

## EDITORIAL

# OCBIL theory: a new science for old ecosystems

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This paper is an introduction to the special issue of the *Biological Journal of the Linnean Society* entitled *OCBIL theory: a new science for old ecosystems*. Firstly, we elaborate on the origins and development of OCBIL theory, which argues that landscape age, climatic buffering and soil fertility are key environmental dimensions shaping ecological and evolutionary processes across different scales. We then consider the 21 contributions made in this special issue in terms of cutting edge advances in the Southern Hemisphere that test, explore and apply aspects of OCBIL theory at the end of its first decade of formal publication. More attempts at refutation are urged, as untested aspects remain controversial. Lastly, a concluding discussion is offered on promising new lines of enquiry to develop the theory further and ensure its global application to pressing conservation issues facing biological and cultural diversity. Although OCBILs are absent or rare in much of the postglacial and periglacial Northern Hemisphere, we demonstrate, in south-west Europe and North America, starting with California, that they are likely to be found, thus extending the implications and applications of OCBIL theory in new directions. We also propose that, in many ways, Noongar Aboriginal cosmology from south-west Australia has developed sophisticated insights about ancient uplands that are precursors to key ideas in OCBIL theory.

ADDITIONAL KEYWORDS: *campo rupestre* – First Nations – *fynbos* – inselbergs – *kwongkan* – OCBIL – YODFEL.

## INTRODUCTION

Latitudinal gradients in species diversity are probably the most obvious of global ecological and biogeographical patterns. The so-called ‘latitudinal diversity gradient’ (LDG) has stimulated research across generations of biologists; however, after more than half a century since publication of the key paper by Pianka (1966), we still know embarrassingly little about the drivers of diversity. A plethora of ecological and evolutionary factors have been invoked to explain the LDG (Schemske & Mittelbach, 2017), but key factors shaping species richness, endemism and functional traits have been largely overlooked. Although the validity of the LDG remains undisputed,

centres of diversity and endemism worldwide occur in sites that do not precisely conform to its predictions. Two emblematic examples include the temperate floras of the Greater Cape Floristic Region and the Southwest Australian Floristic Region (SWAFR). These ‘anomalies’ in the LDG strongly suggest that ancillary environmental drivers are needed to explain ecological patterns and mechanisms at population- and community-levels, as well as evolution at both the micro- and macro-evolutionary scales.

The development of OCBIL (‘old climatically-buffered infertile landscape’) theory over the past decade arose from initial recognition that subdued uplands within 500 km of ancient coastlines in the Southern Hemisphere were unusually rich in species and local endemics of sedentary organisms (Hopper, 2009; Hopper *et al.*, 2016). OCBIL theory, a decade

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on, is based on multiple hypotheses predicting patterns of evolution, ecology, cultural diversity and conservation that are at variance, to some extent, from mainstream theory in these disciplines, and therefore remain controversial (Mucina & Wardell-Johnson, 2011). Yet increasing evidence highlights that prolonged persistence of landscapes with equally prolonged oceanic climatic-buffering has offered opportunities for sedentary organisms to persist and evolve in remarkable ways. As is evident in this special issue, OCBILs appear to be centres for major ongoing biological and anthropological discovery.

In this introduction to the special issue on *OCBIL theory: a new science for old ecosystems*, we review the significance and major findings of the 21 contributions (authors' names are given in bold). We conclude with some pointers to the next phase of research on these remarkable, overlooked and under-studied landscapes.

## ORIGINS AND DEVELOPMENT OF OCBIL THEORY

First Nations, ecologists, evolutionary biologists and anthropologists have long observed unusual biological and cultural patterns associated with OCBILs. This body of work has translated ultimately into cosmologies embracing appropriate behaviours for persistence in or near OCBILs where cultures have endured long enough for humans to begin to understand how they function (see below). Settler cultures, however, have a record of invasive destruction of OCBILs, trying unsuccessfully to mould these ancient landscapes and their First Nations into supporters of ways of living developed on young, often-disturbed fertile landscapes ['YODFELS' (Hopper, 2009)].

The concept of OCBILs crystallized after decades of research on the conservation biology of threatened plants in the SWAFR. It was noticed that the subdued uplands of this region, in the form of granitic and quartzitic outcrops, lateritic mesas and high sandplains, usually within a few hundred kilometres of present-day coastlines, had unusually high species richness and concentrations of threatened local endemic plants (Hopper *et al.*, 1990). In contrast, lowlands such as fertile alluvial floodplains and coastal dunes, now recognized as YODFELS, were comparatively species-poor in such plants. Upland floras exhibited a range of patterns and processes that were unexpected in the context of mainstream ecological, evolutionary and conservation theory. For example, limited seed dispersal was evident across OCBILs. Dramatic change in species communities occurred over short distances, rather than a few species dominating over vast distances. Shrublands (known locally as *kwongan* in the SWAFR) were the dominant

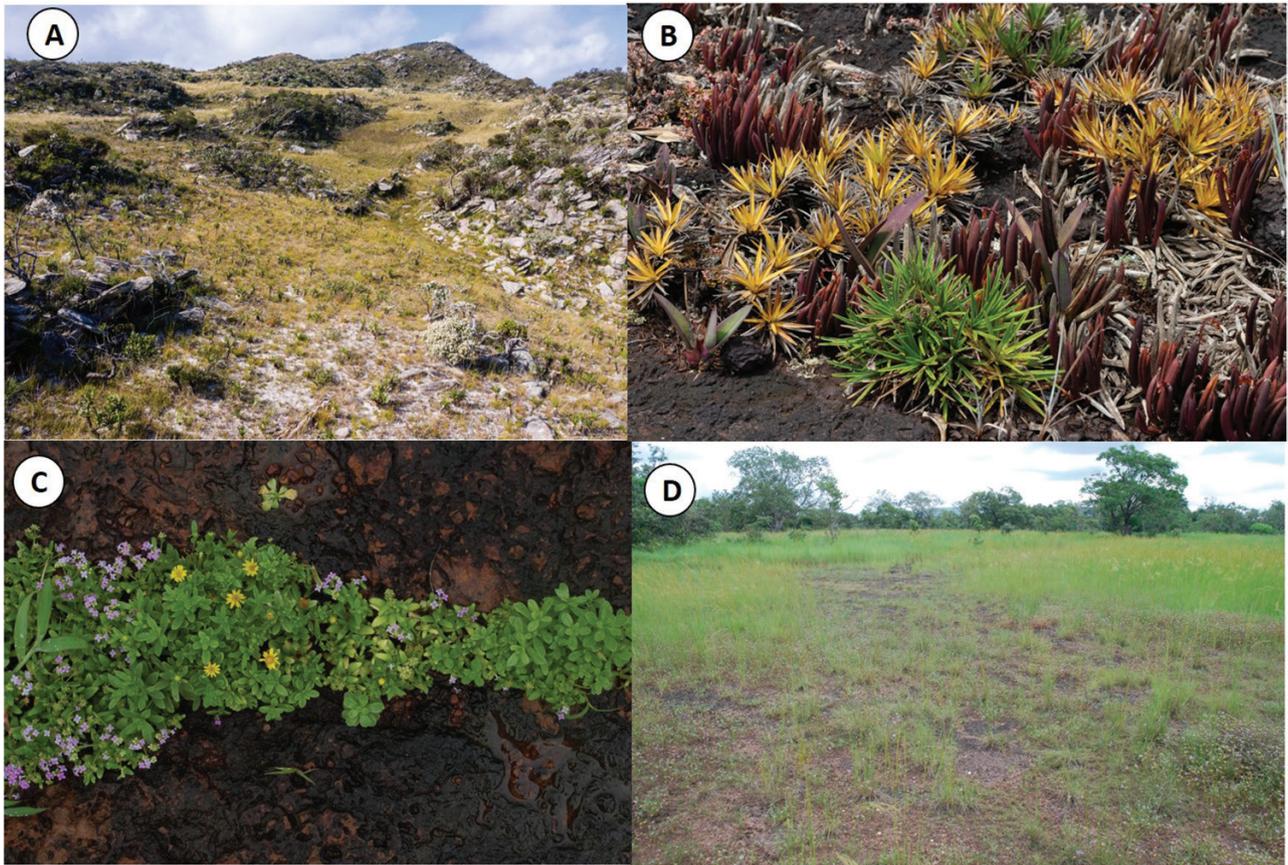
vegetation on many uplands. Overstorey forests of just a few species of eucalypts were another feature in higher rainfall regions. Dramatic conversion to swathes of invasive exotics occurred when the OCBIL uplands were cleared of native topsoil and fertilizers applied. Exceptional numbers of bird-pollinated plants were found in the uplands dominated by a small number of plant families.

Attempts to grow many native plants from the uplands through conventional nursery practice failed. Similarly, Aboriginal cultures did not respond favourably to attempts to convert their methods of caring for the land to those of European agricultural practices. Such unusual patterns and processes were beyond the experience of the colonial nations. The response to European agriculture was nearly always destructive of both native biodiversity and First Nations' cultural traditions.

OCBIL theory is an attempt to rethink the ecology and evolution of sedentary biota on these remarkable ancient uplands and, at least in SWAFR, learn from the cultural approaches of Aboriginal people that ultimately may develop sustainable ways of contemporary living on or near OCBILs. To formulate hypotheses, the early work on OCBIL theory focussed on three regions: the *kwongan* vegetation in SWAFR, the *fyntos* in South Africa's Greater Cape Floristic Region, and the Pantepui Neotropical uplands of South America (Hopper, 2009). Subsequently, OCBILs have been recognized in a third of the world's Global Biodiversity Hotspots (Hopper *et al.*, 2016). The list of global regions is being further expanded (Hopper *et al.*, 2021b; Fig. 1). In particular, recent years have seen an almost exponential increase in the literature on *campo rupestre* vegetation as an example of where OCBIL theory has provided inspiration to guide contemporary research. The potential for similar research has emerged in the Northern Hemisphere (see below), especially Mediterranean California, the North American Eastern Coastal Plain, and other Northern Hemisphere OCBILs that are yet to be explored (Klein *et al.*, 2005; Porembski *et al.*, 2016; Fig. 1).

## CONTRIBUTIONS IN THE SPECIAL ISSUE

A little more than a decade ago, Hopper (2009) offered a new scientific path to understanding ancient landscape mosaics, and provided seven hypotheses to enable and encourage others to test them. This special issue illustrates the advancement of OCBIL theory in the last half-decade, including the addition of five new hypotheses and seven conservation management postulates that are the logical outcomes of a more mature landscape theory (Hopper *et al.*, 2016). Contributions to the special issue illustrate the



**Figure 1.** OCBILs are distributed worldwide, but are concentrated in the Southern Hemisphere. A, an example of a recently identified OCBIL is the *campo rupestre*, a montane megadiverse vegetation mosaic in South America. Granitic outcrops (inselbergs) and ironstone outcrops (ferricretes) occur worldwide (Klein *et al.*, 2005; Porembski *et al.*, 2016) where OCBILs potentially occur. B, endemic orchids and desiccation-tolerant *Vellozia* in south-eastern Brazil. C, *Spermacoce articularis* and *Senecio* in the Western Ghats. D, ferricretes near Bondoukou, Ivory Coast. Photos: R. Solar (A), F.A.O. Silveira (B), A. Watve (C) and S. Porembski (D).

validity and far broader reach of OCBIL science than when Hopper (2009) first proposed his deep synthesis of the evolutionary history of Western Australian landscapes. This collection of 21 articles represents a more comprehensive assessment of OCBIL theory than when it was reviewed five years ago (Hopper *et al.*, 2016). It is an advancement of OCBIL theory for two particular reasons. First, it contains papers explicitly testing the predictions of OCBIL theory in areas beyond the original formulation of OCBILs (e.g. Arruda *et al.*, 2021; Monteiro *et al.*, 2021), including an extensive review of OCBILs in New Caledonia (Pillon *et al.*, 2021). Second, it expands the range of organisms that can be studied under the scope of the theory (e.g. Magalhães *et al.*, 2021), suggesting comparative studies on the flora and fauna using an OCBIL framework may prove useful for understanding the ecology and evolution of sedentary biota in ancient, nutrient-poor landscapes (see also Kok *et al.*, 2017; Fouquet *et al.*, 2021).

Hopper *et al.* (2021b) review recent studies addressing the predictions of OCBIL theory and find that most hypotheses are supported from empirical data; however, studies are biased towards the SWAFLR and the *campo rupestre*. Support for some hypotheses is still controversial, pointing out the need for testing the predictions using different approaches and in different biogeographical regions. Hopper *et al.* (2021b) also provide mechanistic explanations for the predictive hypotheses of OCBIL theory and examples of ways of testing them through direct and indirect evidence.

An accurate testing of hypotheses is scale-dependent, meaning that definitive proof or disproof of OCBIL hypotheses must tackle the problem at the right level of specificity. Cortez *et al.* (2021) predict that an association exists between ancient seed plant lineages and OCBILs if selected environmental characteristics of OCBILs are both significantly and consistently correlated with older communities. These authors gathered environmental, phylogenetic and geographic

distribution data for the biodiverse floras of the *campo rupestre*, Cape Floristic Region (CFR) of South Africa, and the Southwest Australia Floristic Region at half degree latitude  $\times$  longitude scale. The authors have been able to confirm their prediction for only one of the three OCBIL-rich regions, the CFR. However, because of habitat heterogeneity, the correct identification of OCBILs across the landscape is better done at a very small scale. Therefore, **Cortez *et al.*'s (2021)** lack of support for the OCBIL prediction of ancient lineages in a global context may simply be a function of attempting to answer a question on the wrong scale.

Another major contribution to the special issue is the authoritative review by **Pillon *et al.* (2021)**. The authors present extensive geoeological, pedological and climatic evidence suggesting how New Caledonia might qualify as a classic OCBIL, and they scrutinize the predictions of OCBIL theory for the island. **Pillon *et al.* (2021)** find support for many hypotheses of OCBIL theory, including a high rate of micro-endemism, accumulation of relict lineages, a high incidence of dioecy, myrmecochory and nutritional specializations in plants. They also explore some anthropological aspects of New Caledonian ecosystems, summarizing evidence that humans developed specific horticultural practices in the ultramafic landscapes of New Caledonia.

Significant advances in OCBIL theory have been made in Brazil and Western Australia that illustrate the importance of embracing a geological timescale and concomitant evolutionary history in understanding the biogeographic patterns of OCBIL megadiversity. **Gosper *et al.* (2021b)** offer a detailed, meticulous demonstration of what is often only intuited when enough time has been spent in the field—that is, that rare (or the human/conservation construct, 'listed') species are neither randomly nor uniformly distributed—a thorough demonstration of a fundamental tenant of OCBIL theory. Instead, rarities are vastly disproportionately restricted to OCBILs' long exposed ancient geographic features. Using surface geology to define OCBILs, YODFELs and intermediate landscapes, the authors test a suite of predictions about the role of landscape history in shaping the distribution of Western Australia's rare flora. Not only are the rarities concentrated on ancient landforms, but also they are largely represented as narrow range endemics. Perhaps **Gosper *et al.*'s (2021b)** most significant contribution is setting the groundwork for fully informed stewardship protocols for preventing plant extinctions in one of the world's most biodiverse botanical hotspots.

**Gosper *et al.* (2021a)** further explore the loss of Western Australia's rich flora by examining the likelihood of exposure to various threats, such as land clearing, mining, pathogens, etc., and the susceptibility to them, in both OCBILs and YODFELs. Methodically

examining seven predictions about threat exposure and susceptibility, the authors find ample support that OCBIL flora are more susceptible than YODFEL flora to pathogens and to extremes of contemporary fire management practices, and that the two floras face different degrees of exposure to land clearing, mining and fragmentation. The argument that time's arrow should play a significant role in the formulation of conservation management is conclusively made.

OCBIL theory is still in its infancy, and as such, new hypotheses are emerging across the spectrum. Only a few years after the original publication, OCBILs were expanded from landscapes to seascapes [old, climatically buffered infertile seascapes (**Langlois *et al.*, 2012**)], and additional hypotheses that fleshed out the theory were added (e.g. **Hopper, 2018**). A paper in this special issue adds yet another. The genus *Eucalyptus* is practically synonymous with Australia in popular Western culture, and in the botanical world, it is both revered for its evolutionary creativity and success, and despised for its invasiveness potential. Yet it is also a keystone genus of OCBILs in every way imaginable, from the 'ultimate self' to the extreme endemic, from restricted dispersal to a singular reliance of some species on bird pollination, from Noongar totem to keystone species, and so on. **Hopper (2021)** turns conventional thinking about the evolution of the genus on its head, offering strong evidence that *Eucalyptus* is not a remnant of the former fabled Gondwanan rainforests that covered much of Australia in the late Cretaceous, but instead, that the genus likely evolved on ancient contemporaneous landscapes—OCBILs—and then spread across the continent and beyond.

**Robins *et al.* (2021a)** test the OCBIL hypothesis that highly differentiated intraspecific population systems of *Banksia seminuda* on OCBILs should contrast with more limited differentiation on YODFELs. As expected, genomic analyses revealed strong structuring within *B. seminuda*, with high differentiation across narrow geographic scales among OCBIL populations vs. lower differentiation across much larger geographic scales among YODFEL populations. Genomic and morphological divergence between OCBIL and YODFEL populations provide comprehensive quantitative evidence to support segregation into two subspecies.

The *campo rupestre* vegetation provides a second Southern Hemisphere template to examine the validity and universality of OCBIL theory, and nine contributions of this special issue rise to the challenge. **Miola *et al.* (2021)** revisit the geographical distribution of the *campo rupestre* in South America and show that, rather than being restricted to the Espinhaço Range as previously thought, *campo rupestre* communities are distributed as isolated and naturally fragmented sky islands in Central and

Eastern Brazil, eastern Bolivia and in the Guyana Shield. Significant areas across the Amazon, Cerrado, Atlantic Forest, Caatinga and Pantanal suggest that OCBILs are more widespread across Neotropical ecosystems than suggested by previous assessments (Silveira *et al.*, 2020a), and represent excellent models for the study of the ecology and evolution of the Neotropical biota. Miola *et al.* (2021) propose research avenues to fill persistent knowledge gaps in the *campo rupestre*, with the ultimate goal of improving biological conservation.

The Pantepui in the Guayana Highlands was originally identified as a classical OCBIL region (Hopper, 2009). These table mountains ('tepui') are characterized as cradles of diversity, richness and endemism for an ancient flora (Barbosa-Silva *et al.*, 2020) and fauna (Fouquet *et al.*, 2021). Summits of the tepuis represent the northernmost distribution of *campo rupestre* (Barbosa-Silva *et al.*, 2020; Miola *et al.*, 2021). Campos *et al.* (2021) evaluated the effect of fine-scale geoenvironmental gradients on phylogenetic communities in the iconic Roraima table mountain. An astonishing 40% of the flora is endemic to the Guayana Highlands. However, more importantly, Campos *et al.* (2021) find that soil texture explained most of the variation in phylogenetic metrics across the three microhabitats. This result may be related to the long-term geological history of tepuis and the accumulation of lineages over tens of millions years.

Studies on diversification in *campo rupestre* are rare; however, the recent compilation by Vasconcelos *et al.* (2020) challenges the idea that *campo rupestre* is rich in ancient lineages. Rapini *et al.* (2021) explore the 'escape-to-radiate' model for explaining the high plant diversity and endemism in *campo rupestre*. They modelled the palaeo-range distribution of 1123 endemic plant species from the Espinhaço Range and revealed the virtually constant suitable area for *campo rupestre* across the last glacial cycle. Rapini *et al.* (2021) challenge the great importance placed on Pleistocene climatic oscillations in the diversification in *campo rupestre* and offer an alternative explanation that emphasizes niche shifts.

Perhaps because research has focused on plant life in *campo rupestre*, studies on animal ecology and evolution are still scarce. Two studies in this special issue focused on the ecology and diversification of animal life. Neves *et al.* (2021) evaluate how habitat specialization of species contributes to metacommunity nestedness in insect groups with different dispersal capacities in a vegetation mosaic characterized by OCBILs (*campo rupestre*) and YODFELs (naturally fragmented mountaintop forest islands). The metacommunity was nested in structure, with habitat generalist species contributing more to nestedness than habitat specialists. Neves *et al.* (2021) reveal that

species sorting (for habitat specialists) and mass effects (for habitat generalists) are concurrent processes in the mountaintop forest-grassland mosaic, thus opening the way to improve our ability to predict and manage how land use and climate change will affect mosaics characterized by fine-scale OCBIL-YODFEL transitions. Magalhães *et al.* (2021) present a bold study that used two endemic leaf frog species specifically to test Hopper's (2018) 'reduced hybridization hypothesis', which was originally formulated for OCBIL plants. Hopper (2018) proposed that, due to reduced extinction rates on OCBILs, rates of natural hybridization, introgression and hybrid speciation are reduced due to heightened reproductive incompatibilities when compared with such evolutionary processes among congeners on YODFELs. Using molecular data and ecological niche modelling, Magalhães *et al.* (2021) found haplotype sharing and/or lack of differentiation in four nuclear fragments, one of them associated with introgression. Coalescent models support introgressive hybridization unidirectionally from *Pithecopus megacephalus* to *Pithecopus ayeaye*, occurring ~300 Kya, thus contradicting the expectation of reduced hybridization. The reduced hybridization hypothesis needs to be further investigated because the results of Magalhães *et al.* (2021) suggest that it may have unrealistic assumptions, at least for some animals. For plants, recent work upholds the hypothesis (Bradbury *et al.*, 2021; Hopper *et al.*, 2021b; Robins *et al.*, 2021a, 2021b).

Arruda *et al.* (2021) explore the hypothesis that organisms restricted to OCBILs exhibit reduced or limited dispersibility. Working in the *campo rupestre* grasslands of south-eastern Brazil for over a year, the authors experimentally examined seed rain across the complex mosaic of quartzite outcrops and nutrient-poor grasslands intermixed with sclerophyllous trees. In addition to confirming limited dispersal across the flora of this region of the *campo rupestre*, Arruda *et al.* (2021) find significant differences between the seed rain in disturbed and undisturbed plots, a result that may explain in part the comparatively poor recovery of *campo rupestre* communities after soil removal (Nerlekar & Veldman, 2020).

Monteiro *et al.* (2021) test the prediction of OCBIL theory for the prevalence of long distance pollinators ensuring cross-pollination (Hopper, 2009). Using different sources of information, their study is the most comprehensive synthesis on pollination systems in *campo rupestre*. Among the 636 plant species studied, Monteiro *et al.* (2021) found that bee pollination was dominant (56%), followed by wind and hummingbird. Large bee and hummingbird long-distance pollination systems remained unchanged with elevation and were more frequent in the highly isolated rocky outcrops, thus providing firm support to OCBIL theory.

OCBILs are characterized by stressful environmental conditions, which suggests that native species have evolved adaptations to cope with extremely impoverished soils and seasonality. **Caminha-Paiva *et al.* (2021)** conducted a functional trait analysis on four different community types of *campo rupestre* vegetation from four different ironstone and quartzite soil/rock types. Stem, leaf and plant architectural functional traits were determined to be tightly correlated at the individual and plot levels of analysis. **Caminha-Paiva *et al.* (2021)** demonstrate that plant species appear to exhibit resource conservation strategies in *campo rupestre*, adding additional evidence in support of OCBIL hypotheses that OCBIL taxa have evolved specialized traits that facilitate survival in nutrient-poor soils. In line with these results, **Tameirão *et al.* (2021)** find that OCBIL plant species have a high degree of stress tolerance and virtually no ruderalism. Despite a major edaphic filter selecting stress tolerance, fine-scale microhabitat variability represented by soil parameters related to fertility (i.e. P, Ca, Mg) and water retention capacity (i.e. clay content) was associated with subtle variation in ecological strategies and functional traits of species in the ironstone *campo rupestre*, probably explaining species coexistence. In Western Australia, **Ottaviani & Marcantonio (2021)** examined the functional ecology of granite outcrop plants along the stark aridity gradient that occurs in the region. They find that plants display more acquisitive and variable trait values with increasing precipitation seasonality, and argue that these patterns are likely to be associated with the long-term effect of the stable and predictable precipitation regime in the old SWAFR that may have fine-tuned plant water use strategies to maximize water acquisition during the most favourable season.

Geographical gradients are to be expected at the scale in which OCBILs are most common. **de Paula *et al.* (2021)** offer compelling research on the extremophilic mat vegetation communities of 24 remarkable ‘sugar loafs’ of south-eastern Brazil. These inselbergs—ancient and paradigmatic infertile habitats of solid rock, little soil and strong environmental gradients—support highly specialized communities, none more novel than the extreme mat communities that sprawl across barren rock. **de Paula *et al.* (2021)** demonstrate a coast-to-inland gradient (as might be expected), and that climate controls a large fraction of the beta diversity, despite much it remaining unexplained. Another coast-to-inland gradient is explored by **Hopper *et al.* (2021a)**. Working in a quite remote and far less explored region of Western Australia, the authors plumbed a unique 40+ year dataset of plant distribution across the SWAFR’s OCBILs to determine whether floristic patterns on 89 inselbergs conformed to OCBIL predictions. Indeed, a trimmed dataset

confirmed (among other things) that rare species were abundant, hybrids were rare and that there was a decrease in species richness from coast-to-inland for most plant life forms.

An emerging paradigm of OCBIL theory is the intricate role of humans and human culture in the characterization of OCBILs. **Lullfitz *et al.* (2020)** exemplify the insightful exploration of cultural plants, their geographic distributions, and the genetics of plant cultivation in the mosaic landscape of Western Australia’s OCBILs and YODFELs. They focus on the plant genus *Platysace* (Apiaceae) which is not particularly showy nor memorable to the average botanist. However, to the Noongar traditional owners, certain species of this tuber-producing group are to this day an essential food crop that could not be more important. **Lullfitz *et al.* (2020, 2021a, 2021b)** exemplify the vanguard of the renewed field of ethnobotany, with the result of better science and long overdue cultural respect.

The application of OCBIL theory to human cultural adaptations has been mooted (**Hopper *et al.*, 2016**), but not explored in any detail until recently. **Lullfitz *et al.* (2021a)** used oral history interviews and multivariate statistical analysis to determine the traditional ecological knowledge of Noongar families regarding use of, and reverence for, OCBIL granite uplands compared with YODFEL creekline lowlands. Patterns of human disturbance in these landscapes aligned closely with OCBIL theory predictions and maximized biodiversity conservation. Camping, burning, travelling through country and hunting were, and are, primarily YODFEL rather than OCBIL activities. Noongar activities usually avoid OCBIL disturbance. Although not involving explicit consideration, these behaviours ensured that the rich concentrations of narrow endemics with complex biology atop OCBILs remained intact. Further research of First Nations’ responses to OCBILs and YODFELs is recommended by the authors.

## FUTURE DIRECTIONS

OCBIL theory proposes a set of hypotheses across different levels of ecological and evolutionary scales (reviewed in **Hopper *et al.*, 2021b**), so testing the validity of the theory will only be achieved through independent tests across taxa and biogeographic regions. The papers in this special issue have tested the predictions of OCBIL theory; however, the studies were concentrated in the SWAFR and the *campo rupestre*. Some papers provided empirical support for some hypotheses, while others have not. Further comparisons among biogeographic regions are desirable to develop the OCBIL theory into a more robust, quantitative and generalized testable framework.

Ecology, biogeography and evolution all have historical roots in the Northern Hemisphere, which is largely dominated by YODFELs (Hopper, 2009; Eicchorn *et al.*, 2020). Unsurprisingly, such legacies of colonial relations have resulted in misunderstandings and a lack of scientific appreciation of Southern Hemisphere science and scientists, including the ecology and conservation of OCBILs, with unintended detrimental policies for these ecosystems (e.g. Silveira *et al.*, 2020b). The ultimate goal of OCBIL theory is to call attention to the uncritical extrapolation of scientific practice and policy developed in YODFELs to understand, manage and conserve biodiversity in OCBILs. OCBIL theory calls for the development of conservation strategies tailored to ancient, nutrient-poor ecosystems. One example is the fast change in the course of conservation in *campo rupestre*. Five years ago, this ecosystem was barely known to the scientific community. However, inspired by the tenets of OCBIL theory, a review on the ecology and evolution of plant life in *campo rupestre* (Silveira *et al.*, 2016) triggered an extraordinary interest in this ecosystem (Miola *et al.*, 2021; fig. 1). A positive consequence of increasing awareness of *campo rupestre* is its recent inclusion in the IUCN Global Ecosystem Typology (Keith *et al.*, 2021).

In the SWAFR, McQuoid (2014) offered an example of the application of OCBIL theory to landscape restoration in a very practical way. He examined the SWAFR's wheatbelt woodlands as compromised ecosystems in need of restoration, using the analogy of restoring abandoned cars, in terms of character, components and function. OCBIL theory provides the framework for understanding function of these woodlands. Thus, quite different behaviours are expected from eucalypts endemic to YODFEL alluvial flats, such as the freely seeding and self-recruiting *Eucalyptus kondinensis* and *Eucalyptus loxophleba*, compared with OCBIL upland endemics, such as *Eucalyptus caesia*, in need of very special circumstances to recover from disturbances (Bezemer *et al.*, 2019). Also, a strong reliance on clonality and ancient hybridization for persistence on OCBILs continues to be revealed in contemporary eucalypt studies (Bradbury *et al.*, 2021; Hopper, 2021).

Because of their localized and often insular occurrence embedded in a matrix of YODFELs, investigating OCBILs at a fine geophysical scale is essential (Fig. 4). Exciting developments in recent species distribution modelling research (Tomlinson *et al.*, 2019; Ball *et al.*, 2020) now offer the potential to work at this fine scale and therefore devise experiments aimed at rigorous future testing of OCBIL hypotheses.

#### CANDIDATES FOR NORTHERN HEMISPHERE OCBILS

Since the original publication of OCBIL theory (Hopper, 2009), additional geographies and ecosystems have

been proposed that bear most, if not all, of the signature characteristics of OCBILs. Indeed, as researchers look deeper into Earth's history, particularly in regions recognized as biodiversity hotspots (Roberts *et al.*, 2002; Mittermeier *et al.*, 2004, 2011; Williams *et al.*, 2011), additional candidates for testing OCBIL hypotheses have rapidly been identified (see, for example, Silveira *et al.*, 2016). Although some areas in the north may not exactly fit in the extremes of soil infertility, climatic buffering and geological antiquity, it is very likely more OCBILs will emerge, even in the most unlikely of places, e.g. Northern Hemisphere hotspots in glaciated landscapes. Thus, novel areas may be recognized in the multivariate space of the OCBIL-YODFEL continuum (see Hopper *et al.*, 2016; fig. 2).

The extensive glaciation in the mid and high latitudes during the Quaternary is well documented. In the Southern Hemisphere, significant glaciation began in the eastern Antarctic and then southern South America during the late Oligocene (c. 35 Mya), which was followed by mountain glaciation in the mid latitudes for both hemispheres (Ehlers *et al.*, 2017). Glaciation in the Northern Hemisphere began later and was less expansive initially; however, ice sheets increased significantly at the start of the Quaternary. Glaciers increased in frequency and scale throughout the rest of the Cenozoic, with extremely high levels of glacial extent in the Middle-Late Pleistocene. Ehlers *et al.* (2017: p. 79) concluded that, "based on the distribution of land mass in higher latitude land mass, worldwide glaciation is in effect a northern-hemispheric phenomenon."

Where to start and what do we look for in the North? Likely answers come from biodiversity hotspots (Myers, 2000; Mittermeier *et al.*, 2004, 2011) with modulated climates that are also rich in palaeoendemics (Stebbins & Major, 1965; Harrison & Noss, 2017; Brown *et al.*, 2020). Thus the California Floristic Province (CFP) and the Mediterranean Basin—two Mediterranean biomes—are prime candidates for recognition as additional OCBILs (Rundel *et al.*, 2016). Supporting evidence comes from Valiente-Banuet *et al.* (2006), who argue that a significant number of ancient lineages from the Palaeogene and Neogene persist today in Mediterranean biomes due to the facultative (nurse) effects of more modern (Quaternary) species. With respect to the latter, Molina-Venegas *et al.* (2016) analysed the Baetic-Rifan biodiversity hotspot of the southern Iberian Peninsula and northern Morocco to reveal that within this long-climatically buffered region, palaeoendemics are mostly clustered in the south-western tip of Europe and the north-western tip of Africa, where increased water availability is key to their persistence. Neoendemism (recently arisen endemism) is pronounced towards the eastern drier margins of this hotspot in places such as Cabo de Gata National Park (Fig. 2), just as predicted



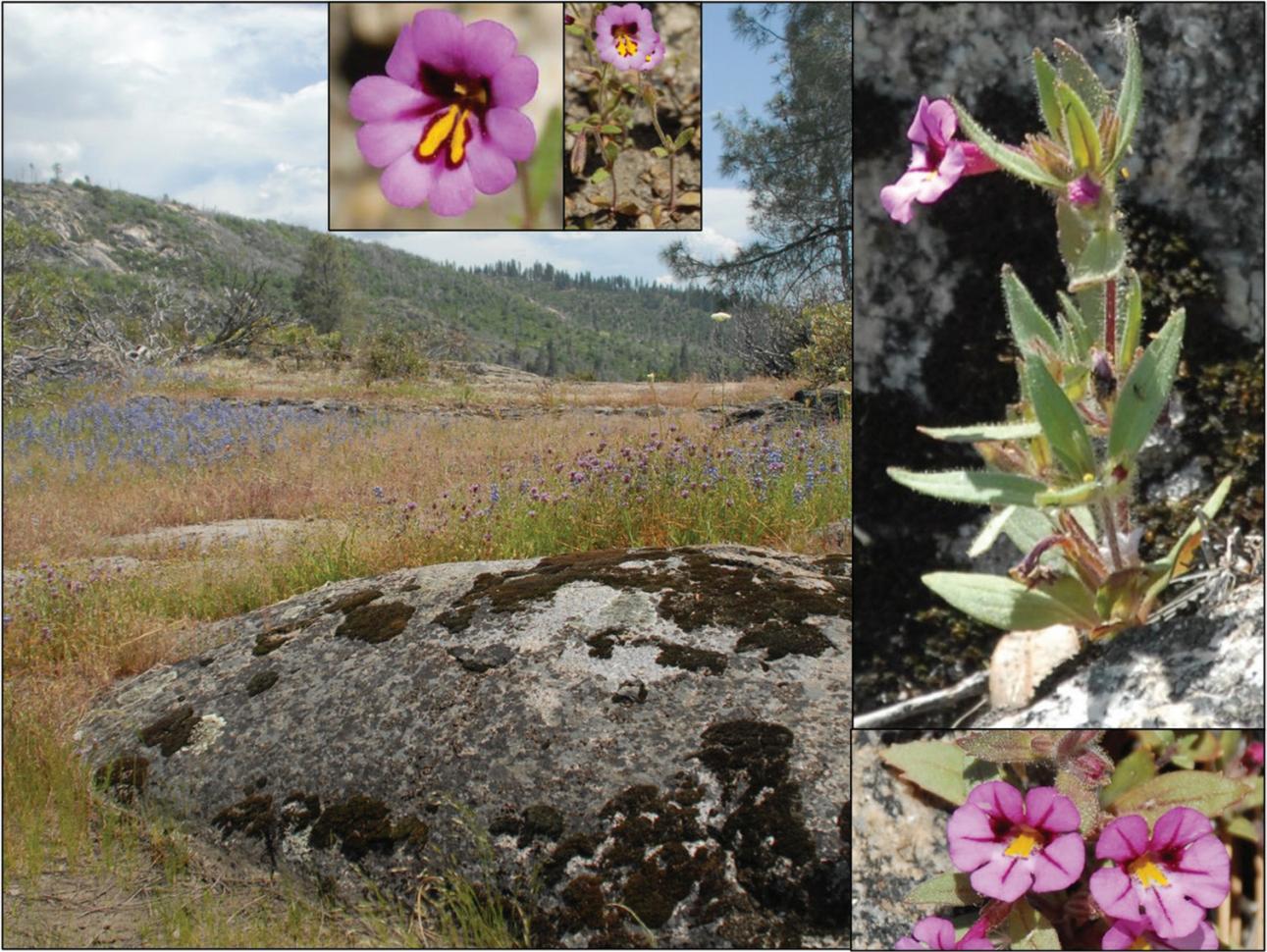
**Figure 2.** A, C, *Helianthemum alypoides* (south-east Spain in Cabo de Gata National Park), a narrow range neoendemic from the potential OCBIL Baetic-Rifan biodiversity hotspot centred on the Strait of Gibraltar. B, flowers of *Helianthemum almeriense* (left), a hybrid (centre) and *H. alypoides* (right), highlighting the evolutionary dynamism of this centre of neoendemism on the semi-arid margins of the biodiversity hotspot. Photos: S.D. Hopper.

from the Semiarid Cradle Hypothesis of OCBIL theory (Hopper, 2009; Hopper *et al.*, 2016). Thus the region around the Strait of Gibraltar may be a place within this expansive biodiversity hotspot rife with OCBILs, but it awaits further investigation. More generally, research on southern European glacial refugia (Feliner, 2011) points to several potential OCBILs on the Iberian, Balkan and Italian peninsulas characterised by persistent high species richness and endemism, relatively stable Quaternary climates, complex microrefugia and limited dispersal capabilities.

#### OCBILS IN NORTH AMERICA

With respect to the other Northern Hemisphere Mediterranean-type biodiversity hotspots that are

likely to be rich in OCBILs, the CFP may seem an unlikely place to look. However, recent research on a topographic signature of life (Dietrich & Perron, 2006) using new methods to connect lithology with vegetation, suggests that some of the granite landscapes of the CFP may indeed represent OCBILs. Granite rocks have been determined to have a median phosphorus (P) content of 436 ppm, which is considered significantly lower than other common rocks, particularly those that are iron-rich such as andesite with a median P concentration of 1000 ppm. Importantly, within-rock type variation can be nearly as large (Porder & Ramachandran, 2012; Porder, 2014), providing an important starting point to examine how microsite differences (e.g. variable substrate P levels) can lead to vast differences in landscape evolution.



**Figure 3.** Wildflowers and granite bornhardts, potential OCBIL country, near Hetch Hetchy in Yosemite National Park, California, with two local endemic annuals, *Erythranthe filicaulis* (top centre) and the recently described *Diplacus graniticola* (right column), from this site. Photos: S.D. Hopper.

Granite rock comprises roughly 20% of California's land (Graham & O'Geen, 2010), with the granitic batholiths of the central and southern Sierra Nevada making a significant contribution to this percentage (Fig. 3). Additional granites in California are found in various locations across the state, with the granite rocks of the Peninsular Ranges in southern California and Baja California's spine dominated by tonalite (quartz diorite) (Graham & O'Geen, 2010) and coincident with phylogenetic diversity (Thornhill *et al.*, 2017).

The Sierra Nevada batholith is not one, but a collection of related Mesozoic plutons that are at the core of California's most notable mountain range (Norris, 1990; Stock *et al.*, 2004), whose pluton composition ranges across several granite types, although granite, granodiorite and tonolite are the most common (Callahan *et al.*, 2019). Most of the Sierra Nevada land surface is geologically young, with active uplift

in some areas. However, other areas are remnants of the earlier Nevadan Mountains dating back to the late Tertiary (Norris, 1990). Also persisting in the central and southern Sierra Nevada is the palaeoendemic giant sequoia (*Sequoiadendron giganteum*), an ancient massive conifer with an evolutionary history dating back at least 200 million years. It survived the glacial cycles of the Cenozoic in zones devoid of ice, and today exists in 75 groves in granite-derived residual and alluvial soils.

Hahm *et al.* (2014), working across the Sierra Nevada Batholith, hypothesized that the transition between soil-mantled hillsides and exposed bedrock may result from variation in the bedrock P content of different plutons. Their study area focused on a region of the Sierra Nevada in the Kings and San Joaquin watersheds underlain by different plutons differing in dominant rock type (e.g. granite vs. tonolite vs. andesite). Study sites devoid of vegetation were not glaciated during

the Pleistocene, yet striking differences in ecosystems exist adjacent to bald landscapes. Specifically, much of the Sierran landscape is characterized by bornhardts (granite domes), inselbergs and vegetation-free slopes next to forested areas such that bald mountain tops are surrounded by woody vegetation, a condition described as “bimodal” (Jessup *et al.*, 2011).

Examining the geochemistry of the bedrock, Hahm *et al.* (2014) discovered that the difference in P content between vegetated and bare regions varied by a factor of 20, which the authors hypothesized might demonstrate that bedrock geochemistry may be as equally influential as climate in regulating vegetation in the Sierra Nevada. What is remarkable is that researchers are now able to demonstrate that subtle microsite differences in rock properties correlate with extreme differences in vegetation, including zones free of plants and others that support groves of giant sequoia (Hahm *et al.*, 2014). Small differences in initial conditions can have dramatic effects on the evolution of a landscape (Porder, 2014).

Whether these Sierra Nevada mountain ecosystems qualify as OCBILs remains to be examined, but they are likely candidates (Hahm WJ, pers. comm.). Other mountain ecosystems in the American West that are equal or better OCBIL candidates are found as inselbergs or isolated ranges such as Timbe Nabor (Independence Rock), and the Granite, Shirley or Laramie ranges of the Rocky Mountains, all in central Wyoming—unglaciated, erosion-resistant expressions of the Wyoming Batholith.

The Peninsular Ranges of southern California and northern Baja California, as well as the Cape Region of Baja California, Mexico (particularly the Sierra de la Laguna Biosphere Reserve, Rascón-Ayala *et al.*, 2018), are all rich with endemic species. All but the Cape Region are encompassed within the CFP, while Baja’s Cape Region could be considered part of the Mesoamerican biodiversity hotspot (Myers *et al.*, 2000; Mittemeier *et al.*, 2004, 2011). The Baja Peninsula is a relative recent geological feature of the North American continent, being sheared from Mexico’s mainland by the San Andrea Fault system and transferred from the North American to the Pacific Plate between 3 and 4 million years ago (Nix 2013). With the increasingly sophisticated analyses of climate change velocity pioneered by Loarie *et al.* (2009), considered in the context of biodiversity and endemism (Sandel *et al.*, 2011; Molinos *et al.*, 2016; Harrison & Noss, 2017), mapping tools to examine ancient landscapes in the Northern Hemisphere rich in biodiversity will become increasingly useful to identify OCBILs, particularly in the North American West.

Relatedly, Noss *et al.* (2015) argue that it is too easy to overlook biodiversity hotspots, although the same could be said about OCBILs. These authors argued

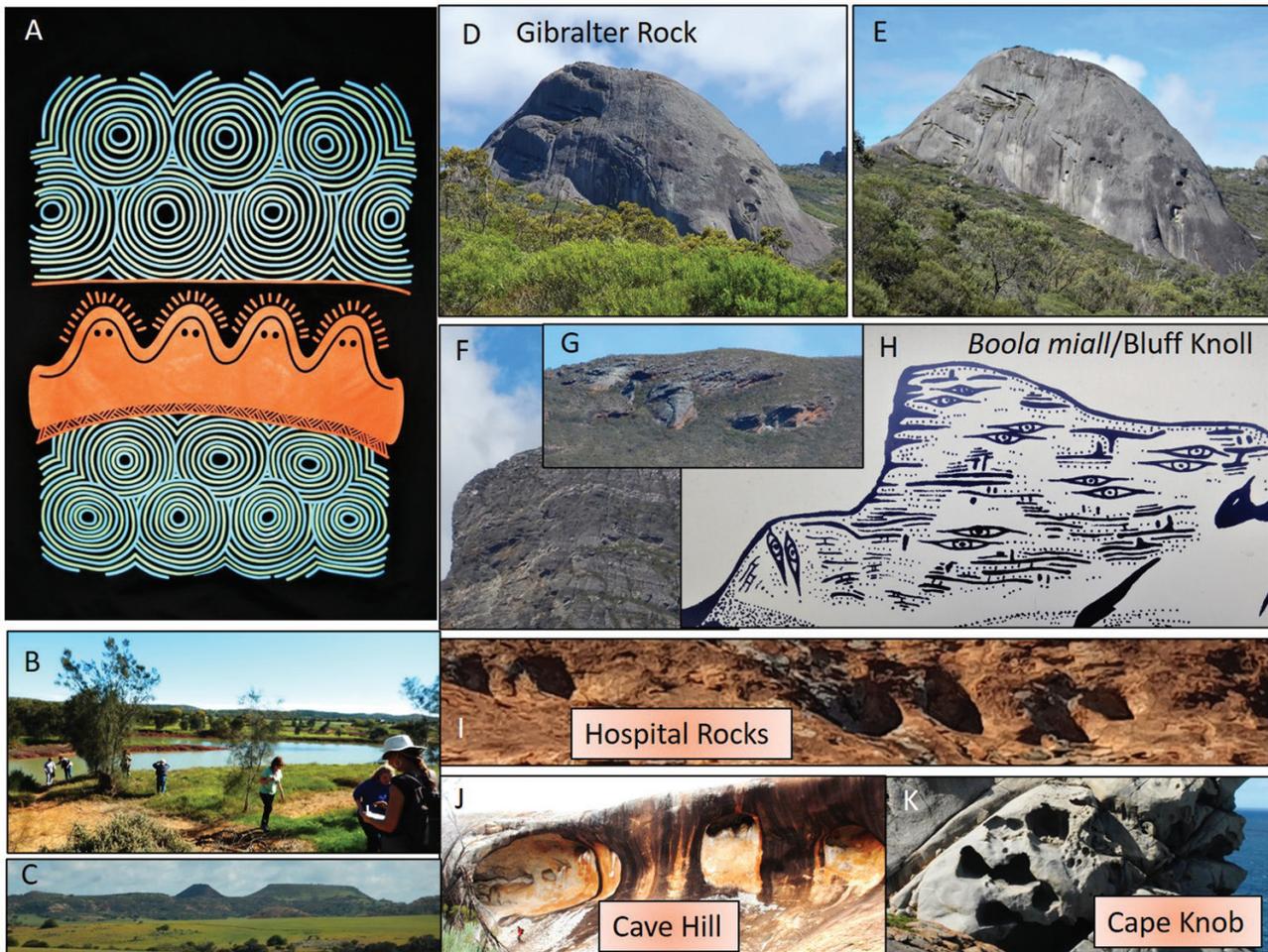
that a 36<sup>th</sup> biodiversity hotspot is found in the North American Coastal Plain (NACP), termed the Coastal Plain Floristic Province [CPFP (Takhtajan, 1986)], a 1.06 million km<sup>2</sup> region stretching from the Gulf coast of southern Texas northwards and eastwards along the Gulf of Mexico, encompassing much of northern Florida and extending along the Atlantic coastal plain as far north as southern Massachusetts. These authors evaluated a suite of misconceptions (in addition to ignorance and biases) that examined key characteristics of OCBIL theory, such as geological age, climate stability and the relationship between topographic complexity and floristic richness and diversity. In addition, Noss *et al.* (2015) successfully tackle two myths about the NACP, i.e. that closed canopy forests represent ‘climax’ vegetation and that fire is a recent and primarily anthropogenic ecological driver.

Our point in reviewing this work is twofold. First, ecology, while one of the younger natural sciences, has built up sufficient myths and dogma to bias observers into accepting existing theory as fully resolved, with little reason to re-examine accepted truths. Second, Noss *et al.* (2015) provide an elegant protocol for looking for additional biodiversity hotspots that could be modified for searching for OCBILs. As the authors state “[b]iodiversity is not distributed randomly or uniformly on Earth ... [t]rue hotspots may go unrecognized” (Noss *et al.*, 2015: 236), and they give three reasons: data are not sufficiently organized to facilitate discovery; long-standing systematic biases exist in the field of biogeography (see also Eicchorn *et al.*, 2020); and misconceptions about regional biodiversity discourage investigation. Exactly the same can be said for OCBILs.

As OCBIL theory develops, is refined and corroborated, we are encouraged to continue the search for more examples. Although the 36 recognized biodiversity hotspots provide an obvious starting point, other regions presumed not as likely (e.g. glaciated landscapes in the Northern Hemisphere) should not be automatically dismissed. The search for additional ancient landscapes that conform to OCBIL theory can and should continue, if for no other reason than their conservation is of utmost importance and urgency (Porembski *et al.*, 2016).

#### KAAT AND BEELIAR—NOONGAR COSMOLOGY

It is sobering to consider, briefly, the insights on OCBILs of First Nations who have lived with these landscapes for tens of thousands of years. Noongar Aboriginal people occupy most of the SWAFR (*sensu* Hopper & Gioia, 2004), and have been there for at least 48 000 years (Turney *et al.*, 2001). From their perspective, Noongars have been present in spirit and body since the time of creation (Nannup Karda, 2006; Robertson *et al.*, 2016).



**Figure 4.** First Nations believe OCBILs are enspirited. A, ‘Dreamtime’, 50 000+ years of Aboriginal occupation, by south-west Australia’s *Amangu* artist Wayne Ronan (with permission), highlighting YODFELs—circles of *beeliar* [fresh water pools, e.g. (B) Bootenal Spring, Greenough River] and OCBILs [e.g. (C) from Elephant Hill Lookout, Moresby Range]—haunting *kaat* (hills, OCBILs) containing the *Waarkarl* (rainbow serpent) and eyes forever overlooking their *boodjar* (country) keeping watch on the behaviour of people below. The eyes sometimes only reveal themselves at certain times of day [e.g. (D, E) Gibraltar Rock, Porongurup Range]. Peaks in the SWAFR, such as Bluff Knoll in the Stirling Range (F–H, artwork by Maria Ann Penny (Tyrdir) and Grant Mason Williams), is replete with eye-like caverns in its quartzite cliffs, and is known as *Boola miall* (many eyes). Granite inselbergs (I–K) feature eye-like caverns across the SWAFR and beyond. Photos: S.D. Hopper.

Creation stories are deeply embedded in landscape, at a time when the Earth was soft and malleable, and the sky pressed heavily upon its surface. Spirit beings roamed the dark, cold landscape. One, the *waarkarl* (rainbow serpent), moved across the surface, moulding it as it moved, forcing the sky and land apart, enabling sunlight to reach the land. A select group of spirit animals and humans discussed who should care for everything, ultimately deciding that each would play a part, but humans would take the lead. How this came to be is expressed in journeys taken by the original spirit man and woman across south-western Australia. Their

travels and exploits with spirit animals and plants created many features of the landscape, including the OCBIL uplands, ultimately leading to people becoming real, and dreaming into being language and culture, with clear directives as to proper behaviour for all, and dire consequences for those who transgressed social norms (Nannup Karda, 2006). This cosmology enabled Noongar society to evolve and respond adaptively to dramatic changes associated with late Pleistocene climatic cycles and sea level fluctuations.

When introducing their culture, Noongars often start with describing *boodjar*, their country, and

the interconnectedness of people and biodiversity to it. In this process, first base is to recognize the distinction between the words *kaat* and *beeliar* (Fig. 4). Interconnectedness is emphasized by these words having dual meanings. *Kaat* is the Noongar word for head, but also hill or upland. *Beelair* means fresh water, but also mother's milk. Merningar Noongar Elder Lynette Knapp (pers. comm., 3 March 2017) described it this way:

“Rivers are especially important to us because, it's *beeliar*. We say *beeliar*, mainly for freshwater. *Beeliar*...And also *beeliar* is mother's milk. Mother's milk is the life giver, so is the freshwater. So you see the relationship that we've got with rivers. Mountains we call *kaat*; we [also] call our heads *kaat*. So that when we're walking along the Earth we're walking along the shoulders of our Mother Earth so we can't do anything wrong because we know that those *kaats* have got eyes [Fig. 4] and if you do anything wrong you get punished cause they see you! So when you're walking on country [past] mountains you get a feeling that someone is watching you and they look at you and make sure you're doing the right thing. So when you leave country you make sure you leave it clean, you leave it as if it's untouched and you respect it of all things. If you don't put that respect back into your country you've lost out there.”

There are diverse songlines and dreamtime stories held by Aboriginal families that reinforce this rational reverence shown by Noongars towards *kaat* and *beeliar* (e.g. Nannup Karda, 2006; Knapp, 2011; Yorkshire-Selby, 2011). This deep cultural history exemplifies the long-standing recognition by Southern Hemisphere First Nations of the importance of OCBILs and appropriate behaviour associated with them (Lullfitz *et al.*, 2021a, b). Essentially, such recognition predates OCBIL theory by tens of thousands of years.

## CONCLUSION

OCBILs are extremely rich in biodiversity and endemism, yet many have been neglected. The combination of megadiversity with scientific dismissal makes them prime scenarios for ecological surprises, defined as unexpected findings about the natural environment (Lindenmayer *et al.*, 2010). The findings of underground, nematode-trapping leaves (Pereira *et al.*, 2012), fly-mimicking weevils (Guerra, 2019), rock-eating plants (Abrahão *et al.*, 2020), faecal-mimicking seeds (Midgley *et al.*, 2015), and pseudoflowers produced by fungi on *Xyris* (Laraba *et al.*, 2020) are but a few recent examples of fascinating natural histories that attest to the potential of ecological surprises in

OCBILs. Whether every hypothesis, explanation and conclusion in this special issue falls into place lies in the understanding and experience of the reader, but we urge all to set aside long held assumptions and Northern Hemisphere theoretical biases, and seek to understand the extraordinary world of OCBILs. We encourage ecologists, evolutionary biologists and biogeographers to test widely the predictions of OCBIL theory. Recognizing the specific needs for conservation and restoration of OCBILs is an urgent and necessary step in the global conservation agenda.

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