral winter and peaking over spring and summer. Individual El Niño and La Niña events follow their own development and decay timetables, as well as differing in peak intensity.

An analogous coupled event also occurs periodically in the tropical Indian Ocean. The Indian Ocean Dipole (IOD) is defined as a difference in sea surface temperatures in two regions across the western and eastern Indian Ocean. In its most developed form, there is also a coupled atmospheric response across the tropical Indian Ocean. Opposite phases of the phenomenon are more prosaically called IOD-negative or IOD-positive events.

IOD events develop during the austral winter and peak during spring, usually lasting some 4–6 months at most. They can act to either enhance (IOD-negative) or suppress (IOD-positive) rainfall over central and eastern Australia during winter and spring. Notable IOD-negative events in 2010 and 2016 brought record seasonal rains to much of Australia. Driven by warming ocean temperatures around Indonesia, northwest cloud bands and other tropical moisture inflow can interact with low-pressure systems over southern Australia to bring rainfall inland (Bureau of Meteorology 2016a).

ENSO and IOD events can occur individually in any one year, or in combination to either reinforce or cancel out impacts on rainfall. The resulting time series of seasonal rainfall across Australia is accordingly highly variable from year to year. As well as these two tropical modes of climate variability, there is also a southern higher-latitude mode just to complicate interactions further. This is the Southern Annular Mode (SAM) (Bureau of Meteorology 2008d), which describes the strength and latitudinal positioning of the string of alternating high- and low-pressure weather systems between Australia and Antarctica.

As with the IOD, SAM has positive and negative phases. When SAM is positive, the belt of strong westerly winds and low-pressure systems contracts towards the South Pole. This results in weaker than normal westerly winds and higher pressure over southern Australia. A negative SAM phase describes an equatorward expansion of the belt of strong westerly winds. This results in more storm systems and lower pressure over southern Australia. These phases have different impacts on rainfall during the year. If SAM is positive, during autumn and winter, rainfall tends to be reduced over southern Australia, especially towards the coast. Conversely, a positive phase over spring in summer can bring more rain to the south-east and inland of Australia.

The frequency of weather systems that occur, and seasonal rainfall totals, is the result of interactions between the three major climate events discussed above. They can occur singly or in combination in any one year. Such complexity of interactions is one reason why global climate models are primary tools for investigating current and future climate.

Climate Change Modelling

At its most basic level, what is popularly called ‘global warming’ or ‘climate change’ is an amplification of a natural atmospheric process. Gases such as carbon dioxide, methane and nitrous oxide (as well as the wider family of chlorofluorocarbons) have major impacts on global temperature, despite being in relatively low concentrations in the atmosphere. They achieve this by strongly absorbing longwave radiation upwelling from the Earth’s surface and atmosphere and then reradiating the energy in all directions. Most energy eventually exits the atmosphere by a process of radiative transfer, and some is radiated downwards. The resulting increase in longwave radiation reaching the surface increases its temperature until radiative equilibrium is reached with the incoming shortwave radiation from the Sun. This process occurs on an extreme level on Venus (closer to the Sun, with a thick absorbing atmosphere), as well as to a small extent on Mars (further from the Sun and with a thin atmosphere).

The presence of absorbing gases (otherwise called greenhouse gases, GHG) keeps the Earth’s global mean temperature some 18 °C warmer than otherwise at present concentrations. The concentration of GHGs at any time is the result of a dynamic balance between sources of emission (such as respiration, combustion and geological processes) and extraction from the atmosphere into oceans and plants. Over geological timescales, gas concentrations and global temperatures have varied widely, driven by interactions between the Earth's orbit, geology and the biosphere. More recently, additional GHGs, especially carbon dioxide, have accumulated in the atmosphere since the onset of the Industrial Revolution in the mid-1750s. The use of fossil fuels (such as coal and petroleum) adds an extra emission component to the carbon budget that has not been mitigated by matching extraction and sequestration of carbon dioxide from the atmosphere.

To simulate how increasing atmospheric GHG concentrations may affect future climate, scenarios describing long-term economical and industrial development are used to provide trajectories of future concentrations of GHGs. Four scenarios of future emissions have been defined for use in simulations. They are called Representative Concentration Pathways (RCP) and cover cases of high-, intermediate- and low-emission trajectories. Responses of global atmosphere and ocean processes to these RCP options are simulated in Global Climate Models (GCMs) to assess possible impacts. GCMs simulate the physical relationships behind the major weather and climate features (as outlined in Introduction) and how they interact with the land and ocean. They are a major tool for understanding the dynamics and feedbacks of earth systems (i.e. integrating the atmosphere, hydrosphere, cryosphere and biosphere) and sensitivities of responses.

Modelling studies of climate change are commonly run as ensembles of multi-model simulations. This is to deal with uncertainties arising from the internal variability of the oceans and atmosphere and from limitations in the models' ability to simulate all processes in sufficient detail. To account for this variability (or uncertainty) among models, it is usual to present the results from a suite of models and present both the range of values and the median projection. Most of the variability in near-term climate simulations (e.g. up to 2020) results from differences among GCMs, rather than emission trajectories; however, differences in emission trajectories become increasingly important in determining medium- and longer-term (2050 and 2070) climate responses (CSIRO and Bureau of Meteorology 2015). Differences in climate projections reported in the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (providing the beloved acronym IPCC AR5) from previous reports largely stem from differences in the emission scenarios, rather than outputs from the GCMs.

Current Trends and Projections

Temperature: Current Trends

Between 1910 and 2015, average annual temperature increased by around 1 °C across most of the arid zone of Australia (Bureau of Meteorology 2016b *State of the Climate 2016*, Fig. 3).

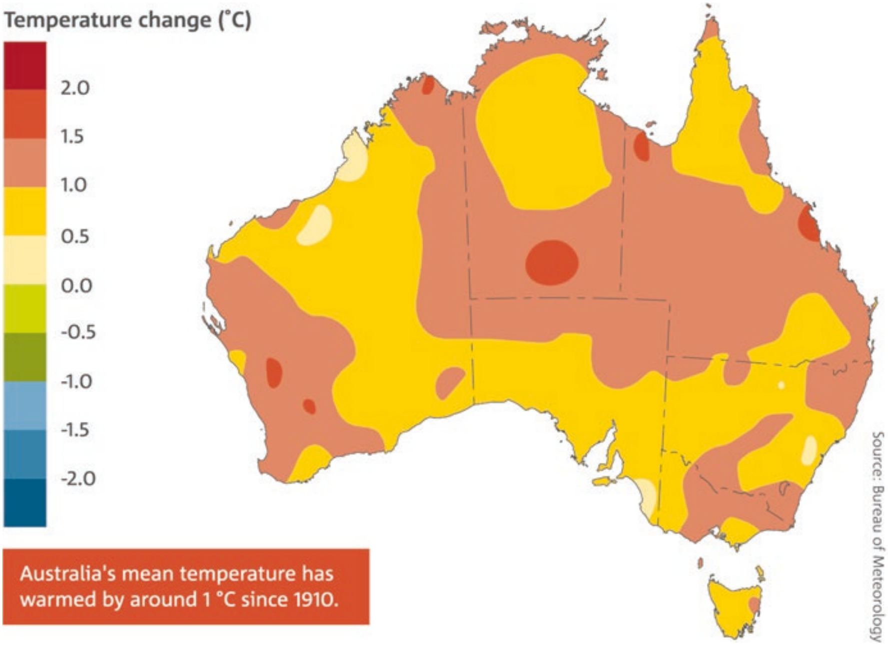


Fig. 3 Change in mean annual surface temperature since 1910. (Source: Bureau of Meteorology State of the Climate 2016, http://www.bom.gov.au/state-of-the-climate)

While average annual temperatures have increased, changes in seasonal average temperatures have been mixed. Increased rainfall over northern Australia in summer has been responsible for a cooling trend in recent years. The number of hot days (defined as the number of days over 35 °C) has increased over much of the inland (Fig. 4).

While the numbers appear small, a trend of 0.2 days per year means an extra 12 days with maxima above 35 °C in 2015 when compared with 1957. This type of statistic is important as an indicator of severe impacts from high temperatures. Risks of wildfire behaviour, heat stress on animals and water stress on plants are strongly elevated as temperature rises. A shift in mean temperature of 1 degree may seem innocuous (given diurnal changes will be commonly ten times greater) but can translate into a greatly increased frequency of extreme events.

The State of the Climate 2016 report has noted increasing frequency of extreme fire weather and a longer fire season over inland, southern and eastern Australia since the mid-1970s. This has been attributed to a broad trend of increasing temperatures and decreasing rainfall, though in context of large interannual variability of the fire danger index.

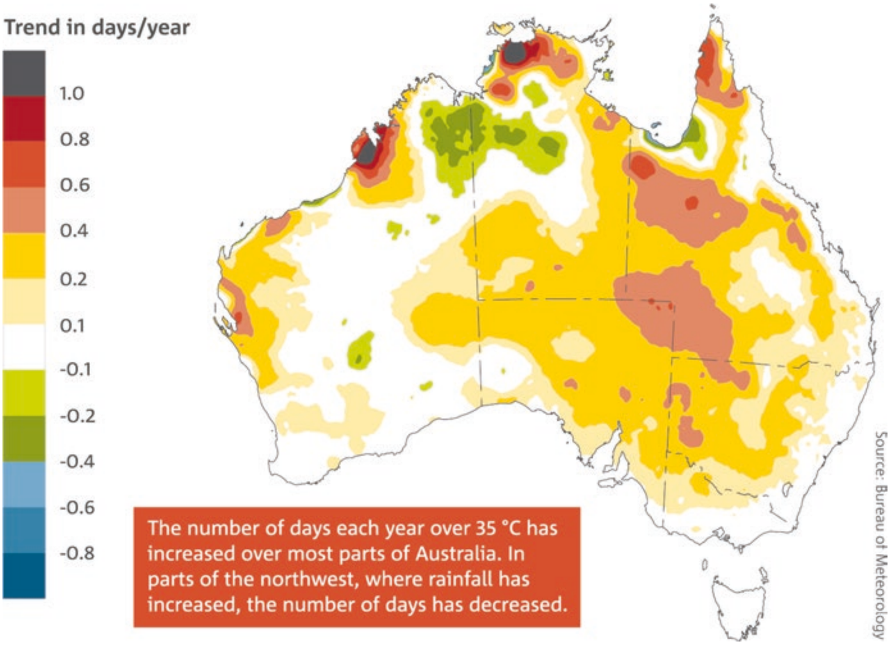


Fig. 4 Trend in number of days above 35 °C for 1957–2015. (Source: Bureau of Meteorology State of the Climate 2016, http://www.bom.gov.au/state-of-the-climate)

Table 1 Projected temperature change (°C) over inland Australia for 20-year periods centred on 2013 and 2090, compared with 1986–2005

	RCP2.6 (low)	RCP4.5 (intermediate)	RCP8.5(high)
2030	0.9 (0.6–1.3)	1.0 (0.6–1.4)	1.0 (0.8–1.4)
2090	1.1 (0.6–1.8)	2.1 (1.5–2.9)	4.3 (2.9–5.3)

The median projected temperature is shown for each Representative Concentration Pathway (RCP), with ranges of 10th and 90th percentile temperatures in brackets. This has been adapted from the Rangelands Cluster Report at https://www.climatechangeinaustralia.gov.au/en/publications-library

Temperature: Future Projections

There is very high confidence in projections that average, maximum and minimum temperatures will continue to increase to the end of the century (Watterson et al. 2015). Temperatures increase for all emission scenarios but are greater for higher emission scenarios, with a high level of agreement between global climate models. Average annual temperature across central Australia is projected to increase by 0.6–1.4 °C by 2030 under intermediate- and high-emission scenarios (RCP 4.5 and RCP 8.5, respectively), compared with average conditions from 1986 to 2005. By 2090, average annual temperature is projected to increase by 1.5–2.9 °C and 2.9–5.3 °C under RCP 4.5 and RCP 8.5, respectively (Table 1). Average maximum and minimum temperatures are projected to increase by similar amounts as the average daily mean temperature. Some appreciation of the significance of these changes can be gained from comparison with the change in temperature already observed. Mean annual temperature has increased by about 1 degree over the past 100 years, while the middle of the range for RCP4.5 (intermediate emissions) is 1 degree by 2030. That represents a fivefold increase in the rate of warming (i.e. 0.1 °C per decade since 1910 compared with 0.5 °C per decade to 2030).

Temperature extremes can be expected to increase as projected average temperatures rise (Steffen et al.2014; Moise et al. 2015). Extremes can be manifested as a wider temperature range (i.e. record new maximum or minimum temperatures), a change in the frequency of occurrence above or below thresholds or as sequences or runs of days exceeding temperature thresholds. The intensity of hot spells (daily maxima above 35 °C) is projected to increase over most of arid Australia, as is their duration. The overall frequency of hot days is also expected to increase.

An inland site such as Alice Springs can expect the average number of days above 35 °C to increase from 94 under current climate to 113 days at 2030 under an intermediate emissions future (RCR4.5). This continues to rise with time, so that by 2090, more than a third of the year would experience maxima above 35 °C. Coastal areas will not be immune. In Broome, the number of days with maxima over 35 °C is projected to increase from 56 currently (1971–2000 average) to 87 in 2030 for RCP 4.5, and to 133 in 2090 for RCP 4.5 (Moise et al. 2015).

Higher temperatures and more hot days, coupled with higher evaporation, are expected to raise the atmospheric component of bushfire risk by promoting faster curing of biomass as well as contributing to stronger fire behaviour. Combined fire risk is heavily dependent on fuel availability, and this is determined by rainfall, so the overall trend in fire risk remains uncertain over inland Australia.

How mean temperatures and extremes evolve over coming decades will be modulated by changes in rainfall. If rainfall increases, some easing of warming can be expected (as has occurred in recent years; Fig. 2). Given there is little agreement among the current generation of climate models on future rainfall trends over inland Australia, the overall temperature trajectory remains towards rising temperatures.

Rainfall: Current Trends

Over the last 50 years, annual rainfall has increased over northern and inland Australia and declined in the south and far west. It reflects contrasting trends between summer and winter rainfall that appear to have intensified in recent decades. Rainfall for April to October for the past 20 years has been markedly lower than normal over much of southern and western Australia (Fig. 5).

The decline in autumn and winter rainfall over the western Pilbara and southwest of western Australia is attributed to the southward shift in the subtropical ridge and midlatitude weather systems (Bates et al. 2012; Cai et al. 2012; Charles et al. 2013; Abram et al. 2014). Consequent rainfall reductions are associated with the persistence of high-pressure systems over the region, so while intense rainfall events

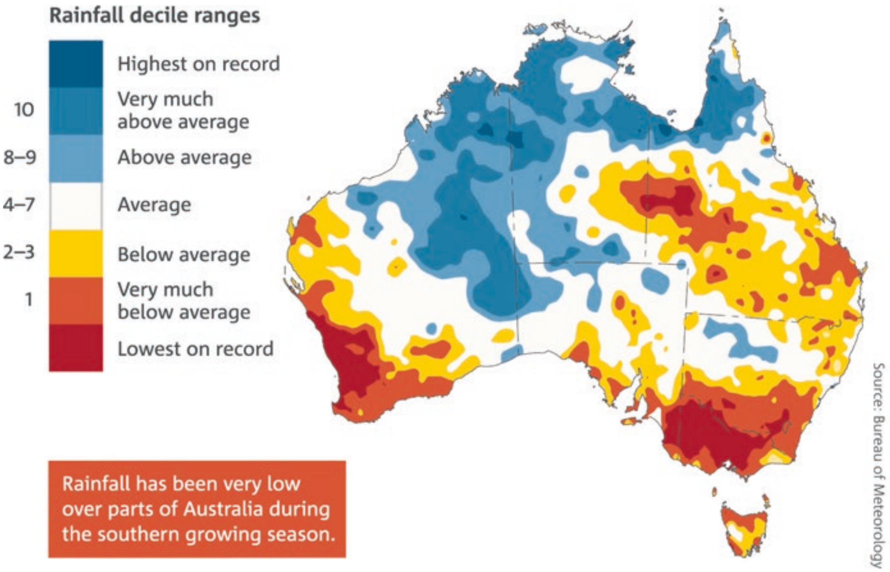


Fig. 5 Southern growing season (April to October) rainfall deciles for the last 20 years (1996–2015). A decile map shows where rainfall is above average, average or below average for the recent period, in comparison with the entire rainfall record from 1900. (Source: Bureau of Meteorology State of the Climate 2016, http://www.bom.gov.au/state-of-the-climate)

still occur, they are often interspersed by longer dry periods. The trend to more rainfall over inland and northern Australia during April to October should be taken in context that this period is usually dry. Seasonal mean rainfall is mostly under 200 mm or less. The decline in growing season rainfall over the south-west is consistent with increasing greenhouse gas concentrations and cannot be explained solely by natural climate variability or changed land use such as land clearing (Bates et al. 2012). Increasing rainfall over inland and northern Australia during warmer months has been more significant (Fig. 6). Most of this change has occurred in summer (December to February) and appears to have intensified in the past two decades. A recent study of tree growth in the Pilbara found that 5 of the 10 wettest years in the last 210 years occurred in the last two decades (O'Donnell et al. 2010, 2011).

Bates et al. (2012) linked increased rainfall in the Kimberley and the Eastern Pilbara to an increase in the growth rate of north-west cloud bands and an increase in the variability of the Madden-Julian Oscillation. Bates et al. (2012) also suggested that particulate pollution from Southeast Asia might be influencing tropical weather patterns, decreasing the amount of solar radiation reaching the surface in some regions. An additional climate influence has been increasing sea surface temperatures to the north of Australia (Bureau of Meteorology 2016b State of the Climate 2016). Causes are likely to be a combination of global warming and climate events (such as ENSO and IOD events). Warmer sea temperatures have been associ-

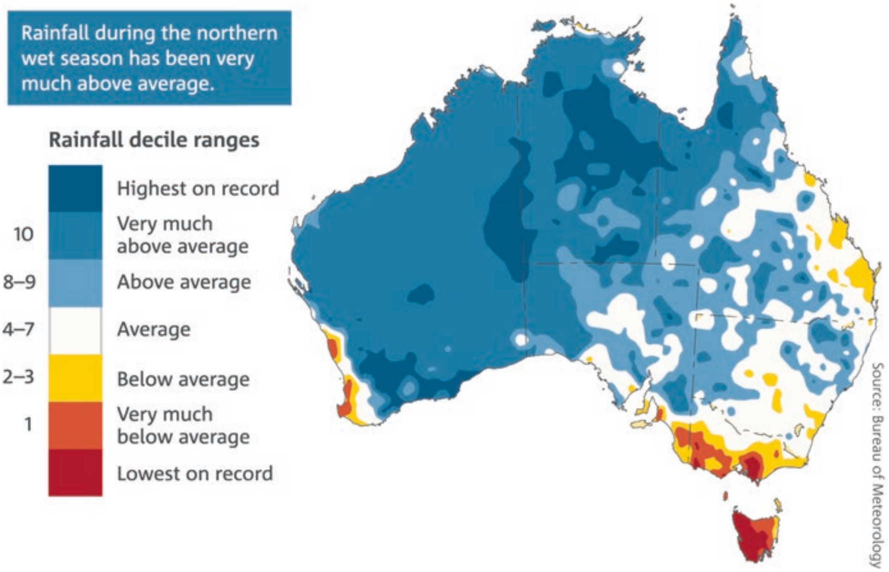


Fig. 6 Northern wet season (October to April) rainfall deciles for 1995–2016. (Source: Bureau of Meteorology State of the Climate 2016, http://www.bom.gov.au/state-of-the-climate)

ated with increasing rainfall during stronger IOD events, such as in 2010 (Lim et al. 2016). In addition to increased annual rainfall, the seasonality—the difference between rainfall amount in the driest and wettest periods—has also increased in northern WA (Feng et al. 2013).

Rainfall: Future Projections

On a global scale, climate modelling indicates a general expansion of the tropics, a southward shift of the subtropical ridge and a contraction of midlatitude low-pressure systems closer to the pole. For southern and south-western Australia, this means continuation of the drying trend during autumn and winter as greenhouse gas concentrations increase. Southern parts of inland Australia are likely to be similarly affected as winter weather systems become either weaker or less frequent. The overall increase in average pressure will likely drive a further shift to a more settled weather regime, with more high pressure systems persisting for longer (Bates et al. 2012). There is high confidence that annual, winter and spring rainfall will decline in regions dominated by winter-type weather systems. Climate models have been consistent in projecting such changes in mid- and high-latitude weather systems. Interannual rainfall variability will remain high over inland Australia, and this will tend to mask projected rainfall trends. Changes in projected rainfall for the Monsoonal North are small compared with current natural variability, and there is generally low confidence in projected rainfall changes. This most likely comes from

Table 2 Projected rainfall difference (percent) compared with 1986–2005 for inland Australia, for 20-year periods centred on 2030 and 2090

	RCP4.5 2030	RCP4.5 2090
Annual	+11 to +6	−15 to +7
Summer	−16 to +7	−16 to +10
Autumn	−23 to +20	−23 to +27
Winter	−20 to +14	−34 to +7
Spring	−21 to +19	−26 to +11

Given the high uncertainty in projections, only the range between the 10th and 90th percentiles and for one RCP (4.5) are shown. This has been adapted from the Rangelands Cluster Report at https://www.climatechangeinaustralia.gov.au/en/publications-library

the dominance of interannual climate events such as ENSO and IOD, and climate models currently are not consistent in simulating changes in their future variability (Table 2).

Warmer sea surface temperatures in the future may be expected to contribute to higher daily or seasonal rainfall via increased availability of water vapour. How much rain actually occurs will depend on interactions between water availability and seasonal weather events. It may mean that when a climate event favourable to rainfall occurs (such as a La Niña), higher sea surface temperatures may act to enhance rain from that event. There is some evidence of this interaction occurring during 2010 (Lim et al. 2016). Projections of future tropical cyclone frequency and strength reflect complex interactions between climate influences. While the frequency of occurrence of tropical cyclones could decrease by the end of the twenty-first century, the region of cyclone formation and decay could move about 100 km southward. On one hand, changes to the frequency of El Niño events may reduce cyclone occurrence in the Australian region; on the other hand, warmer ocean temperatures can allow cyclones to form and persist further south. Tropical cyclones could increase in size, and the most intense tropical cyclones could become more powerful. An increase in the intensity of rainfall associated with tropical cyclones is also expected.

Summary

Australia’s climate has changed over the last century, particularly over the last 50 years:

- Average temperature has increased by about 1 °C.
- Rainfall has increased slightly over the north and interior but declined along the west and south. Rainfall has declined by about 20% over the far south-west.
- Fire risk has increased in many areas, especially inland eastern Australia.

These changes are greater than what would be expected from purely natural climate variability and are consistent with global warming as a result of greenhouse gas emissions.

Climate projections suggest:

- Average temperatures will be 0.5–1.3 °C higher by 2030, regardless of emission scenario, and 1.1–2.7 °C and 2.6–5.1 °C higher at the end of the century under intermediate- and high-emission scenarios, respectively, compared with average conditions from 1986 to 2005.
- The intensity and duration of hot spells are expected to increase.
- Annual rainfall in the south-west will be 5–6% less by 2030 and 1–15% and 5–35% less by 2090 for intermediate- and high-emission scenarios, respectively, compared with average conditions from 1986 to 2005.
- Annual rainfall will remain relatively unchanged in northern and central regions.
- The frequency of rain events will decrease, but storm intensity will increase.
- Tropical cyclone frequency may decline, but tropical cyclones may increase in intensity and travel further south.
- Evaporative demand will increase.
- Fire risk according to temperature will increase but be co-determined by fuel loads.

References

Abram J, Mulvaney R, Vimeux F, Phipps S, Turner J, England M (2014) Evolution of the Southern Annular Mode during the past millennium. Nature Climate Change 4:564–569

Bates B, Frederiksen C, Wormworth J (eds) (2012) Western Australia's weather and climate: a synthesis of Indian Ocean Climate Initiative Stage 3 Research. Indian Ocean Climate Initiative, CSIRO and Bureau of Meteorology, Australia

Bureau of Meteorology (2007) Frontal systems. Commonwealth of Australia. http://www.bom.gov.au/climate/about/?bookmark=fronts

Bureau of Meteorology (2008a) The Monsoon. Commonwealth of Australia. http://www.bom.gov.au/climate/about/?bookmark=monsoon

Bureau of Meteorology (2008b) The sub-tropical ridge. Commonwealth of Australia. http://www.bom.gov.au/climate/about/?bookmark=stridge

Bureau of Meteorology (2008c) El Niño Southern Oscillation (ENSO). Commonwealth of Australia. http://www.bom.gov.au/climate/about/?bookmark=enso

Bureau of Meteorology (2008d) Southern Annular Mode Commonwealth of Australia. http://www.bom.gov.au/climate/about/?bookmark=sam

Bureau of Meteorology (2012) The Madden-Julian Oscillation. Commonwealth of Australia. http://www.bom.gov.au/climate/about/?bookmark=mjo

Bureau of Meteorology (2014) El Niño. Commonwealth of Australia. http://www.bom.gov.au/climate/about/?bookmark=elnino

Bureau of Meteorology (2016a) Indian Ocean. Commonwealth of Australia. http://www.bom.gov.au/climate/about/?bookmark=iod

Bureau of Meteorology (2016b) State of the Climate 2016. Commonwealth of Australia. http://www.bom.gov.au/state-of-the-climate

Cai W, Cowan T, Thatcher M (2012) Rainfall reductions over Southern Hemisphere semi-arid regions: the role of subtropical dry zone expansion. Scientific Reports 2(1)

Charles S, Fu G, Silberstein R, Mpelasoka F, McFarlane D, Hogson G et al (2013) Interim report on the hydroclimate of the Pilbara: past present and future. CSIRO, Australia

CSIRO and Bureau of Meteorology (2015) Climate change in Australia information for Australia's natural resource management regions: technical report. CSIRO and Bureau of Meteorology, Australia. https://www.climatechangeinaustralia.gov.au/en/publications-library/technical-report/

Feng X, Porporato A, Rodriguez-Iturbe I (2013) Changes in rainfall seasonality in the tropics. Nat Clim Chang 3:811–815

Lim E, Hendon H, Arblaster J, Chung C, Moise A, Hope P, Young G, Zhao M (2016) Interaction of the recent 50 year SST trend and La Niña 2010: amplification of the southern annular mode and Australian springtime rainfall. Clim Dyn 47:2273–2229

Moise A, Abbs D, Bhend J, Chiew F, Church J, Ekström M et al (2015) In: Ekström M et al (eds) Monsoonal North cluster report, Climate change in Australia projections for Australia's Natural Resource Management Regions: cluster reports. CSIRO and Bureau of Meteorology, Australia http://www.climatechangeinaustralia.gov.au/media/ccia/2.1.5/cms_page_media/

O'Donnell AJ, Cullen LE, Lachlan McCaw W, Boer MM, Grierson PF (2010) Dendroecological potential of Callitris preissii for dating historical fires in semi-arid shrublands of southern Western Australia. Dendrochronologia 28:37–48

O'Donnell AJ, Boer MM, McCaw WL, Grierson PF (2011) Climatic anomalies drive wildfire occurrence and extent in semi-arid shrublands and woodlands of Southwest Australia. Ecosphere 2:1–15

Steffen W, Hughes L, Perkins S (2014). Heatwaves: hotter, longer, more often. Climate Council of Australia Limited. http://www.climatecouncil.org.au/heatwaves-report

Watterson I et al (2015) Rangelands cluster report, climate change in Australia projections for Australia's natural resource management regions: cluster reports (ed. Ekström M et al). CSIRO and Bureau of Meteorology, Australia. https://www.climatechangeinaustralia.gov.au/en/publications-library/cluster-reports