

REVIEW

Out of the OCBILs: new hypotheses for the evolution, ecology and conservation of the eucalypts

STEPHEN D. HOPPER*,

Centre of Excellence in Natural Resource Management, School of Agriculture & Environment, The University of Western Australia, 35 Stirling Terrace, Albany, WA 6330, Australia

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OCBIL theory is a multi-hypothesis formulation aimed towards an understanding of the evolution, ecology and conservation of biological and cultural diversity on old, climatically buffered, infertile landscapes (OCBILs). OCBILs have been in existence contemporaneously with rainforest since Gondwanan times. Such landscapes are common in areas of eucalypt species richness embraced by Australia's two Global Biodiversity Hotspots, the Southwest Australian Floristic Region and the Forests of East Australia. Here, I summarize evidence pertaining to the eucalypts in the context of a recent reformulation of OCBIL theory into 12 evolutionary, ecological and cultural hypotheses and ten conservation management hypotheses. A compelling argument emerges for a new interpretation of the eucalypts evolving out of the OCBILs, rather than out of the rainforests as traditionally interpreted. This calls for a significant reinterpretation of best conservation management of the eucalypts. For example, traditional ideas on application of fire in eucalypt communities regarded as well adapted to this disturbance need to give way to a more nuanced and cautious view. This review of eucalypts seen as evolving out of the OCBILs helps in understanding the group from several new perspectives. Interpretation of other sedentary plant and animal groups as out of the OCBILs is commended for further study.

ADDITIONAL KEYWORDS: *Angophora* – *Arillastrum* – conservation management – *Corymbia* – *Eucalyptus* – evolution – rainforest – YODFEL.

INTRODUCTION

Australia's iconic trees, the eucalypts, are a species-rich assemblage of some 850 named and 50 unnamed species (Brooker, 2000; Slee *et al.*, 2006; Nicolle, 2019) in three genera: ~800 in *Eucalyptus*, 95 in *Corymbia* and ten in *Angophora*. Some uncertainty remains with delineation of the genus *Corymbia* (Schuster *et al.*, 2018; Thornhill *et al.*, 2019).

Only 12 of the 900 species extend beyond Australia or are endemic to adjacent islands to the north (Gonzalez-Orozco *et al.*, 2014). Fossil eucalypts are documented further afield from Argentina, Antarctica and New Zealand (Gandolfo *et al.*, 2011; Hermesen *et al.*, 2012; MacPhail & Thornhill, 2016).

The eucalypts range in size from the world's tallest angiosperms (*Eucalyptus regnans* F. Muell. and

Eucalyptus diversicolor), soaring 90–100 m above the forest floor, to shrubby prostrate coastal mallees < 1 m high that resprout from underground lignotubers (e.g. *Eucalyptus diversifolia* Bonpl., *Eucalyptus tetraptera* Turcz. and *Eucalyptus sweedmaniana* s.s. Hopper & McQuoid). Their dominance in all but the most arid or upper montane environments means that eucalypts provide vital habitat for countless organisms, in addition to diverse cultural and economic values for the Australian people.

There is a significant literature now available on the biology of eucalypts, with several modern books documenting this burgeoning knowledge from diverse perspectives (for references, see Wrigley & Fagg, 2010; Keith, 2017; Thornhill *et al.*, 2019). The exponential increase in data on eucalypts has not been matched, in some quarters, by a similar effort in developing theoretical perspectives updated with modern sources of evidence. For example, given the fundamental

*E-mail: steve.hopper@uwa.edu.au

differences in landscape history between most of the Northern Hemisphere and much of the Southern Hemisphere, it is possible that processes of evolution, ecology and conservation management might differ sufficiently to warrant new theoretical approaches to understand eucalypt biology or at least require a broadening of mainstream theory to account for poorly investigated patterns and processes now emergent in Southern Hemisphere studies (Lusk & Bellingham, 2004; Hopper, 2009; Hopper *et al.*, 2016).

Mainstream narratives concerning the evolution and ecology of eucalypts assume that the emergence of the group to dominance is intimately linked to fire dependence, facilitated by evolutionary adaptations such as the emergence of lignotubers and epicormic buds for resprouting. Increased prevalence of fire is inferred with the onset and intensification of aridity in the mid- to late Tertiary in Australia, coincident with substantial diversification of eucalypts. Moreover, fires are hypothesized to have become significant in the late Cretaceous–early Tertiary, when ancestral eucalypts evolved (Griffiths, 2001; Orians & Milewski, 2007; Crisp *et al.*, 2011; Burrows, 2013; MacPhail & Thornhill, 2016). Given that sister genera to the eucalypt group are tropical (Bayly, 2016; Schuster *et al.*, 2018; Thornhill *et al.*, 2019), as was the oldest (Eocene) macrofossil habitat of eucalypts in Argentina (Gandolfo *et al.*, 2011; Hermsen *et al.*, 2012), it has been inferred that the ancestors of the eucalypts arose in or adjacent to rainforests, in landscapes where volcanic eruptions regularly enriched the soil and provided ready sources of ignition for bushfires alongside monsoonal lightning strikes (Gandolfo *et al.*, 2011; Hill *et al.*, 2016).

Such a narrative has profound implications for conservation management of eucalypts and the use of prescribed burning in eucalypt communities (Gosper *et al.*, 2016; Bradshaw *et al.*, 2018; Barker & Price, 2018; Santín *et al.*, 2018), especially given the prevalence of speculation that eucalypts have traits specifically adapted to fire (Gill, 1981; Burrows *et al.*, 2010; Crisp *et al.*, 2011; Keeley *et al.*, 2011; Burrows, 2013). Given that this speculation was rigorously critiqued from a modern evolutionary perspective (Hopper, 2003; Bradshaw *et al.*, 2011), some authors have been more cautious in routinely invoking adaptation to fire in plants such as eucalypts (Clarke *et al.*, 2013; Midgley, 2013; Bowman *et al.*, 2014; Miller & Dixon, 2014; Hill *et al.*, 2016; Hopper *et al.*, 2016; Poulos *et al.*, 2018). Others have not (Keeley *et al.*, 2012; Groom & Lamont, 2015; He & Lamont, 2017; Rundel *et al.*, 2016, 2018).

Cautious reviews by Florence (1996) and Gill (1997) argued cogently for the need to appreciate the diversity of apparent interdependence and independence of eucalypts in their relationships to complex fire regimes. A plea was made by Gill (1997), still valid, for much more work on eucalypt demography under varying disturbance

regimes, including those caused by fire. Florence (1981, 1996) noted that traits of eucalypts enabling fire tolerance might be ‘byproducts’ (i.e. exaptations in the sense of Gould & Vrba, 1982) to ‘...declining soil fertility and a drying climate’. The eucalypt’s outstanding capacity to respond to a number of environmental stresses could reflect ‘...prior adaptation of its progenitor to more specialized and disturbed niches within the Gondwanan rainforests’ (Florence 1996: p. 52).

Building on Florence’s insights and a wealth of new data now available, the aim here is to construct new hypotheses for the evolutionary ecology, conservation and cultural uses of eucalypts within a new theoretical framework and to review the veracity of these hypotheses against available empirical evidence. Specifically, this paper examines the evolution, ecology and conservation biology of eucalypts viewed from the perspective of the special attributes of old, climatically buffered, infertile landscapes (OCBILs; Fig. 1). These landscapes are prominent in the two regions where eucalypts are most diverse and rich in endemic species, namely the Southwest Australian Floristic Region (SWAFLR *sensu* Hopper & Gioia, 2004; Gonzalez-Orozco *et al.*, 2014; Gioia & Hopper, 2017) and the Forests of East Australia (Williams *et al.*, 2011; Fig. 2). Both regions are now included among the world’s 36 Global Biodiversity Hotspots (Mittermeier *et al.*, 2011; Noss *et al.*, 2015), which are places on Earth richest in endemic plants and animals under significant threat of extinction. A focus on the two regions, therefore, will serve to highlight some of the exciting modern advances in eucalypt biology and conservation in a new light.

A key conclusion of this review is that the ancestors of eucalypts evolved not in young, often disturbed, fertile volcanic landscapes. Instead, they emerged out of the late Cretaceous–early Tertiary OCBILs in the Southern Hemisphere (Carpenter *et al.*, 2015), preadapted (exapted) with a unique set of life-history attributes, including gigantism, epicormic buds and the mallee lignotuberous habit, that enabled prolonged persistence. Ancestral life histories, selected for in ancient OCBILs, enable eucalypts to cope with canopy-consuming disturbances, such as fire, herbivory, disease, infertile soils, flooding, freezing and drought. This inherited resilience has complex origins during eucalypt diversification with reduced extinction rates across southern lands from the late Cretaceous onwards. Aboriginal and colonial cultures have recognized implicitly the significance of such landscape origins of the eucalypts. Much more experimental research, combined with modern investigative techniques, is needed to strip away correlations from underlying causation and enable significant advances in understanding the evolutionary ecology, conservation and cultural uses of eucalypts.

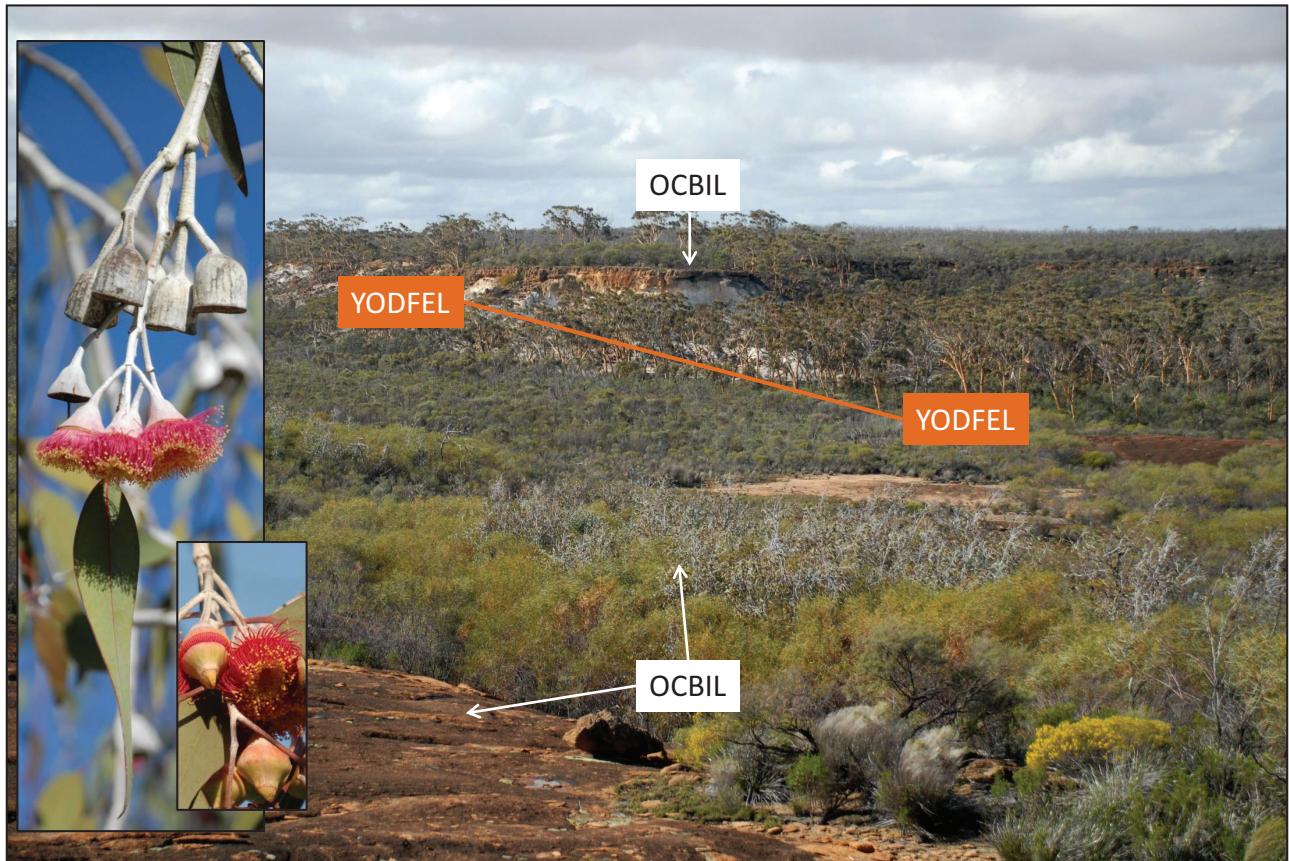


Figure 1. Old, climatically buffered infertile landscapes (OCBILs) feature prominently in the Southwest Australian Floristic Region, immersed as insular uplands and rock outcrops amidst younger, often disturbed, more fertile lowlands (YODFELs). Here at Chiddarcooping Nature Reserve, a classic OCBIL endemic, *Eucalyptus caesia* Benth. subsp. *magna* Brooker & Hopper (flowers, buds and fruits in the inset), wisps above *Acacia lasiocalyx* CRP Andrews adjacent to a granite outcrop OCBIL, while behind a more widespread species of YODFELs, *Eucalyptus capillosa* Brooker & Hopper, stands emergent with orange bark along an alluvial YODFEL creekline and the eroding edge of a flat-topped OCBIL mesa. Photographs by S. D. Hopper.

A NEW THEORETICAL APPROACH

Explaining variation of biodiversity and endemism across the Earth, and for eucalypts, is demonstrably more complex than single-factor causation. Although reasonable predictors, latitudinal gradients are not uniformly richer in species from the poles to the Equator. Mediterranean climate vegetation at intermediate latitudes has floras as species rich as many tropical rainforests (Cowling *et al.*, 1996; Rundel *et al.*, 2016), and eucalypts are richer in species in southern Australia than in the tropical north (Gonzalez-Orozco *et al.*, 2014). Moreover, in taxonomic groups where they apply, energy hypotheses alone cannot always explain the latitudinal gradient in species richness. Energy and water availability combined are better, but not comprehensive, predictors of global species richness patterns (Hawkins *et al.*, 2003). Likewise, not all places richest in species and endemics are mountainous. For

example, the SWAFR has exceptional richness and endemism on predominantly subdued topography (Hopper & Gioia, 2004; Gioia & Hopper, 2017). Furthermore, the reasons why mountains are species rich remain elusive and complex and are not explicable from single-factor perspectives (Bertuzzo *et al.*, 2016). This is also evident in studies of Australian rainforest boundaries, where attempts to explain the patchiness of rainforests in a sea of sclerophyll eucalypt vegetation as attributable to topography or soil fertility or climate or fire regimes (Bowman, 2000) are much less compelling than invoking multiple causal factors that vary in space and time. The challenge, therefore, to a general theory of biodiversity and species richness, is to apply Occam's razor and come up with the smallest number of factors that, combined, account for the global patterns (Hopper *et al.*, 2020). So, too, is the specific challenge for understanding eucalypt diversity, endemism, evolutionary ecology and ethnobotany.

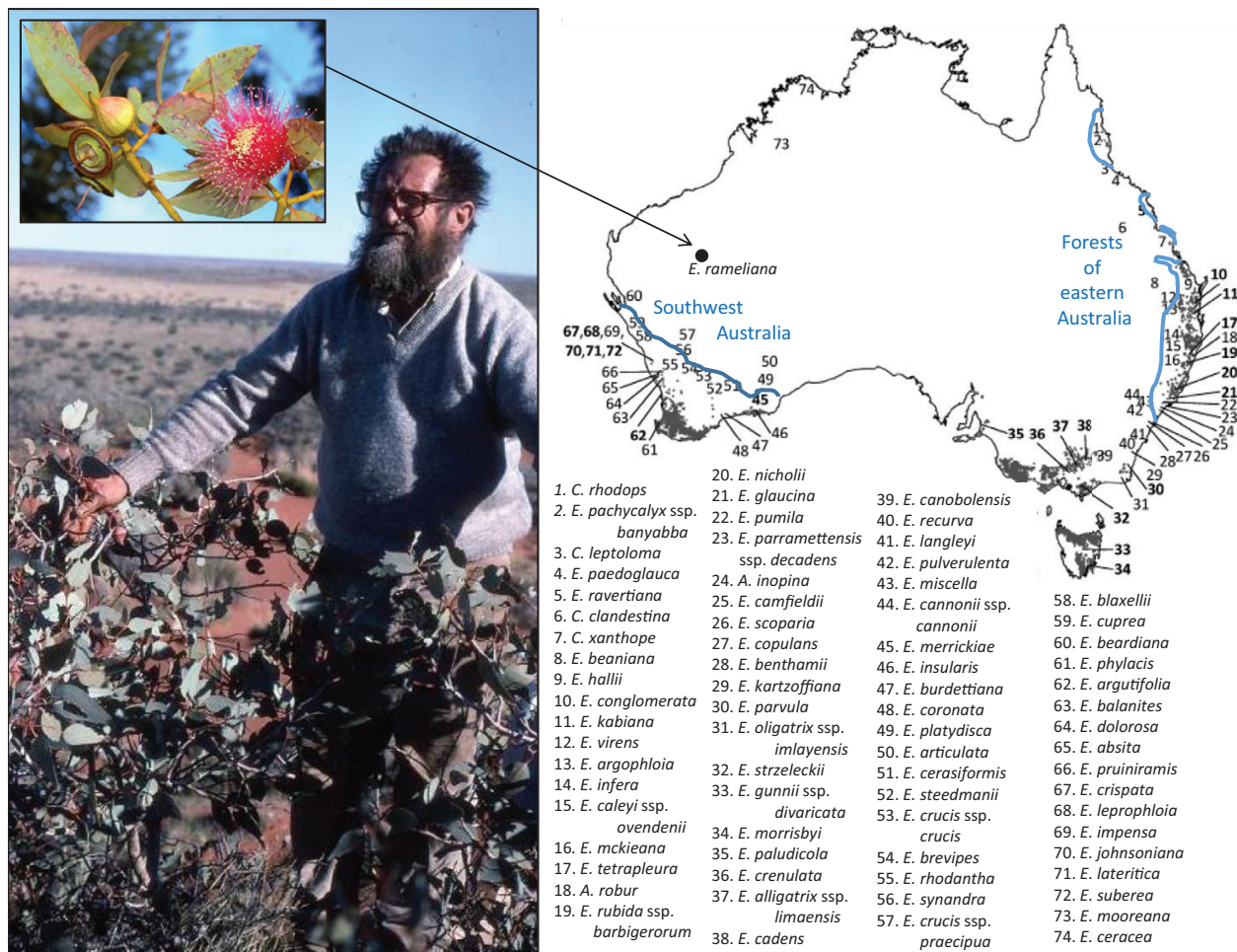


Figure 2. Australia's two global biodiversity hotspots (blue boundaries) and geographical distribution of 74 nationally listed rare and threatened eucalypts (for authorities see [Wrigley & Fagg, 2010](#)), many confined to old, climatically buffered infertile landscapes (OCBILs) in the temperate, semi-arid and subtropical south of the nation. Areas in black are 950 000 ha of eucalypt plantations, mainly of *Eucalyptus globulus* Labill. (64% of area) and *Eucalyptus nitens* (H. Dean & Maiden) Maiden (20%). Conservation geneticists exploring risks to the threatened species from hybridization with plantation species established surprising resistance to this threat, mainly owing to the limited seed and pollen dispersal of most eucalypts and to genetic incompatibility mechanisms. Photographs, taken in 1991, are of desert dweller Nick Foote at his rediscovery site (dot, arrowed) of Australia's only presumed extinct eucalypt (*Yalpiri*, Giles' mallee, *Eucalyptus rameliana*; [Sampson et al., 1995](#)), in Western Australia's Little Sandy Desert, with a flower and bud in the inset. Map from [Barbour et al. \(2010\)](#). Photographs by S. D. Hopper.

OCBILs have emerged as landscapes of special interest and new discoveries regarding biodiversity pattern and process in ≥ 15 of the 35 Global Biodiversity Hotspots, mainly in the Southern Hemisphere ([Hopper et al., 2016, 2020](#)). The three defining attributes of OCBILs, first identified in biogeographical studies of rare and endangered plants in the SWAFR ([Hopper et al., 1990](#)), are as follows: (1) ancient landforms, in place for tens of millions of years; (2) moderate disturbance regimes attributable to factors such as climatic buffering through prolonged proximity to oceans; and (3) deeply weathered, relatively infertile, P-limited soils ([Hopper, 2009](#); [Lambers et al., 2010](#); [Cowling et al., 2015](#); [Bui et al., 2017](#)). Most

of the Northern Hemisphere was extensively covered by glaciers over the past 2 Myr, rejuvenating landscapes that were former OCBILs by reworking landforms, grinding up rocks to create new fertile mineral soils and imposing severe climatic extremes that caused massive local extinction of plants and animals ([Hopper, 2009](#)). In contrast, except for Antarctica and significantly elevated mountains on other continents and islands, the Southern Hemisphere largely escaped glaciation, enabling the persistence of OCBILs and their greatly diversified plants and animals.

Predictions have been developed regarding the patterns and processes of evolution, ecology, conservation

and ethnobotany in OCBILs differing qualitatively or quantitatively from those well documented for organisms of young, often-disturbed, fertile landscapes (YODFELs) of glaciated regions of the world (Hopper, 2009, 2018; Hopper *et al.*, 2016; Lullfitz *et al.*, 2017, 2020). The value of this approach to gain a better understanding of a single large genus has yet to be explored in detail. Here, I follow a recent update of OCBIL theory (Hopper *et al.*, 2020), in which 12 evolutionary, ecological and cultural hypotheses and ten conservation management hypotheses (Fig. 3) are used as a framework to reconsider the evolution, ecology and conservation of eucalypts.

OCBIL PREDICTIONS: EVOLUTIONARY, ECOLOGICAL AND CULTURAL HYPOTHESES

REDUCED DISPERSABILITY

This is a fundamental hypothesis of OCBIL theory. Vagile animals and plants can occur on OCBILs, but they are not subject to the same series of predictions as given herein. Sedentary OCBIL species should exhibit reduced dispersibility, linked with long-term climatic buffering and persistence, edaphic endemism and costs associated with dispersal (Hopper, 2009; Bonte

et al., 2012). This hypothesis proposes that selection should favour the evolution of seeds adapted for short-distance dispersal because optimal conditions for establishment occur near the parental plants. Thus, failure in establishment should increase with increasing distance from the parental plants, resulting in a competitive advantage to seedlings growing close to their relatives (Hopper, 2009; Hopper *et al.*, 2020).

Studies of the seed dispersal process of eucalypts are too few to determine statistically whether species of OCBILs have more restricted seed dispersal than those of YODFELs (House, 1997; Potts & Wiltshire, 1997; Booth *et al.*, 2015; Booth, 2017). Such studies have been carried out mainly for commercially important species that occupy younger landforms, not OCBILs. A general estimate for eucalypt dispersal is 1–2 m/year (Booth 2017), but this is based on very few studies, including how far into bushland of Perth's Kings Park the South Australian sugar gum (*Eucalyptus cladocalyx* F. Muell.) had migrated over 70 years (Ruthrof *et al.*, 2003). Also on Angel Island in San Francisco Bay, *Eucalyptus globulus* Labill. seedlings were found ≤ 133 m downwind from the original 1915 plantings after 73 years (Booth, 2017). For tall *E. regnans*, attaining canopy heights of 55–76 m, the standard deviation of seed dispersal

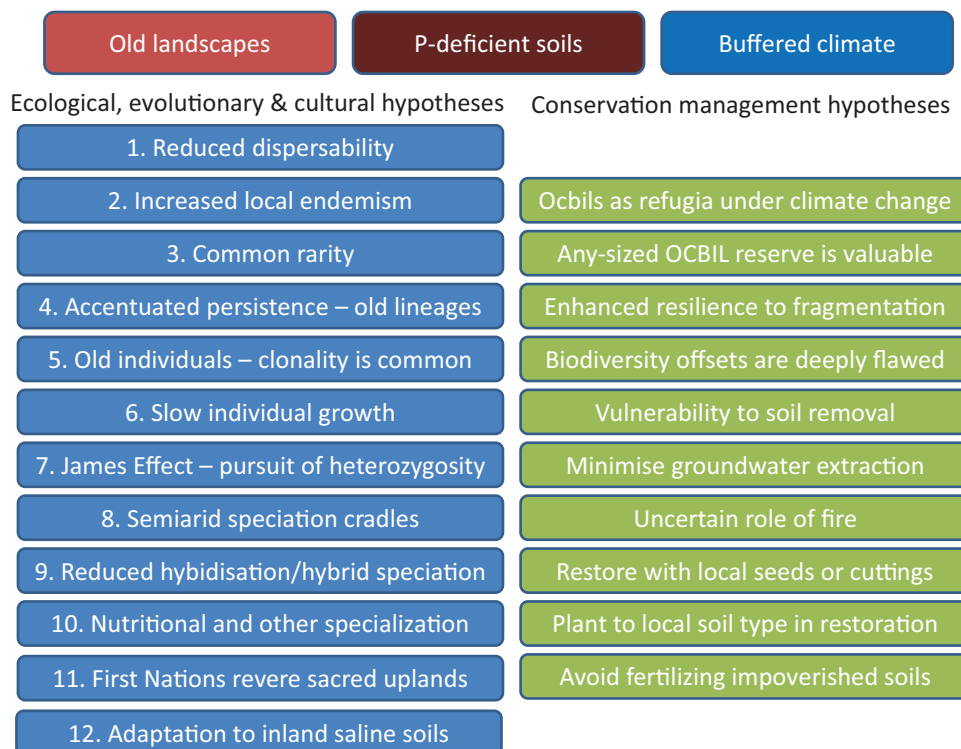


Figure 3. The three key concepts of old, climatically buffered infertile landscape (OCBIL) theory (old landscapes, P-deficient soils and oceanically buffered climate), with 12 predictive hypotheses for general biology and anthropology of OCBILs (blue bars) and 12 predictive conservation management hypotheses for OCBIL biodiversity (green bars). From Hopper *et al.* (2020).

ranged from 30 to 48 m (Potts & Wiltshire, 1997). In contrast, an isolated tree of the 2- to 10-m-high *Eucalyptus risdonii* Hook.f. inhabiting dry infertile Permian mudstone near Hobart dispersed seed mainly downwind over distances of 0.5–10.7 m (mean of 4.7 m; Potts & Wiltshire, 1997).

In the unusual case of seed dispersal by resin-collecting stingless bees for *cadaghi* (*Corymbia torelliana* (F.Muell.) K.D.Hill & L.A.S.Johnson), distances of ≤ 300 m have been recorded (Wallace & Trueman, 1995; Wallace *et al.*, 2008; Leonhardt *et al.*, 2014). Dispersal of seed via water can achieve much greater distances, although even this has failed to prevent significant genetic differences within river systems in the most widespread eucalypt in Australia, the river red gum (*Eucalyptus camaldulensis* Dehnh.; Butcher *et al.*, 2009). Thus, eucalypts appear to be characterized predominantly by exceptionally limited seed dispersal, a key feature of OCBIL organisms.

Pollen dispersal, too, appears to be limited in eucalypts (Sampson & Byrne, 2008; Ottewell *et al.*, 2009). 'Dispersal studies suggest that eucalypt pollen regularly travels at least 1 km, though most is distributed within 200 m and seed crops are dominated by genetic material from nearby trees' (Booth *et al.*, 2015: p. 20).

In the case of eucalypts on OCBILs, there are very few seed dispersal data published. However, recent work on post-fire recruitment of *Eucalyptus caesia* Benth. subsp. *magna* Brooker & Hopper (Fig. 1) over three decades on a granite rock OCBIL at Chiddarcooping, inland from Perth, has shown that successful recruitment of new plants after wildfire has occurred downstream on ephemeral drainage lines ≤ 20 m from existing mature plants (Yates *et al.*, 2003; Bezemer *et al.*, 2019c; S. D. Hopper, unpublished data). At Boyagin Rock after wildfire, seed dispersal and subsequent germination might have been even more limited for *E. caesia* subsp. *caesia*. Seedlings were all located beneath the canopy of burnt adults, except for two that were found downslope only 2 m from the canopy edge of burnt adults (Bezemer, 2018). However, using microsatellite DNA markers to determine the probable maternal plants of seedlings, Bezemer (2018) found that the maximum distance from a presumed mother for one of 118 seedlings was 362 m, and a maximum dispersal distance under the most stringent criterion (95% confidence limits) for determining likely mother trees was 23 m. Seed dispersal over such distances could have been attributable to fruit transport by parrots (Fig. 4), by water downslope along drainage lines or by convectional updrafts during fire, lifting fruiting branches and blowing them away from the mother tree (Bezemer, 2018).

Very rare long-distance dispersal must have occurred in the evolution of this species because it has 25 populations distributed across island-like granite outcrops ≤ 275 km apart. Moreover, its rooting strategy

places *E. caesia* at a strong competitive disadvantage in deep soils interspersed among outcrops (Poot *et al.*, 2012; Hamer *et al.*, 2016). DNA studies suggest that populations of *E. caesia* among even closely adjacent rocks 7 km apart have been genetically independent for hundreds of thousands of years, indicating how rare such long-distance dispersal events might be (Byrne & Hopper 2008; Bezemer *et al.*, 2019c).

There are two other indirect ways to test for evidence of restricted seed dispersal in eucalypts of OCBILs: investigating the geographical concentrations of local endemic species with narrow geographical ranges, and examining the population genetics of such local endemic species to see whether they have strongly divergent systems among populations, as documented for *E. caesia* (Byrne & Hopper, 2008; Bezemer *et al.*, 2019c).

INCREASED LOCAL ENDEMISM

Local endemic eucalypts are most commonly found in both of Australia's Global Biodiversity Hotspots (Figs 1, 2), especially the SWAFR (Gonzalez-Orozco *et al.*, 2014). In the Forests of East Australia Hotspot, The Blue Mountains World Heritage Area has ≥ 96 eucalypts, 54 widespread and 42 of more restricted geographical distribution (NSW National Parks and Wildlife Service, 2003a; Hager & Benson, 2010). Of the 14 areas of local eucalypt endemism identified recently (Gonzalez-Orozco *et al.*, 2014), most are centred on OCBILs.

Among the ~ 900 eucalypts, 8% (74) were classified as endangered or vulnerable in 2009 (Barbour *et al.*, 2010). The vast majority of these are range-restricted local endemics (Fig. 2). Several more local endemics have been described subsequently (e.g. Bell & Nicolle, 2012; Gioia & Hopper, 2017); therefore, it is reasonable to estimate that $\sim 10\%$ of eucalypts are local endemics and rare.

The assumption that narrow-range endemics are threatened has come into question increasingly (Fensham *et al.*, 2020). Being long lived, eucalypts often persist in very small populations for decades without obvious decline. Hence, narrow-range endemics that show such persistence without obvious threats are now being proposed for delisting as threatened taxa. Fensham *et al.* (2020) listed 59, not 74 (Barbour *et al.*, 2010), narrow-range species as of conservation concern, most threatened by mining, urbanization or very low population numbers.

Population genetic studies of narrow-range OCBIL eucalypts reinforce these findings. Moran & Hopper (1983) discovered low genetic variation within granite rock populations of *E. caesia* but high divergence between populations, a pattern reinforced by subsequent DNA studies (Bezemer *et al.*, 2019c).



Figure 4. Black cockatoos consuming and carrying Southwest Australian Floristic Region eucalypt fruits. A, B, red-tailed black cockatoo eating seeds of *Eucalyptus caesia*. C, white-tailed black cockatoo on *yorgum* (red flowering gum, *Corymbia ficifolia* (F.Muell.) K D.Hill & L.A.S.Johnson). D, red-tailed black cockatoo with fruit of *jarrah* (*Eucalyptus marginata* D.Don ex Sm.) arrowed. E, red-tailed black cockatoos eating seeds of *E. caesia*. F, seed of *E. marginata*. G, seed of *marri* (*Corymbia calophylla* (Lindl.) K.D.Hill & L.A.S.Johnson) with 1 cm scale bar. H, seed of *yorgum* (*C. ficifolia*). I, white-tailed black cockatoo in full flight carrying a fruit of *marri* (*C. calophylla*). J, red-tailed black cockatoo eating seeds of *Eucalyptus erythrocorys*. K, red-tailed black cockatoo eating seeds of *yorgum* (*C. ficifolia*). L, red-tailed black cockatoo eating seeds of *E. caesia*. Photographs by Keith Lightbody (C, D, I–K), Margaret Owens (B, L), Luke Sweedman (F–H) and S. D. Hopper (A, E).

Comparisons of *E. caesia* with widespread and regionally restricted eucalypts of YODFELs (Moran & Hopper, 1987) highlighted significant differences. Widespread eucalypts show high diversity within populations and relatively little geographical divergence. Nevertheless, a review of genetic diversity in the Australian flora (Broadhurst *et al.*, 2017), in which eucalypts constituted 25% of the 235 case studies examined, revealed that Australian trees exhibit double the genetic differentiation compared with Northern Hemisphere and tropical trees (Broadhurst *et al.*, 2017). A notable impact of range disjunction was evident in the Australian data, understandable in the context of the disjunct distribution of OCBILs, with

their high narrow-range endemism, on the continent. This insight was not made by Broadhurst *et al.* (2017).

Although the authors were unaware of OCBILs, an investigation in *Gariwerd* (Grampians) National Park was a world first for relating genetic variation in a small area to OCBILs (rocky, high-elevation ridgelines) and YODFELs (flanking slopes and valleys) (Pollock *et al.*, 2013). Three local endemics on ridgelines (Grampians gum, *Eucalyptus serraensis* Ladiges & Whiffin, Mt Abrupt stringybark, *Eucalyptus verrucata* Ladiges & Whiffin, and Victoria Range gum, *Eucalyptus victoriana* Ladiges & Whiffin) and one widespread relative (brown stringybark, *Eucalyptus baxteri* (Benth.) Maiden & Blakely ex J.M.Black) on slopes and valleys were

sampled for DNA. The predictions of OCBIL theory were met in this study. Populations of the local endemics displayed low genetic variation within stands but major divergence between sites, exactly like the pattern found in *E. caesia* (Fig. 5). In contrast, the widespread *E. baxteri* populations on YODFELs displayed high genetic diversity within stands but relatively low variation across the sampled slopes, except where they extended onto OCBIL ridgelines, where their genetic diversity pattern matched that of the three *Gariwerd* endemic eucalypts. More topographically precise studies

like this, comparing genetic and taxonomic diversity between OCBILs and YODFELs in close proximity, such as in mountain ranges, are needed across Australia and elsewhere. This will, no doubt, help to make sense of the enormous complexity of variation evident in the world's Global Biodiversity Hotspots that are rich in OCBILs.

Importantly, genetic studies of other OCBIL eucalypts are slowly being published, affirming what is now the common pattern of a combination within species of clonal growth (as old mallees), with low genetic variation within stands, and high variation

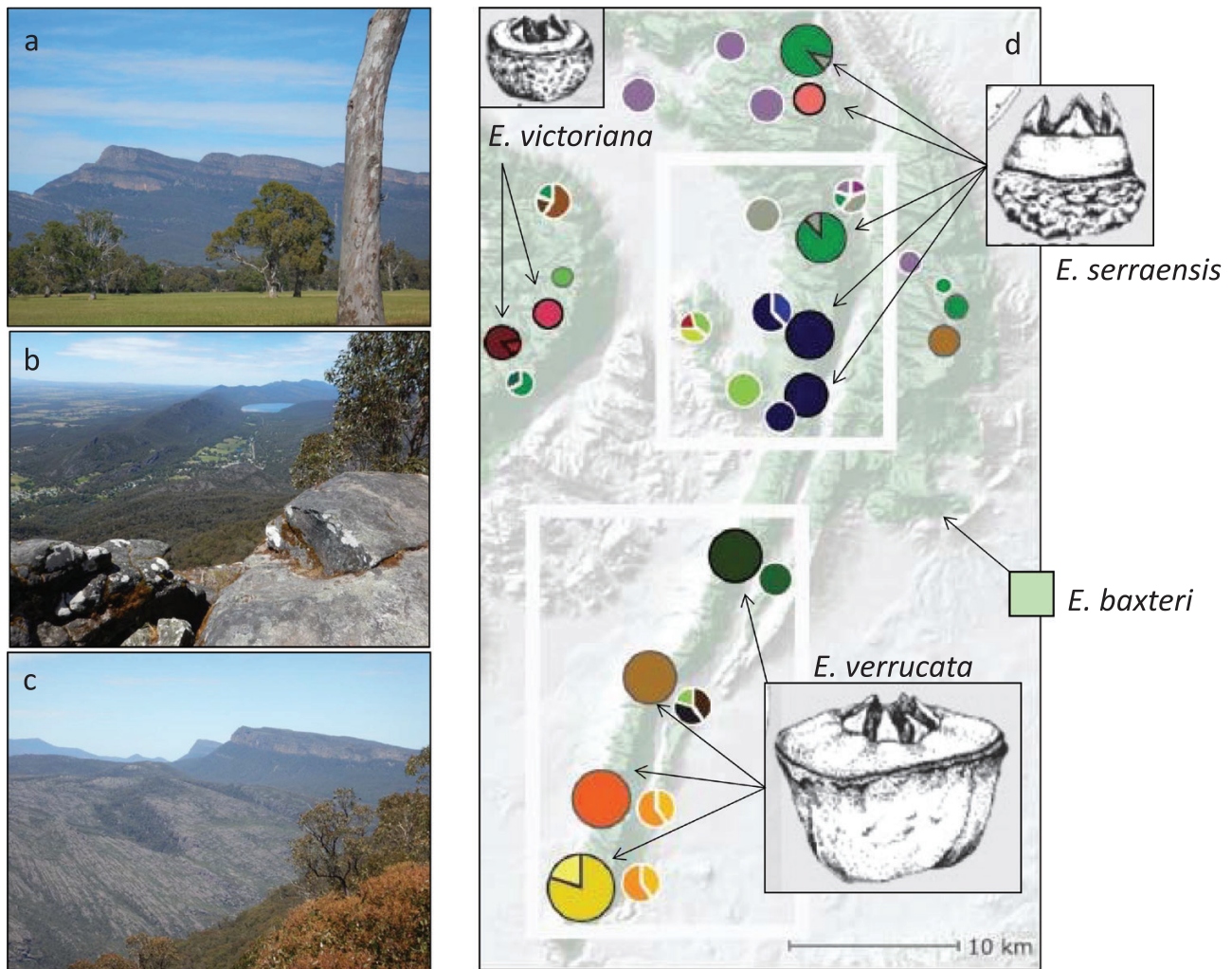


Figure 5. Genetic variation in four related eucalypts, three endemics on the old, climatically buffered infertile landscapes (OCBILs; rocky, high-elevation ridgelines, A–C) and the fourth *Eucalyptus obliqua* with *Eucalyptus baxteri* (Benth.) Maiden & Blakely ex J. M. Black widespread but mainly on young, often-disturbed, fertile landscapes (YODFELs; flanking slopes and valleys) of *Gariwerd* (Grampians) National Park in western Victoria. Background map is from a digital elevation model. Circle size indicates relative numbers of plants sampled; colours are chloroplast DNA haplotypes; white outlines encircle *E. baxteri* populations, black the three endemics. OCBIL endemics exhibit low genetic variation within populations but high divergences between different populations (arrowed). *Eucalyptus baxteri* has more variable populations (multicoloured pies) but shows less divergence across the *Gariwerd* ranges, except where hybridizing with local endemics (e.g. at South Serra range, bottom of map). Modified from Pollock *et al.* (2013). Photographs by S. D. Hopper.

between locations (Sampson *et al.*, 1989; McGowen *et al.*, 2001; Smith *et al.*, 2003; Sampson & Byrne 2008, 2016; Bezemer *et al.*, 2016, 2019c; Bradbury *et al.*, 2016). We are now entering a phase where genomic studies at the population level have enabled careful elucidation of species complexes in eucalypts (e.g. Rutherford *et al.*, 2015; Gosper *et al.*, 2019; Robins *et al.*, 2020). Sample sizes for genetic studies of narrow-range eucalypts of OCBILs and YODFEL are approaching a point where reasonable confidence can be placed in tests of pertinent predictions of OCBIL theory.

COMMON RARITY

Although this phenomenon has yet to be the subject of detailed study, the evidence above for narrow-range endemism suggests that rarity of taxa is commonly observed in species-rich communities. Mallee (*muert*) communities in the SWAFLR exemplify this pattern (Yates *et al.*, 2017). More than 60 species were found in cells measuring $0.75^\circ \times 0.75^\circ$ of latitude \times longitude, and many species in such hotspots are rarely seen.

Most species of eucalypts are found in southern Australia, where the greatest concentration of geographically restricted local endemic species occur (Gonzalez-Orozco *et al.*, 2014; Fig. 2). Six of the ten richest places are found in southern coastal Western Australia, where 86–116 eucalypts per 10 000 km² grid are found. The other four places richest in eucalypts (86–92 per 10 000 km² grid) occur in the Sydney region

and in the north coastal New South Wales–Queensland border region.

ACCENTUATED PERSISTENCE: OLD LINEAGES (GONDWANAN HERITAGE HYPOTHESIS)

Niche conservatism is well established for plants as a common evolutionary strategy (Crisp & Cook, 2012; Jordan *et al.*, 2016). The habitats of rare taxa from ancient lineages are therefore likely to retain the ancestral ecological characteristics they possessed at original speciation.

Using DNA sequence data, combined with much improved understanding of the diversity and morphology of eucalypts and their fossils, modern studies have clarified the evolutionary tree of *Eucalyptus* and the broader alliance of genera to which it belongs (the tribe *Eucalypteae*; Fig. 6; Thornhill *et al.*, 2019). Available evidence suggests an origin of the eucalypt group in the early Tertiary, some 59 Mya, supporting the accentuated persistence hypothesis. There are seven genera recognized, four of which are tropical trees (the mesicalypts) and comprise in total only five species, and the remaining three of which are typical eucalypts, with tough sclerophyll leaves, comprising ≥ 850 species or subspecies.

Eucalyptus fossil fruits and leaves from the Caldera Lake Flora of Patagonia, Argentina have been dated as Early Eocene (52 Mya; Hermsen *et al.*, 2012). Australian fossil eucalypt pollen is known from the Palaeocene–Early Eocene (60–50 Mya), and later

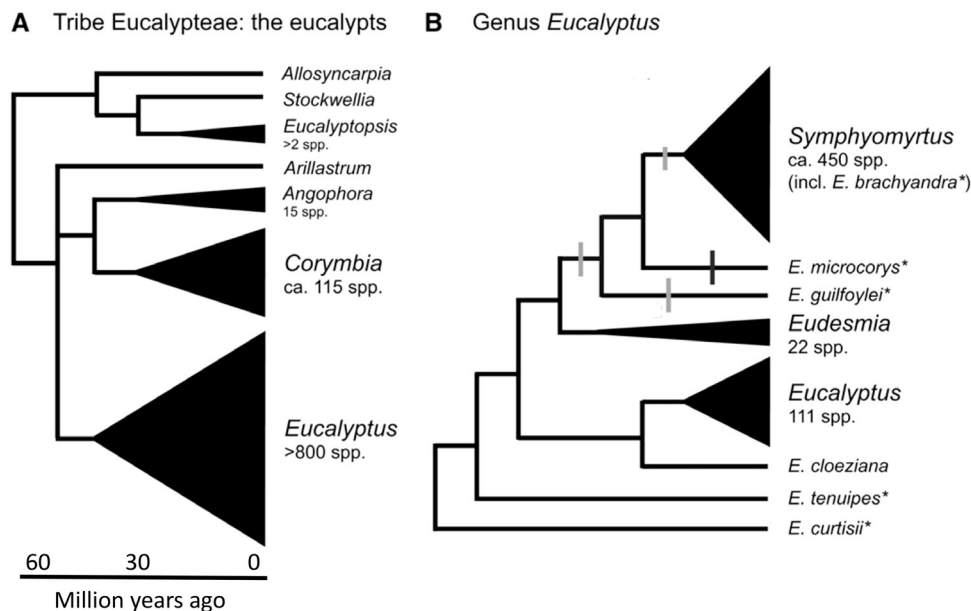


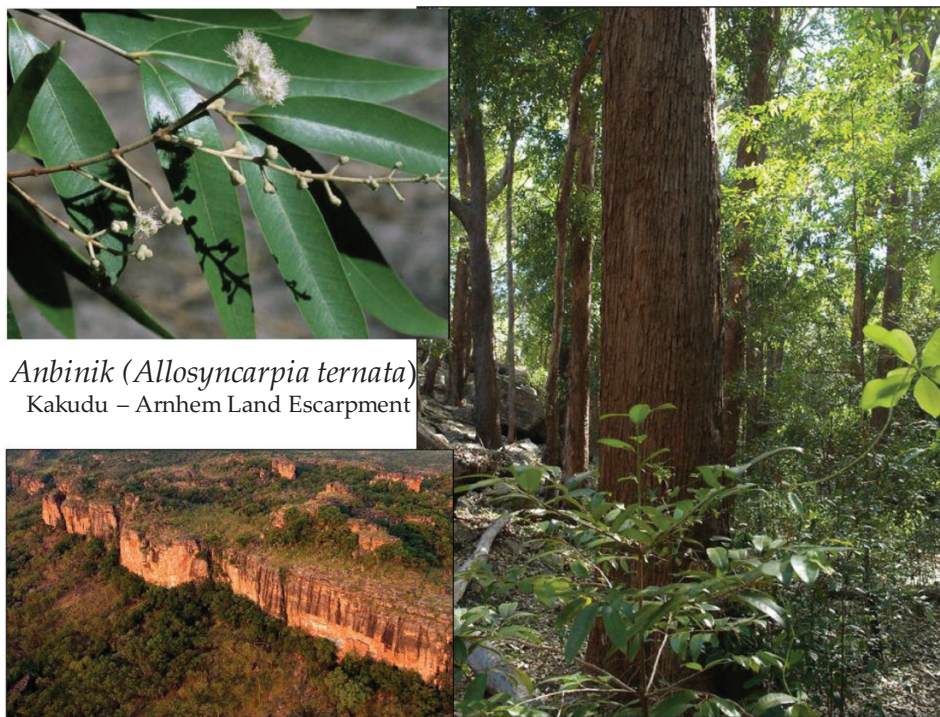
Figure 6. Hypothesized evolutionary (phylogenetic) relationships of the broader group of genera to which *Eucalyptus* belongs (A, tribe *Eucalypteae*, with a very approximate time scale below) and of subgenera within *Eucalyptus* on recent DNA studies (B). Modified from Hermsen *et al.* (2012), for which see detailed references.

fossils of nuts and leaves have been found, including leaves from New Zealand. The typical eucalypts (today's *Eucalyptus* L'Hér., *Corymbia* K.D.Hill & L.A.S.Johnson and *Angophora* Cav.), were thus more widespread early in their evolution than now. They radiated extensively as the climate of Australia became warmer and drier from ~30 Mya, associated with a northward drift and separation from Antarctica as Gondwana rifted apart.

The small relictual mesicalypt rainforest genera include three from tropical OCBIL regions. *Arillastrum gummiferum* (Brongn. & Gris) Pancher ex Baill. is endemic to New Caledonia and is a classic Gondwanan relict, diverging from true eucalypts at ~59 Mya. *Anbinik* (*Allosyncarpia ternata* S.T.Blake; Fig. 7) is from sandstone OCBILs of Arnhem Land in the Northern Territory. *Stockwellia quadrifida* D.J.Carr, S.G.M.Carr & B.Hyland is from the Atherton Tableland in north-east Queensland. *Eucalyptopsis*, with two species, occurs on younger landscapes of New Guinea and the eastern Indonesian archipelago. These

three genera are sister to the large group comprising *Arillastrum* Pancher ex Baill., *Eucalyptus*, *Corymbia* and *Angophora*. *Allosyncarpia* S.T.Blake diverged some 46 Mya from the lineage that would give rise to *Stockwellia* D.J.Carr, S.G.M.Carr & B.Hyland and *Eucalyptopsis* C.T.White. The mesocalypts thus emerged as the monsoonal systems of northern Australia established and the Australian continent drifted northwards, isolating the contracting rainforests in refugial regions, such as the Wet Tropics of north Queensland, Arnhem Land and New Guinea. *Arillastrum* arose as New Caledonia became independent of the Australian continental plate.

All three genera of typical eucalypts have OCBIL species with ancestors that evolved early. There are three subgenera branching early in the evolutionary tree of *Eucalyptus* itself (Fig. 6), each with a single relictual species. Plunkett mallee (*Eucalyptus curtisii* Blakely & C.T.White), the sole species of *Eucalyptus* subgenus *Acerosae* Brooker, is found as a mallee or rarely a tree in south-east Queensland



Anbinik (*Allosyncarpia ternata*)
Kakadu – Arnhem Land Escarpment

Figure 7. *Anbinik* (*Allosyncarpia ternata* S.T.Blake), a fire-intolerant eucalypt relative confined to the western Arnhemland escarpment old, climatically buffered infertile landscape (OCBIL). This tree has a dark green canopy and occurs at the foot and above the escarpment wall. Photographs clockwise from top left were sourced from: John Wrigley, <https://www.flickr.com/photos/plantnerd/4202555199/in/photolist-7pncfg-VTn2MW-RhSdHV-4dW649-24rMjx6-24rMjB4-2gi7Ewy-2dXj9Hj-24rMjzF-2gi7k8z-2gi7EvX-2gi7EvB-2gi76qx-n9Y8gx-kiM2AB-kiPsLS-nruX35-7pneVK-4t2En2-4t6K85-fiVvPpS-fiFNg6-fiFPoe-fiW5AW-au9mfC-2isYi7F-2isYihF-fiFTs4-dmRrRc>; https://www.google.com/search?q=goatshiteambulance.com+kakadu&tbm=isch&ved=2ahUKEwjnh_aqy5rsAhWMK7cAHaJeC8IQ2-cCegQIABAA&oq=goatshiteambulance.com+kakadu&gs_lcp=CgNpbWcQDDoECCMQJ1CaigNYqIMEYMGTBGgAcAB4AIABtgKIAc0ykgEGMi0yNC4xmAEAoAEBqgELZ3dzLXdpei1pbWfAAQE&scient=img&ei=CZF5X6ffn4zX3LUPor2tkAw&bih=969&biw=1920#imgcr=ul3AN2uUjp-eYM



Figure 8. Plunkett mallee (*Eucalyptus curtisii* Blakely & C.T.White), from Bahr's Scrub, south-east Queensland, the sole representative of *Eucalyptus* subgenus *Acerosae*, hypothesized to be sister to all other *Eucalyptus*. Photographs by G. Leiper.

(Fig. 8). Plunkett mallee is found predominantly on sandstone outcrops and ridges or, occasionally, in poorly drained deep sands, such as at Beerwah, north of Brisbane (Smith *et al.*, 2003), within open forest or *Banksia* L.f. shrubland (*wallum* communities), which are classic OCBILs. Plunkett mallee is today an understory species. Its ancestor evolved some 50 Mya and might have been sister to all other *Eucalyptus*. There is incomplete resolution at present about precise relationships at this period of time for eucalypts. The significant observation for *E. curtisii*, however, is that it is a truly ancient mallee from subdued OCBIL uplands, not a rainforest tree from fertile lowlands.

The Duaringa stringybark or narrow-leaved white mahogany (*Eucalyptus tenuipes* (Maiden & Blakely) Blakely & C.T.White; *Eucalyptus* subgenus *Cuboidea* Brooker) comes from a lineage of similar age but is more widespread than *E. curtisii*. *Eucalyptus tenuipes* occurs in eastern central Queensland, with isolated occurrences northwards. It is recorded from sandy or lateritic soils in

open forest on gently sloping country. Whether or not this species occurs on OCBILs will require further research. A third taxonomically isolated species, Gympie messmate (*Eucalyptus cloeziana* F.Muell.; *Eucalyptus* subgenus *Idiogenes* L.D.Pryor & L.A.S.Johnson ex Brooker), is a tree scattered down the Queensland coastline from Cooktown to Gympie. Its ancestor arose ~45 Mya. It grows in open forest or woodland, notably on mesas and plateaus, characteristic OCBILs.

There are a number of species within the various other subgenera of *Eucalyptus* that have early-branching ancestors in the phylogenetic trees, suggesting OCBIL origins similar to those of *E. curtisii* and *E. cloeziana*. For example, among the 111 species of *Eucalyptus* subgenus *Eucalyptus* (Ladiges *et al.*, 2010) there is a major branch with members endemic to the SWAFR. The earliest group to diversify in the south-west comprises four extant species occurring in the highest rainfall forests of the south coast, including the narrow-range endemic tingles *Eucalyptus jacksonii* Maiden and

Eucalyptus brevistylis Brooker (Wardell-Johnson & Coates, 1996), and the more widespread *jarrah* (*Eucalyptus marginata* D.Don ex Sm.) and its sister Albany blackbutt (*Eucalyptus staeri* (Maiden) Kessel & C.A.Gardner). All four species occur on OCBILs. So, too, do the five members of the next group to branch off, mostly mallees, including Mount Lesueur mallee (*Eucalyptus suberea* Brooker & Hopper) and laterite mallee (*Eucalyptus lateritica* Brooker & Hopper) from laterite mesas north of Perth, prickly bark (*Eucalyptus todtiana* F.Muell.) and Johnson's mallee (*Eucalyptus johnsoniana* Brooker & Blaxell) from deep, infertile sands near the west coast, and blackbutt (*Eucalyptus patens* Benth.), a tree from swamps and riverine margins throughout the forested high-rainfall regions of the south-west. This relictual pattern, including many narrow-range endemics confined to rocky OCBIL uplands, recurs in subsequent diversification of the subgenus in the south-west.

Likewise, yellow tingle (*Eucalyptus guilfoylei* Maiden) is another south-west Australian high-rainfall, narrow-range endemic with an ancestor in an early-branching position in the evolutionary tree, sister to all of the 450 species of *Eucalyptus* subgenus *Symphomyrtus* (Fig. 6). It is found on OCBILs (Wardell-Johnson & Coates, 1996), and its lineage diverged from the rest of the species in this largest *Eucalyptus* subgenus > 40 Mya.

In the red bloodwoods (*Corymbia* subgenus *Corymbia*), two major branches occur in their phylogeny, diverging ~33 Mya (Schuster *et al.*, 2018) *Corymbia gummifera* (Gaertn.) K.D.Hill & L.A.S.Johnson, in eastern near-coastal New South Wales and adjacent parts of Queensland and Victoria, is sister to *Corymbia trachyphloia* (F.Muell.) K.D.Hill & L.A.S.Johnson. *Corymbia gummifera* is found on OCBILs, such as the Hawkesbury sandstones in the Sydney region, or on low-fertility sands. *Corymbia trachyphloia* occurs widely in eastern coastal Queensland down to the Hunter River region of New South Wales, inhabiting sandstone uplands and sandy plains (Fig. 4). These two species are, in turn, sister to south-west Australian representatives of the genus. *Marri* (*Corymbia calophylla* (Lindl.) K.D.Hill & L.A.S.Johnson), a high-rainfall forest endemic in the south-west, is sister to all other members of one branch. It is found on OCBILs. The closest relatives of *marri* are the two other local endemics, *yorgum* or red-flowering gum (*C. ficifolia*, Fig. 4) and mountain *marri* (*Corymbia haemotoxylon* (Maiden) K.D.Hill & L.A.S.Johnson), both of which also are found in sands on or adjacent to rocky country.

The third genus of true eucalypts, *Angophora*, has 15 species. *Angophora* diverged from *Corymbia* ~40 Mya. *Angophora exul* K.D.Hill and *Angophora melanoxylon* R.T.Baker arose from early-branching lineages whose common ancestor split from that of all other species

Table 1. Maximum width of clonal mallee eucalypt lignotubers ranked according to size

Taxon	Width (m)	Reference
<i>Eucalyptus</i> × <i>phylacis</i> L.A.S.Johnson & K.D.Hill	39.2	Rossetto <i>et al.</i> (1999)
<i>Eucalyptus cuprea</i> Brooker & Hopper	35	Sampson & Byrne (2016)
<i>Eucalyptus buprestium</i> F.Muell. × <i>marginata</i> D.Don ex Sm.	25.2	Robins <i>et al.</i> (2020)
<i>Eucalyptus</i> × <i>erectifolia</i> Brooker & Hopper	24.4	Robins <i>et al.</i> (2020)
<i>Eucalyptus caesia</i> Benth.	17.7	Bezemer <i>et al.</i> (2019c)
<i>Eucalyptus absita</i> Grayling & Brooker	17	Bradbury <i>et al.</i> (2016)
<i>Eucalyptus curtisii</i> Blakely & C.T.White	13.5	Smith <i>et al.</i> (2003)
<i>Eucalyptus recurva</i> Crisp	12	NSW National Parks and Wildlife Service (2003b)
<i>Eucalyptus imlayensis</i> Crisp & Brooker	12	James & McDougall (2007)
<i>Eucalyptus argutifolia</i> Grayling & Brooker	11	Kennington & James (1997)
<i>Corymbia gummifera</i> (Gaertn.) K.D.Hill & L.A.S.Johnson	10.5	Mullette (1978)
<i>Eucalyptus</i> × <i>graniticola</i> Hopper	8	Rossetto <i>et al.</i> (1997)
<i>Eucalyptus amygdalina</i> Labill. × <i>risdonii</i> Hook.f.	5.5	Tyson <i>et al.</i> (1998)
<i>Eucalyptus</i> × <i>bennettiae</i> D.J.Carr & S.G.M.Carr	5	Walker <i>et al.</i> (2009)

at 23 Mya. *Angophora exul* is a rare species confined to a ridge of acid volcanic outcrops on Gibraltar Rock, near Tenterfield in New South Wales. *Angophora melanoxylon* is widespread on sandy soils of inland northern New South Wales and adjacent Queensland. Narrow leaved apple (*Angophora bakeri* E.C.Hall) occurs usually on OCBILs: sandstone ridgetops and upper slopes with Hawkesbury sandstone geology in central New South Wales. Further north, it occupies infertile sands. Several other species of *Angophora* are typically found on Hawkesbury sandstone, including the iconic smooth-barked apple (*Angophora costata* (Gaertn.) Britten), a sinuous red-barked tree typical of Sydney sandstone habitats, and the shrub of heathlands, *Angophora hispida* (Sm.) Blaxell.

OLD INDIVIDUALS: CLONALITY IS COMMON (ULTIMATE SELF HYPOTHESIS)

The prediction that OCBILs favour the accentuated persistence of long-lived individuals is also well supported by eucalypt studies. Indeed, the ultimate self hypothesis is evidenced by all species of eucalypts being perennial woody plants and by two especially striking attributes.

Firstly, several mallees have been tentatively aged at well over 1000 years old, with one estimate of 3000–11 000 years old for clonal growth forms ≤ 17 m across for *Eucalyptus absita* (Maiden) K.D.Hill & L.A.S.Johnson, a rare mallee of OCBILs north of Perth (Bradbury *et al.*, 2016). The maximum width of other clones occupying SWAFR OCBILs and south-east Australia is 39 m (Table 1). In eastern Australia, large mallee clones of the relictual *E. curtisii* attained 13.5 m, across with an estimated age range of 3970–9000 years (Smith *et al.*, 2003). *Eucalyptus imlayensis* Crisp & Brooker is known from a single population atop *Balawan* (Mt Imlay), comprising Devonian metasedimentary rocks at 886 m a.s.l. in the southern coastal ranges of New South Wales (Keith & Sanders 1990). Comprising only five clones, the largest 12 m across, *E. imlayensis* matches south-west Australian examples of very rare mallee clonal taxa, such as *Eucalyptus argutifolia* Grayling & Brooker, *Eucalyptus* \times *graniticola* Hopper and *Eucalyptus* \times *phylacis* L.A.S.Johnson & K.D.Hill.

Secondly, some eucalypts form towering giants, hundreds of years old, including mountain ash (*E. regnans*) and *karri* (*E. diversicolor*), the tallest flowering plants on Earth (Hickey *et al.*, 2000; Mifsud, 2003). Such gigantism has evolved independently in *Eucalyptus* seven times, five in the largest subgenus, *Symphomyrtus*, and two in subgenus *Eucalyptus*. The nine species that attain heights > 70 m occur in tropical to temperate wet habitats, typically receiving > 1000 mm annual rainfall.

Giant eucalypts are typically found in habitats where disturbance regimes, including climatic buffering, are muted. This then allows for the limits to tree height to be achieved in the face of ecophysiological thresholds of water availability and nutrient supplies (Cramer, 2012). The most remarkable eucalypt giant in this context is *karri*, because it grows in landscapes where phosphorus (P) is the limiting nutrient, not nitrogen (N), and manages to exceed 80 m in height nonetheless. Remarkable plasticity in height is evidenced in species such as *tara monadro* (Tasmanian blue gum, *E. globulus*), which attains 15–60 m height in forest formations, but can form stunted shrubs < 4 m tall on granite outcrops, such as on Wilson's Promontory in Victoria (Tng *et al.*, 2012; Tng *et al.*, 2014). Significantly, a recent review recommended that the best management strategy for long-lived eucalypt giants was to let them be (Tng *et al.*, 2014); a clear recommendation made for all OCBIL woody perennials.

SLOW INDIVIDUAL GROWTH

The preceding section on clonality highlights the slow individual growth of some eucalypts. Not only do eucalypts form large clones and giant trees, but the growth rates of lignotubers of the former are estimated to be 1.5 and 3.4 mm outwards per year (Tyson *et al.*, 1998). Hence, clones attaining 30–40 m in diameter (Table 1) could be ≥ 10 000 years old.

Growth rates of forest trees from YODFELs have been studied over many decades. Individual tree diameter at breast height increments range from 0.01 to 0.4 cm/year in southern and central Queensland (Ngugi *et al.*, 2015). Growing commercial eucalypts (*Eucalyptus grandis* W.Hill ex Maiden and *Eucalyptus dunnii* Maiden) from rich soils on rainforest margins under varying levels of P led to depressed growth in *E. dunnii* at zero and low P, as would be found on OCBILs (Wu *et al.*, 2014). Moreover, 'photosynthetic rate and chlorophyll content of the [two] eucalypt species and [four commercial] hybrids were the most sensitive physiological processes to even mild P deficiency compared with seedling growth and biomass production' (Wu *et al.*, 2014: p. 382).

An earlier study comparing predominantly OCBIL-dwelling *C. gummifera* and a provenance of *Eucalyptus pilularis* Sm. from low-P soils with YODFEL-dwelling *E. grandis* and a provenance of *E. pilularis* from fertile soils conformed to expectations (Mulligan & Sands, 1988). Largely owing to high levels of P stored in seeds, the OCBIL eucalypts produced a larger mass and extracted two to five times more P from experimental sands. This strategy enabled earlier accumulation of a large root mass. The commercial eucalypts from fertile

soils were under significant disadvantage in low-P soils.

THE JAMES EFFECT (PURSUIT OF HETEROZYGOSITY, E.G., BIRD POLLINATION, GENOMIC COALESCENCE)

The James effect refers to natural selection for genetic, cytogenetic or phenotypic adaptations that conserve heterozygosity in the face of inbreeding attributable to small population size (Hopper, 2009). Eucalypts are conservative in chromosome number, having 11 pairs across the 135 species counted thus far, with no evidence of polyploidy or dysploidy characterizing speciation (Grattapaglia *et al.*, 2012). An early genome duplication specific to the group of families to which eucalypts belong (order Myrtales) has been documented ~110 Mya, with subsequent extensive tandem gene duplications (Myburg *et al.*, 2014). This duplication, probably attributable to hybridization, has increased the capacity for evolutionary novelty in eucalypts, which display elevated genetic variation within populations and dampened divergence among populations in widespread common species of forests and woodlands (Moran & Hopper, 1987; Broadhurst *et al.*, 2017).

Differentiation between eucalypt species is known to be multigeneic, widely dispersed across the genome and involve different classes of genes at different places along chromosomes. Species-differentiating genetic markers or segments of DNA constitute 1–5% of all markers and are concentrated where gene density is highest, increasing the probability of linked selection (Hudson *et al.*, 2015). Essentially, greater divergence between species occurs in gene-dense chromosomal regions where natural selection is strongly operative. Such clustering of tightly linked genetic loci involved in adaptation can occur through minor chromosomal rearrangements; a mechanism for inheritance for co-adapted gene complexes. Should genes influencing reproductive isolation be included in such gene complexes, such as those determining flowering time or those causing lethality in developing seeds, a clear genomic mechanism for the origin of new species is evident.

The mating system of such eucalypts is one preferentially favouring outcrossing between different plants. Eucalypt nuts contain large numbers of aborted ovules or immature seeds (dross) relative to the number of well-developed seeds. This suggests that strong maternal selection occurs, favouring full development of only the most vigorous seeds.

Typically, outcrossing leads to slightly higher rates of ovule penetration in some species and, in many eucalypts, routinely yields larger seeds that become more vigorous seedlings, exhibiting hybrid vigour compared with seedlings from self-pollination (Pound *et al.*, 2002). One study summarized that: ‘*Eucalyptus*

species are mainly self-pollinating outbreeders with efficient post-zygotic seed selection systems. The ovule wastage [dross] associated with post-zygotic seed selection is here accommodated by high ovule numbers’ (James & Kennington, 1993).

Moreover, mature trees in forests and plantations display higher levels of genetic diversity or heterozygosity than the seeds they produce, indicating that natural selection continues to favour individuals with high heterozygosity through the life cycle, with intense competition among individuals as plants grow up and compete for light and nutrients (Booth *et al.*, 2015). Outcrossing generates heterozygosity and is accentuated in those species that are pollinated by birds (Hopper & Moran, 1981; Bezemer *et al.*, 2019a). South-west Australia has an exceptional number of such bird-pollinated species, characterized by large, colourful flowers, often red or pink or yellow, in contrast to the cream flowers of most species. How could natural selection have resulted in this phenomenon?

When widespread common eucalypts occur in small populations, often owing to land clearing and fragmentation of native vegetation, inbreeding depression is usually expressed. The opportunity to cross-pollinate with other plants is reduced; more seeds are produced from self-pollination, and resultant seedlings may not grow as vigorously nor reproduce as well as outcrossed seeds. The natural occurrence of small, isolated populations of eucalypts is predicted when they grow on OCBILs (Hopper, 2009). It is postulated that the James effect then comes into play. Intense natural selection works on the genome in small, isolated populations to fix in place any mechanisms that enable plants to retain genetic diversity and heterozygosity. Given that seed dispersal is very limited in eucalypts, an obvious alternative to increase the amount of outcrossing is to place pollen on large, mobile pollinators, such as birds. This seems to be the case for the large diversity of bird-pollinated species seen in south-west Australia.

Eucalypts in South Australia that receive more visits by birds than insects, such as cup gum (*Eucalyptus cosmophylla* F.Muell.) and yellow gum (*Eucalyptus leucoxylon* F.Muell.), have more nectar per flower and fewer, larger flowers per cubic metre of canopy (Paton, 1986). In turn, this results in birds spending more time at such flowers, increasing the probability of pollen pick-up and deposition on stigmas. Purple-crowned lorikeets exemplify this process, methodically working over hundreds of eucalypt flowers on a tree but then ensuring outcrossing by flying long distances to the next tree (Hopper, 1980; Fig. 9).

Two studies of specialization towards exclusive bird pollination illustrate the adaptive changes in floral structure and flowering time (Hopper, 2014b). For the two subspecies of the winter-flowering SWAFR



Figure 9. A wide-ranging agent of pollen dispersal of eucalypts in southern Australia, the purple-crowned lorikeet (*Parvipsitta porphyrocephala* (Dietrichsen, 1837)), here on *Eucalyptus utilis* Brooker & Hopper from the Southwest Australian Floristic Region. Photograph by S. D. Hopper.

granite outcrop endemic *E. caesia*, mammals (western pygmy possums) and insects were rarely recorded at flowers (Hopper, 1981). Honeyeaters were abundant, in contrast, with up to eight species of these birds seen feeding on the eucalypt flowers at individual granite rocks in good flowering seasons (Fig. 10).

The flowers of *E. caesia* subsp. *magna* are larger, with more stamens, than those of *E. caesia* subsp. *caesia*. In terms of evolution, it is clear that *E. caesia* subsp. *magna* has been derived from *E. caesia* subsp. *caesia*, and not vice versa (Hopper & Burgman, 1983). *Eucalyptus caesia* subsp. *magna* produced, on average, fewer flowers than *E. caesia* subsp. *caesia* (32 vs. 55). It had more flowers widely dispersed over each tree and produced an exceptionally high number of seeds per fruit. Moreover, experimental studies of nectar production showed that nectar standing crops in the wild of *E. caesia* subsp. *magna* were greater throughout the day than those in *E. caesia* subsp. *caesia*. In *E. caesia* subsp. *caesia*, nectar in bagged flowers is produced overnight, ceasing in the morning, whereas in *E. caesia* subsp. *magna* it is produced continuously

night and day, resulting in three times more nectar per day than *E. caesia* subsp. *caesia* flowers. Cultivated plants behave in the same manner, demonstrating genetic control of these nectar-production traits (S. D. Hopper & R. Wyatt, unpublished).

It was predicted, consequently, that feeding by honeyeaters on *E. caesia* subsp. *caesia* nectar will cease as the supply dries up through the day, and feeding on *E. caesia* subsp. *magna* nectar will be at higher uniform rates throughout the day. Both these predictions were borne out by field studies. Moreover, it was also predicted that honeyeaters would become more aggressive throughout the day on *E. caesia* subsp. *caesia* as the nectar dries up, and that there would be less evident aggression in *E. caesia* subsp. *magna* stands. Again, both predictions were supported by observational data (S. D. Hopper, unpublished). DNA studies of the mating system established that open-pollinated plants of smaller-flowered *E. caesia* subsp. *caesia* averaged only 38% outcrossing, perhaps owing to geitonogamy effected by large numbers of honeybees (Bezemer *et al.*, 2019a). In contrast, open



Figure 10. The James effect: bird pollination is accentuated in Ocbil endemics of the Southwest Australian Floristic Region, e.g. honeyeaters feeding on *Eucalyptus caesia* in midwinter: top right - Brown honeyeater (*Lichmera indistincta*, Vigers & Horsfield, 1827) on *E. caesia* subspecies *caesia* (photo S. D. Hopper); top left - White-eared Honeyeater (*Nesoptilotis leucotis* (Latham 1801)) on *E. caesia* subspecies *magna* (photo N. Bezemer); bottom - Red wattlebird (*Anthochaera carunculata* (Shaw 1790)) on *E. caesia* subspecies *magna* (photo K. Lightbody).

pollination in large-flowered *E. caesia* subsp. *magna* yielded an average of 76% outcrossed seed.

Using DNA markers to document paternity for six mother plants of *E. caesia* subsp. *caesia* at Boyagin (Bezemer *et al.*, 2016), it was found that random mating occurred for plants < 40 m apart, and fathers of seed came from \leq 300 m away from the mother tree. Of 130 outcross pollination events detected by paternity assignment, 74% occurred between trees > 20 m apart, 28% between trees > 60 m apart, and 14% between trees > 100 m apart. Wide within-population outcrossing prevailed at Boyagin. A similar pattern of paternity was found subsequently at Mt Caroline and in *E. caesia* subsp. *magna* at Chiddarcooping (Bezemer *et al.*, 2019a). The contribution of many fathers to seeds in nuts and more extensive pollen dispersal than only among nearest neighbours is a consequence of

pollination by highly mobile honeyeaters and might buffer *E. caesia* against the loss of genetic diversity predicted for small and genetically isolated populations (Bezemer *et al.*, 2019c). Moreover, even when subjected to inbreeding in small populations, *E. caesia* appears to show no ill effects, suggesting that it has purged lethal genes through prolonged operation of the James effect (Bezemer, 2018; Bezemer *et al.*, 2019b).

The second case study was of *Eucalyptus stoatei* C.A.Gardner, an exclusively bird-pollinated eucalypt that belongs to a small group with effectively tubular flowers (Hopper & Moran, 1981). This small tree emerges from *kwongkan* (sensu Hopper, 2014b - sandplain heath) in the south coast region east of Ravensthorpe in the SWAFR. Honeyeaters visited few flowers per tree (average of one to five). Some 18% of the movements of individual birds from one

flower to another were between flowers on different trees in one study during a good flowering season. This figure was elevated to close to 50% during a poor flowering season, when individual trees each carried fewer open flowers. Most inter-tree movements were between trees farther apart than nearest neighbours, as was noted above for *E. caesia*. Hence, a high rate of outcross pollination was inferred. Analysis of the mating system of *E. stoatei* using genetic (allozyme) seed markers in one population indicated an average level of outcrossing of 82%, among the highest then recorded for eucalypts.

Thus, in both *E. caesia* and *E. stoatei*, there appears to be a strong selective premium placed on conservation of heterozygosity (genetic variation) in the face of prolonged inbreeding imposed by a dissected population

structure on OCBILs, as predicted for the James effect. This hypothesis might be tested further by applying DNA-based paternity analysis to bird-pollinated vs. insect-pollinated or generalist plant species.

PROLONGED SPECIATION AT THE MARGINS (SEMI-ARID CRADLE HYPOTHESIS)

Using powerful computer modelling analyses, annual rainfall has been shown to be the key bioclimatic predictor of eucalypt distributions in Australia (Butt *et al.*, 2013). The variable climate in semi-arid regions between mesic and arid regions is proposed to generate fluctuating pressures on populations, enabling expansion and secondary contact, with hybridization of previously isolated populations, during wet periods and forcing contraction of populations into isolated



Figure 11. Phylogenomic studies (Gosper *et al.*, 2019) have identified these three species of old, climatically buffered infertile landscape (OCBIL)-dwelling mallets as early-branching members of the *Eucalyptus redunca* Schauer superspecies in the Southwest Australian Floristic Region: A, B, *Eucalyptus ravensthorpensis* (Brooker & Hopper) Gosper & Hopper (note the characteristic short buds); C, D, *Eucalyptus densa* Brooker & Hopper, with longer buds typical of the superspecies, in clay-based wetland soils high in the landscape, and with Noongar Elder Doc Reynolds for scale; E, F, *Eucalyptus gardneri* Maiden on lateritic uplands. F, prolific seed germination after fire is typical of obligate seeding mallets.

refugia during harsh, arid conditions. Such population volatility sets up opportunities for genetic divergence in isolation, as documented, for example, in granite outcrop endemics, such as *E. caesia* (Byrne & Hopper, 2008; Bezemer *et al.*, 2019c). Should such divergence involve fixation of genes responsible for reproductive barriers, geographical (allopatric) speciation will occur.

In *Eucalyptus* subgenus *Eucalyptus*, Ladiges *et al.* (2010) presented a model of progressive differentiation over tens of millions of years in the SWAFR, from ancestors of lineages that were based in today's highest-rainfall forests of the south coasts. Thereafter, several groups in this subgenus diverged into multiple species, many rare and localized, and most found in semi-arid OCBIL habitats in *kwongan* vegetation to the north of Perth on the west coast and eastwards from Albany along the south coast. This yields a contemporary pattern of what is termed classic allopatric replacement series among relatives, with many species forming geographically separate isolates in the semi-arid country, each genetically and morphologically distinct from its nearest relatives.

A similar pattern has been documented based on morphological studies of *Eucalyptus* series *Levispermae* Maiden (Brooker & Hopper, 1991), containing *Eucalyptus wandoo* Blakely, *E. redunca*, *Eucalyptus gardneri* Maiden and related species. A recent phylogenomic study of the semi-arid country *E. redunca*–*E. gardneri* superspecies within this group resolved that the three mallee tree taxa (*E. gardneri*, *Eucalyptus densa* Brooker & Hopper and *Eucalyptus ravensthorpensis* (Brooker & Hopper) Gosper & Hopper) were early-branching, genetically distinct and mainly OCBIL dwellers (Gosper *et al.*, 2019; Fig. 11). The mallee species (*E. redunca*, *Eucalyptus* aff. *redunca*, *Eucalyptus varia* Brooker & Hopper, *Eucalyptus improcera* (Brooker & Hopper) D.Nicoll & M.E.French and *Eucalyptus pluricaulis* Brooker & Hopper) and their subspecies were less well resolved, except for *E. varia* from the Esperance region. Moreover, most of these mallees occupied YODFELs or intermediate landscapes.

The semi-arid cradle hypothesis was also supported in a study of DNA variation in four subspecies of *Eucalyptus loxophleba* Benth. in semi-arid south-west Australia (Hines & Byrne, 2001). A pattern of morphological and genetic intergradation in semi-arid country of southern Queensland emerged in a study of the origins of a morphological cline between *Eucalyptus melanophloia* F.Muell. and *Eucalyptus whitei* Maiden & Blakely (Holman *et al.*, 2011). In tuart (*Eucalyptus gomphocephala* DC.) along the west coast of south-west Australia, southernmost populations in higher-rainfall country are relatively genetically homogeneous, whereas higher levels of divergence in local patches occurs northwards into the semi-arid area (Nevill *et al.*, 2014).

Speciation of eucalypts in eastern Australia is driven by and large by the influence of the Great Dividing Range. OCBILs are common along this continental north–south divide. Incipient speciation was captured in a study of the blackbutts *E. pilularis* and *Eucalyptus pyrocarpa* L.A.S.Johnson & Blaxell (Shepherd & Raymond, 2010), the former common from subtropical Fraser Island in Queensland to temperate Bega in southern New South Wales, favouring coastal plains and foothills to 900 m a.s.l. *Eucalyptus pyrocarpa* (large-fruited blackbutt) occupies less fertile, higher sites, with soils derived from sandstone, occurring in patches from Woodburn to Wauchope in coastal New South Wales. No hybrids of the two species are known, and they remain morphologically distinct in fruit size and white waxiness of the branches, but sequencing the DNA revealed no genetic differences. Populations of *E. pyrocarpa* might be best regarded as ecotypes of *E. pilularis*, although further genomic studies are needed to determine their status.

Semi-arid conditions on rocky outcrops along the Great Dividing Range are scattered along its length and often afford habitat for mallee eucalypts and local endemics, suggesting support for the semi-arid cradle hypothesis. For example, the Blue Mountains World Heritage Area has a spectacular array of eucalypts (Hager & Benson, 2010). Some 75 species are found in the southern Warragamba Special Area (NSW National Parks and Wildlife Service, 2003a), which includes vegetation types called rock plate heath-mallee, found on exposed rock plates, outcrops and wind-buffed plateau edges ≤ 800 m a.s.l. The sandstone rocks form OCBILs that are rich in mallees, including Blue Mountains mallee ash (*Eucalyptus stricta* Sieber ex Spreng.), narrow-leaved mallee ash (*Eucalyptus apiculata* R.T.Baker & H.G.Sm.), whipstick mallee ash (*Eucalyptus multicaulis* Blakely), privet-leaved stringybark (*Eucalyptus ligustrina* DC.) and Faulconbridge mallee ash (*Eucalyptus burgessiana* L.A.S.Johnson & Blaxell, including *Eucalyptus obstans* L.A.S.Johnson & K.D.Hill). Upslope, these mallee-heaths grade into montane heath-mallee, again on OCBIL sandstones, such as those found on Ti Willa Plateau and along the Narrow Neck Peninsula near Katoomba, but the diversity of mallees drops to two species: *E. stricta* and sporadic narrow-leaved sally (*Eucalyptus moorei* Maiden & Cabbage). Rutherford *et al.* (2015) have unravelled complex relationships among these green ashes, establishing unequivocally that speciation and hybridization of mallee ashes occurs on OCBILs of sandstone and granite outcrops, probably mirroring the pattern discussed above for the Victorian *Gariwerd* (Grampian) National Park endemics (Pollock *et al.*, 2013). New species of eucalypts continue to be discovered in the Blue Mountain

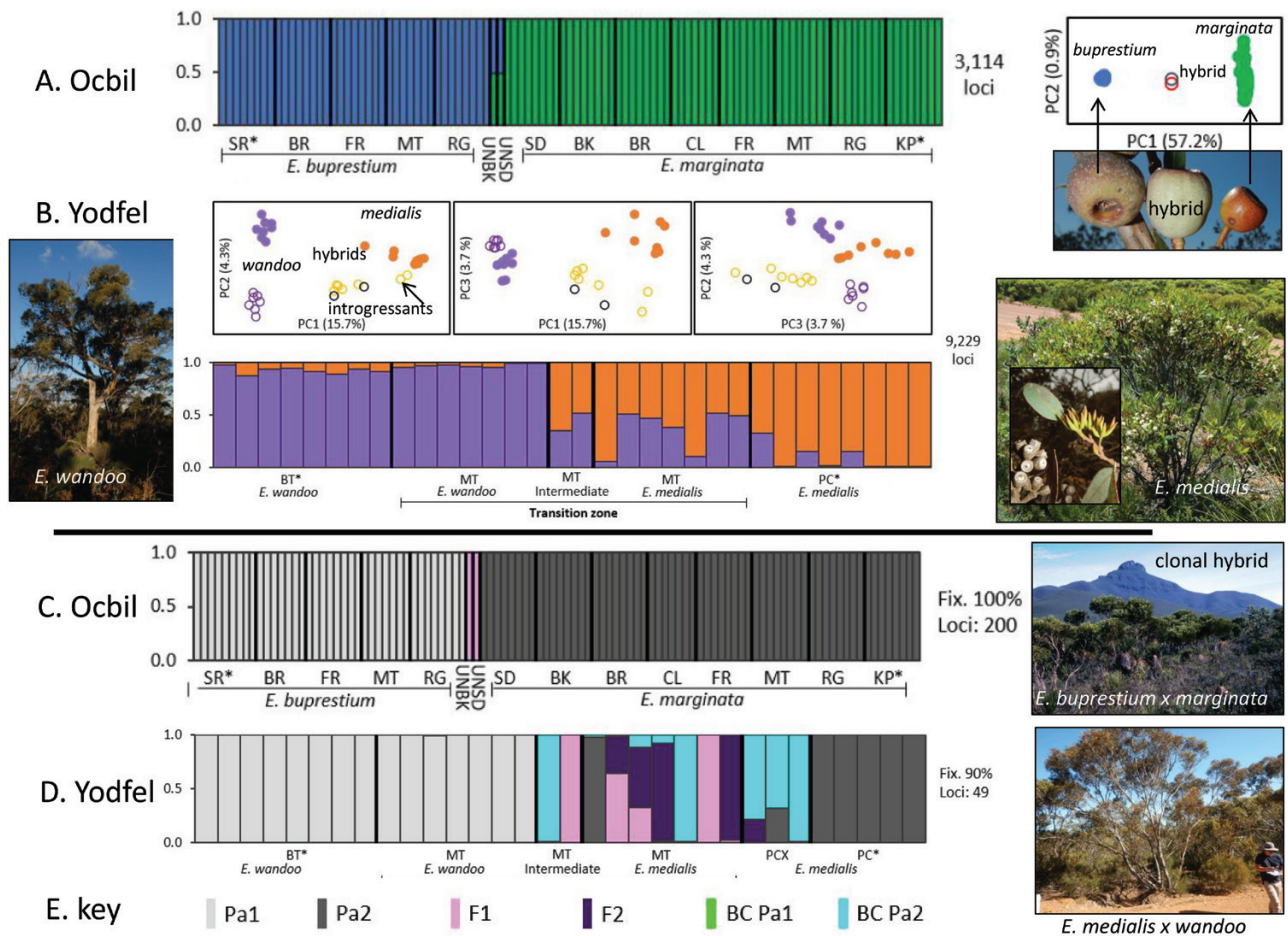


Figure 12. Contrasting DNA patterns in natural hybridization as predicted for old, climatically buffered infertile landscapes (OCBILs) and young, often-fertile, fertile landscapes (YODFELs) of the Stirling Range, Southwest Australian Floristic Region. A, clonal F_1 *Eucalyptus buprestium* F.Muell. \times *marginata* D.Don ex Sm. with no backcrossing from OCBIL sandplain; STRUCTURE results ($K = 2$) for 3114 loci, with the vertical bar plots showing the proportion of each genetic cluster assigned to each specimen sampled at each location. Dark bars indicate separate populations/species. Sampling sites: BK, Bluff Knoll; BR, Bluff Knoll Road; CL, Central Lookout; FR, Formby Road; KP, Kalgan Plains; MT, Mt Talyuberlup; RG, Red Gum Pass; SD, Stirling Range Drive; SR, Salt River Road. *Parental genotype allopatric reference populations used for each analysis; two clonal hybrids are UNSD and UNBK; to the right is a cluster, with principal coordinates analysis performed on each *Eucalyptus buprestium* \times *marginata* hybrid (open circles) and their putative parents (filled circles), with fruits illustrated below. B, introgressant hybrid population of *Eucalyptus medialis* Brooker & Hopper \times *wandoo* Blakely from YODFEL slope at Mt Talyuberlup. Reference parental populations (*) are BT, Bluff Knoll turnoff for *E. wandoo*, and PC, Paper Collar Creek for *E. medialis*; MT, Mt Talyurberlup has both parental taxa and hybrids as highlighted in the STRUCTURE plot. C, NEWHYBRIDS analysis of the OCBIL *Eucalyptus buprestium* \times *marginata* clonal hybrids and allopatric reference parental individuals, with vertical bars indicating the proportion of each hybrid class assigned to each individual. D, NEWHYBRIDS analysis of the YODFEL *E. medialis* \times *wandoo* introgressant hybrid population, as above. The fixation rate and number of loci used for each analysis are shown to the right of each plot. *Parental genotype reference populations used for each analysis. E, key to introgressant hybrid classes: BC Pa1, parent 1 backcross; BC Pa2, parent 2 backcross; F_1 , first generation hybrid; F_2 , second generation hybrid; Pa1, parent 1; Pa2, parent 2. Modified from Robins *et al.* (2020). Photographs by S. D. Hopper.

OCBILs, such as the distinctive Wollemi stringybark (*Eucalyptus expressa* S.A.J.Bell & D.Nicolle; Bell & Nicolle, 2012).

On the western side of the Great Dividing Range, semi-arid conditions become common, but gently

sloping terrain favours widespread species of eucalypts, with few local endemics on unusual geology. For example, white box (*Eucalyptus albens* Benth.) displays high genetic variation within populations but little geographical divergence across its range from

southern Queensland to northern Victoria (Prober & Brown, 1994).

REDUCED HYBRIDIZATION/HYBRID SPECIATION

The reverse of divergence in isolated refugia, hybridization following range expansion and secondary contact, is also evident in many eucalypts, significantly more so in the east than in the west (Potts & Wiltshire, 1997; Hopper, 2018). Evidence of extensive hybridization has emerged from sequencing of chloroplast DNA in eucalypts (Jackson *et al.*, 1995; Byrne, 2008). Rates of hybridization, introgression and hybrid speciation should be reduced on OCBILs because of the prolonged opportunities for genetic divergence of parental taxa and their reduced dispersal capabilities (Hopper, 2018). The reverse prediction is made for YODFELs.

Robins *et al.* (2020) tested these ideas in the Stirling Range of the SWAFLR (Fig. 12). There, the OCBILs (ridge tops, *kwongkan* plains) are the favoured habitat of *E.* subgenus *Eucalyptus* species. YODFELs (steep slopes, lowland, wetland margins) are where species of *E.* subgenus *Symphyomyrtus* (Schauer) Brooker predominate. Based on molecular and morphological analyses, it was concluded:

The older parental taxa assessed within Subgenus *Eucalyptus*, which are widespread on old landscapes, were identified as well-defined genetic entities and all hybrids were exclusively F₁ hybrids. In addition, many combinations showed evidence of clonality, suggesting that the high number of hybrids recorded from some combinations is the result of long-term clonal spread following a few hybridisation events rather than frequent hybridisation. In contrast, the species in Subgenus *Symphyomyrtus*, which typically occur on younger landscapes and are generally more recently evolved, showed less distinction among parental taxa and where hybridisation was detected, there were high levels of introgression (Robins *et al.*, 2020: Abstract).

Hence, the reduced hybridization hypothesis was affirmed in this study (Fig. 12). Further comparative studies of this type are recommended, especially where large, rare clonal hybrids have been found (Table 1).

NUTRITIONAL AND OTHER BIOLOGICAL SPECIALIZATION

It is hypothesized that special nutritional and other biological traits associated with coping with infertile lands should be evident in OCBILs, accentuated

in plants with water-foraging strategies, unusual life histories, symbioses, carnivory, pollination etc. (Hopper, 2009).

More than 150 fungal species of ≥ 60 genera are mycorrhizal with eucalypts, exhibiting little specificity for their hosts (Chilvers, 2000). Experimentally inoculated eucalypts in pots develop more dry weight in the presence of mycorrhizae. For SWAFLR forest trees, for example, *marri* doubles in biomass, and *karri* doubles through to growing > 20 times dry weight. These symbiotic partnerships are clearly advantageous to eucalypts. However, as yet, a careful examination of such interactions, comparing eucalypts on OCBILs with those on YODFELs, has yet to be undertaken.

Labiberté *et al.* (2015) and Lambers *et al.* (2018) hypothesized that mycorrhizae in mallee eucalypts on P-deficient OCBILs conferred resistance to pathogens and enabled coexistence with species of Proteaceae with more efficient nutrient-acquisition strategies but greater susceptibility to pathogens. It is possible that the mycorrhizal eucalypts could tap into nutrients in the rhizosphere made available by their less well-defended neighbours. This offers a promising line of future research to help explain coexistence and facilitation on OCBILs.

Eucalypts provide habitat and food for a diverse array of organisms, with ecological relationships of some perhaps extending back for tens of millions of years. Well-known associations of herbivorous mammals and eucalypts, such as the koala and sugar gliders, are a case in point. However, relatively few specific biological interactions with eucalypts of OCBILs have been documented. One example is the trapdoor spider *Bertmainius tingle* (Main, 1991), which has its burrows in the thick red spongy bark of red tingle (*E. jacksonii*) in south-west Australia (Harvey *et al.*, 2015). This is an ancient lineage of spiders with sister genera in Africa and Madagascar, classic denizens of OCBILs.

Comparative studies of animals on eucalypts of OCBILs vs. YODFELs would best be prosecuted where co-evolutionary species-specific relationships are evident. A promising group of invertebrates from this perspective is the gall-forming bugs (Lin *et al.*, 2015), such as the scale insect genus *Apiomorpha* Rübsaamen. This genus shows evidence of possible co-speciation with eucalypt hosts (Cook & Gullan, 2004), facilitated by exceptional levels of chromosomal divergence (Cook & Rowell, 2007; Mills & Cook, 2014). As molecular DNA tools enable advances in the identification of undescribed species of *Apiomorpha* and their eucalypt hosts, better understanding of the importance of OCBILs in their co-speciation might eventuate.

Rockiness in OCBILs limits rapid growth and favours resource conservation in eucalypts (Pollock *et al.*, 2012). This was demonstrated in experiments

comparing the root foraging strategy in confined spaces of the granite outcrop endemic *E. caesia* subsp. *caesia* with that for *Eucalyptus drummondii* Benth., a species of deeper soils (Poot *et al.*, 2012). It was found that *E. caesia* invested a larger portion of its biomass in roots, distributed its roots faster and more evenly through available root space, and had a lower specific root length. Replication of similar experiments (Hamer *et al.*, 2016) comparing *E. caesia* with eight other SWAFR species of deeper soils confirmed that the rooting strategies of *E. caesia* were the most divergent:

Juveniles of this species did not develop a tap root and produced many relatively thick lateral roots that explored a large portion of the rhizotron, with the majority of finer roots confined to the topsoil. ... Thus, the different architecture and foraging of *E. caesia* roots compared to a range of other *Eucalyptus* species from a variety of deeper soil environments, again confirms that shallow-soil habitats are quite unique and have selected for specialised root architecture (Hamer *et al.*, 2016: p. 226).

This represents a classic test of OCBIL theory, affirming the prediction of accentuated divergence of traits of organisms endemic to OCBILs over long periods of time compared with related congeners of YODFELS.

One other research area provides similar tests for an accentuated evolutionary process on OCBILs; that of specialization towards vertebrate pollination in eucalypts, already mentioned above as a response consistent with the James effect hypothesis. An interesting example concerns the close tie between swift parrots (*Lathamus discolor* (White, J., 1790)) and Tasmanian blue gums (*E. globulus*; Hingston & Potts, 2005). Flowers of this eucalypt are visited by a range of birds and insects (Hingston & Potts, 1998). Experiments allowing animals to feed on only single flowers with virgin stigmas enabled the measurement of seed set after a single flower visit by swift parrots, introduced honey bees and bumble bees, and native insects. It was discovered that the average resultant seed set of a swift parrot visit was 6.2 seeds per gum nut (76% of 8.2 seeds, the maximum possible following experimental outcross pollination of virgin flowers). For honey bees and bumble bees, it was 0.5 seeds (7%), and for native insects it was zero seeds. This compelling evidence that swift parrots were the most effective pollinators highlighted the importance of natural selection for bigger flowers in eucalypts to favour pollination by short-billed birds (and possibly small mammals).

Moreover, the discovery that more outcrossed pollination in *E. globulus* occurred in seeds produced in the upper half of the canopy than in the lower

half led to the suggestion that this was effected by a preference of pollinating birds for the upper canopy. Hingston & Potts (2005) showed that 14 species of birds visiting flowers on 23 trees with equal numbers of flowers in the upper and lower canopies spent an average of 74% of their foraging time in the upper canopy. Two frugivorous parrots were exceptional, spending 45 and 46% of their foraging time in the upper canopy. Of the remaining 12 species, ten were nectarivores, and their time in the upper canopy foraging ranged from 66% (noisy miner, *Manorina melanocephala* (Latham, 1801)) to 96% (crescent honeyeater, *Phylidonyris pyrrhoptera* (Latham, 1801)). Importantly, primary outcross pollinators spent 75% (New Holland honeyeater, *Phylidonyris novaehollandiae*, and musk lorikeet, *Glossopsitta concinna* (Shaw, 1791)), 70% (swift parrot) and 85% (little wattlebird, *Anthochaera chrysoptera* (Latham, 1801)) of their foraging time in the upper canopy. A related study established that the swift parrot and lorikeets carried more pollen within 22 mm of their bill tips than did New Holland honeyeaters, and the parrots contacted stigmas regularly because of their consistent consumption of both pollen and nectar on *E. globulus* flowers (Hingston *et al.*, 2004).

Although *E. globulus* rarely grows on OCBILs (stunted trees on the granite outcrops of southern Victoria might be an exception), these studies demonstrate a convincing case for eucalypts evolving larger flowers to achieve predominant pollination by parrots and other vertebrates. Another species, cup gum (*E. cosmophylla*) from South Australia, essentially has flowers of comparable size, colour and shape to those of *E. globulus* and is also pollinated primarily by birds (Paton, 1986). The overwhelming majority of eastern Australian eucalypts have smaller flowers. It is in south-west Australia where the largest, most colourful eucalypt flowers are to be found. Is there evidence that accentuated evolution towards vertebrate pollination on OCBILs has occurred there?

A spectacular innovation in this line of floral evolution on SWAFR OCBILs is the aggregation of the hypanthial bases of buds, flowers and fruits into a fused mass the size of a cricket ball, seen in *Eucalyptus* subser. *Conjunctae* Brooker (Nicolle *et al.*, 2008), with six species now recognized. These structures are so striking that in 1844 the German Botanist Johannes Conrad Schauer (1813–1848) named a new genus, *Symphyomyrtus*, meaning fused myrtle, for the group of species first collected in 1802 at Lucky Bay east of Esperance by Robert Brown (1773–1858), the Scottish naturalist aboard Flinders' *Investigator*. Today, *Eucalyptus lehmanii* (Schauer) Benth. remains the type for the largest subgenus (*Symphyomyrtus*), because it was realized subsequent to Schauer's

description of the new genus that other south-west eucalypt species with solitary buds, flowers and fruits are closely related to, and hybridize readily with, those of *E.* subseries *Conjunctae*.

The long, finger-like buds of species of the *Conjunctae* probably led to the Noongar name *maarlaq* (*maar* = hand, *aq* = small). Thus, today we recognize Bald Island *marlock* (*Eucalyptus conferruminata* D.J.Carr & S.G.M.Carr). In flower, *Conjunctae* species form a ball of lemon-yellow stamens that clearly favour bird and mammal pollinators. Concentrated in Fitzgerald River National Park, where five of the six species are found and one (Quoin Head *marlock*, *Eucalyptus mcquoidii* Brooker & Hopper) is endemic, the *Conjunctae* are characterized by isolated populations found on OCBILs. Thus, they constitute an independent example of the James effect, parallel to those outlined above for subspecies of *E. caesia* and for *E. stoatei* and allies (Hopper & Moran, 1981). Another selective pressure deserving investigation relates to the advantages of fused fruits as a defence against seed predation; they can also escape incineration in mild canopy fires and conserve moisture during drought. The capacity for new discovery in eucalypts on OCBILs is evident.

FIRST NATIONS REVERE SACRED UPLANDS

This hypothesis, proposed by Hopper *et al.*, (2020), is derived from recent oral history studies with Noongar people of the south coast of the SWAFR (Lullfitz *et al.*, 2017, 2020), in addition to a broader reading of the literature on Aboriginal Australians. Eucalypts are seminal in Aboriginal cosmology, and those of OCBILs feature prominently in matters sacred and profane (e.g. Bodkin & Robertson, 2012).

ADAPTATION TO SALINE SOILS (ONLY FLAT LANDS, SUCH AS IN THE INLAND MARGINS OF THE SWAFR AND GREATER CAPE FLORISTIC REGION)

Studies of tolerance to waterlogging, salinity and both in eucalypts have revealed significant variation among provenances within many of the 20 south-west species tested (van der Moezel *et al.*, 1991). Eight species survived waterlogging plus salinity, with the best survival percentages for individual provenances recorded at 94% (Salt River gum, *Eucalyptus sargentii* Maiden), 75% (*mauw/swamp yate*, *Eucalyptus occidentalis* Endl.), 50% (soak *yate*, *Eucalyptus aspratilis* L.A.S.Johnson & K.D.Hill), 44% (*swamp mallet*, *Eucalyptus spathulata* Hook.), 38% (*Eucalyptus halophila* D.J.Carr & S.G.M.Carr), 31% (salt salmon gum, *Eucalyptus salicola*), 20% (York gum, *E. loxophleba*) and 19% (Kondinin blackbutt, *Eucalyptus kondininensis* Maiden & Blakely). Among

20 northern species tested for salt plus waterlogging, the most tolerant were inland red box (*Eucalyptus intertexta* R.T.Baker), smooth-barked *coolabah* (*Eucalyptus victrix* L.A.S.Johnson & K.D.Hill), black ironbox (*Eucalyptus raveretiana* F.Muell.), kopi mallee (*Eucalyptus striaticalyx* W.Fitzg.) and forest red gum (*Eucalyptus tereticornis* Sm.). These data indicate independent evolution of adaptation to saline soils across many lineages in OCBILs.

Unlike species of *Acacia* Martius, which appear to have evolved in saline habitats ≤ 25 Mya (Bui *et al.*, 2014), the evolution of salt-tolerant eucalypts appears to be more recent. At least one series (*Rigentes* Brooker & Hopper), however, has speciated in south-eastern salt lake systems of south-west Australia (Brooker & Hopper, 1989). This indicates evolutionary adaptation and movement into salt lake habitats for long enough to diversify over 400 km along the south coast. DNA studies suggest that this has happened within the past 1 Myr (Thornhill *et al.*, 2019).

Another surprising discovery was the salt salmon gum (*Eucalyptus salicola* Brooker), long confused with the unrelated salmon gum (*Eucalyptus salmonophloia* F.Muell.), forming a large picturesque tree adjacent to salt lakes in south-west Australia and the adjacent arid zone (Brooker, 1988). A complex of ten species similar to *swamp mallet* (*E. spathulata*) represent two disparate groups that have also diverged in salt lake systems of the south-west (Nicolle & Brooker, 2005). The exceptionally salt-tolerant species *E. sargentii* occurs as two subspecies (*sargentii* and *onesia* D.Nicolle) differing in being either single-trunked trees or lignotuberous resprouting mallees, respectively (Nicolle, 2005). These eucalypts indicate that exploration of ancient salt lake systems forming OCBILs along old palaeodrainage lines clearly merits further examination. Moreover, the use of salt-tolerant eucalypts in reclamation of salinized landscapes has become a major activity in semi-arid landscapes in Australia and elsewhere.

OCBIL PREDICTIONS: CONSERVATION MANAGEMENT HYPOTHESES

A brief outline follows of some conservation management principles and hypotheses derived for eucalypts when considered through the lens of OCBIL theory (Hopper *et al.*, 2020).

OCBILS AS REFUGIA UNDER CLIMATE CHANGE

There is a need for studies addressing climate change impacts on eucalypts to address what is now known

about poor seed dispersal yet prolonged persistence over millions of years of OCBIL endemics. A recent study based on climate envelope modelling (González-Orozco *et al.*, 2016) hypothesized dramatic shifts in predicted geographical ranges for 657 eucalypt species in the period from 2014 to 2085: 'Our models predicted that by 2085, the current geographic range of 91% of the 657 eucalypt species will shrink by an average of 51%, with 2.4% of species predicted to become extinct because their climate space will disappear entirely.' (González-Orozco *et al.*, 2016: p. 1111). Moreover, 'approximately 90% of the current areas with concentrations of palaeo-endemism (that is, places with old evolutionary diversity) are predicted to disappear or shift their location' (González-Orozco *et al.*, 2016: p. 1110). The latter quotation alludes to many narrow-range OCBIL endemics, especially in the SWAFR. The models used to construct these predictions are too coarse to allow for what has clearly happened over considerable periods for many narrow-range endemic eucalypts, i.e. prolonged persistence in microrefugia (Hopper, 1979, 2009; Hopper & Gioia, 2004; Byrne, 2008; Byrne & Hopper, 2008; Keppel *et al.*, 2012). A focus on the microrefugia is needed to bring climate change modelling for eucalypts to more realistic scenarios of conservation implications. A recent example of assembling a 2-m-resolution digital elevation model for narrow-range endemics on inselbergs pioneers the scale at which compelling evidence might be marshalled (Ball *et al.*, 2020).

OCBIL RESERVES OF ALL SIZES HAVE CONSERVATION VALUE

The fact that some 10% of eucalypts are very narrow-range endemics (Fig. 3), with some known only from single populations or clones (Table 1), indicates that even the smallest of OCBIL reserves can have significant conservation value. This was a major point emergent from genetic studies of *E. caesia*, for example, from isolated granite outcrops in the wheatbelt of the SWAFR (Moran & Hopper, 1983; Byrne & Hopper, 2008; Bezemer *et al.*, 2019c).

ENHANCED RESILIENCE TO FRAGMENTATION

Evidence for this concerning eucalypts on OCBILs comes from genetic studies, establishing unexpectedly high genetic diversity in the smallest of populations (e.g. Bezemer *et al.*, 2019c). Population genetic studies also highlight the persistence in small fragments of native vegetation of species from lineages that appeared tens of millions of years ago (e.g. *E. curtisii*; Smith *et al.*, 2003).

BIODIVERSITY OFFSETS IN OCBILS ARE DEEPLY FLAWED

Irreplacibility is a key attribute of the sedentary biota of OCBILs. The notion, therefore, that an exchange could be made for development of one OCBIL for another does not hold. Again, the abundance of narrow-range endemics of eucalypts on OCBILs offers compelling evidence here (Fig. 3).

VULNERABILITY TO SOIL REMOVAL

Continuity of landscape for millions of years is an essential defining attribute of OCBILs. Bulldozing constitutes the major threat. Attempts at restoring and repairing OCBILs face formidable challenges, although success has been achieved after decades of research, with the resources of big mining companies or significant Government investment behind the venture (Hopper, 2009). As yet, little has been published specifically about narrow-range endemic eucalypts and OCBIL repair.

MINIMIZE GROUNDWATER EXTRACTION

Eucalypts are facultatively groundwater dependent, at least in mesic climates adjacent to or on OCBILs (Zolfaghar *et al.*, 2017). There is a significant risk, therefore, that groundwater depletion in shallow soils will place range-restricted eucalypts under water stress. Experiments comparing OCBIL endemics with species from adjacent YODFELs confirm this hypothesis (Poot *et al.*, 2012; Hamer *et al.*, 2016), at least regarding the granite outcrop endemic *E. caesia* compared with eight other SWAFR species of deeper soil. This trend is likely to be exacerbated by global warming.

UNCERTAIN ROLE OF FIRE

Fire is a common disturbance, whether initiated by lightning or by humans, important in the life history of eucalypts (Nicolle, 2006). It will kill adult plants if severe enough, although most species resprout from the basal or underground lignotuber and from vegetative buds beneath thick bark on trunks and branches. Prolific recruitment through seeds released by adult trees is another coping strategy. However, other disturbances have also been shown to be as important for similar behaviours as fire for some eucalypts: flooding regimes, windthrow from stormy winds, grazing by animals, deposition of dust and sand by strong winds, earth movements and landslides, to name a few (Turner, 2010; Bradshaw *et al.*, 2011; Newman, 2019).

Eucalypt biologists vary in their recognition of the importance of fire regimes. Some see them as so all pervasive that they argue that eucalypt responses to fire must have evolved as adaptations to cope (e.g. [Crisp *et al.*, 2011](#)). Others are more cautious, urging the need for research in specific circumstances and for each species of interest before it is assumed automatically that fire has been the singular and driving evolutionary force favouring traits that help plants cope with the disturbance rendered by fire ([Florence, 1996](#)).

Obviously, if all eucalypts are adapted to fire, then managers of wildfire and prescribed burning need not pay attention to when, how and why they burn or control fire. If fire is only one of many disturbance regimes that might have influenced the evolutionary adaptation of eucalypts, a need for better understanding and greater caution in fire management of eucalypts would be the wise course to avoid unexpected outcomes.

Although exceptional, some eucalypts succumb to fire more readily than some rainforest species ([Prior *et al.*, 2018](#)). Even resprouting mallees can be killed by two fires separated by a short interval of 1–3 years ([Noble & Diggle, 2013](#)). In contrast, tropical savanna eucalypts are fire tolerant and unresponsive to reductions in fire frequency and intensity ([Fensham *et al.*, 2020](#)). Coping with fire is an attribute of most species.

However, fire sensitivity occurs in 10% of eucalypts ([Nicolle, 2006](#)). These are called obligate seeders. Adults are routinely killed by fire and some other disturbances, meaning that regeneration is achieved only by the release of seed and subsequent germination. Most obligate seeders are found in the SWAFR (78 species). Nine are found in eastern Australia. Most obligate seeders are found in semi-arid south-west Australia, where they are known by *Noongar* names, such as *mallet*, *marrlak* or *marlock*, and *moort*. Much of this cereal-growing landscape is now relatively fire free owing to extensive agriculture ([Shedley *et al.*, 2018](#)). Obligate seeders are less at risk there, but they remain vulnerable in large conservation reserves subjected to increasing levels of prescribed burning by land managers ([Bradshaw *et al.*, 2018](#)). In Fitzgerald River National Park and nearby, for example, obligate seeders that are threatened by close fire intervals include *Eucalyptus brandiana* Hopper & McQuoid, *Eucalyptus mcquoidii* Brooker & Hopper and *Eucalyptus nutans* F.Muell.

Although much has been written about so-called fire-adapted eucalypts, few authors furnish evidence of genetic inheritance, function of traits in the presence of fire regimes vs. other disturbances, unequivocal natural selection in operation, and compelling phylogenetic evidence to establish evolutionary adaptation of traits such as resprouting from epicormics or lignotuberous

buds ([Bradshaw *et al.*, 2011](#)). There is a clear distinction between adaptations for fire and mechanisms for coping with fire. Compelling research remains elusive, as ably summarized by [Gill \(1997: p. 163\)](#):

Any interdependence between eucalypts and fires can occur only when there is a suitable meshing of life-cycle attributes, fire regimes and environmental characteristics. ... much more discovery must take place if we are to have a quantitative appreciation of the extent to which eucalypt species and fire regimes are independent [coping with fire, but not involving adaptation] or inter-dependent [fire adaptation in place] across the many environments and landscapes of terrestrial Australia.

RESTORE WITH LOCAL SEEDS OR CUTTINGS

The fine-scale genetic divergence among populations of some endemic eucalypts on OCBILs, such as *E. caesia*, necessitates very local seed collections for restoration ([Bezemer *et al.*, 2019c](#)). If this is not adhered to, the risk of outbreeding depression occurs.

PLANT TO LOCAL SOIL TYPE IN RESTORATION

This is another principle pertaining to the high fidelity to local soil type exhibited by OCBIL eucalypts. Although eucalypts are relatively easy to germinate and grow, long-term persistence in the wild requires recognition of local soil types occupied by OCBIL endemics.

AVOID FERTILIZING P-IMPOVERISHED SOILS

Lastly, the P-deficient soils of OCBILs succumb to extensive weed invasion if fertilized with superphosphate. Essentially, this practice converts OCBILs to YODFELs. As yet, experimental studies on the impacts of fertilization on endemic OCBIL eucalypts have not been conducted.

CONCLUSION

The hypothesis that eucalypts evolved out of OCBILs rather than out of volcanically enriched rainforests or their margins rests on several lines of evidence. Many early-branching lineages of the eucalypts today live on OCBILs rather than on rainforest margins (e.g. *E. curtisii*). If niche conservatism predominates in eucalypts, this points to origins on OCBILs. The fossil record of eucalypts might be misleading because it is biased towards young, fertile wetland landscapes, not OCBILs. Moreover, eucalypts have biological attributes

conforming to predictions of OCBIL hypotheses: (1) reduced seed dispersal; (2) 10% of eucalypts are local endemics and rare, with the majority found on OCBILs; (3) the greatest species richness of eucalypts and high population genetic divergence is found in the OCBIL landscapes of Australia's two Global Biodiversity Hotspots; (4) clonality is common and great age achieved; (5) growth is slow in many species; (6) the James effect is evident in some species; and (7) eucalypts exhibit reduced hybridization on OCBILs compared with younger, more fertile landscapes. Thus, this review of eucalypts viewed as evolving out of the OCBILs helps in understanding the group from several new perspectives. Some of the biological hypotheses of OCBIL theory have been investigated extensively in eucalypts. Others have yet to be undertaken. Sufficient is known, however, to accept the out of OCBILs hypothesis as one meriting careful consideration. I would suggest that viewing what is known about other plant genera found across the world as OCBIL endemics also has merit.

There are profound management implications arising from a perspective of eucalypts as originating in OCBIL landscapes. Dire predictions for eucalypt extinction under climate change might not be met if OCBILs are given priority in conservation programmes. Small reserves might play a larger role in conserving eucalypts than previously forecast. Resilience to fragmentation effects might be evident in many eucalypts of OCBILs, and biodiversity offset approaches to conservation should be regarded with considerable caution. Soil disturbance needs careful management, as does the application of prescribed burning on OCBILs. There are significant implications concerning groundwater extraction, seed sourcing for restoration and fertilizing impoverished OCBIL soils. Further research might elucidate these processes better and point the way to improved conservation of these iconic Australian trees and mallees.

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