

OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes

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Received: 16 March 2009 / Accepted: 8 June 2009 / Published online: 14 July 2009
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Abstract OCBIL theory aims to develop an integrated series of hypotheses explaining the evolution and ecology of, and best conservation practices for, biota on very old, climatically buffered, infertile landscapes (OCBILs). Conventional theory for ecology and evolutionary and conservation biology has developed primarily from data on species and communities from young, often disturbed, fertile landscapes (YODFELs), mainly in the Northern Hemisphere. OCBILs are rare, but are prominent in the Southwest Australian Floristic Region, South Africa's Greater Cape, and Venezuela's Pantepui Highlands. They may have been more common globally before Pleistocene glaciations. Based on the premise that natural selection has favoured limited dispersability of sedentary organisms, OCBILs should have elevated persistence of lineages (Gondwanan Heritage Hypothesis) and long-lived individuals (Ultimate Self Hypothesis), high numbers of localised

rare endemics and strongly differentiated population systems. To counter such natural fragmentation and inbreeding due to small population size, ecological, cytogenetic and genetic mechanisms selecting for the retention of heterozygosity should feature (the James Effect). The climatic stability of OCBILs should be paralleled by persistence of adjacent semi-arid areas, conducive to speciation (Semiarid Cradle Hypothesis). Special nutritional and other biological traits associated with coping with infertile lands should be evident, accentuated in plants, for example, through water-foraging strategies, symbioses, carnivory, pollination and parasitism. The uniquely flat landscapes of southwestern Australia have had prolonged presence of saline lakes along palaeoriver systems favouring evolution of accentuated tolerance to salinity. Lastly, unusual resiliences and vulnerabilities might be evident among OCBIL organisms, such as enhanced abilities to persist in small fragmented populations but great susceptibility to major soil disturbances. In those places where it is most pertinent, OCBIL theory hopefully lays a foundation for future research and for better informed conservation management.

Responsible Editor: Hans Lambers.

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Keywords YODFEL · James Effect · Ultimate Self · Gondwanan Heritage · Dispersability · Endemism · Heterozygosity · Mineral nutrition · Salinity · Speciation · Southwest Australia · Greater Cape · Pantepui · Old landscapes · Infertile soils · Climate · Rare species · Conservation · Evolution

Introduction

Much was celebrated in 2007 regarding the tercentenary of the birth of Linnaeus (e.g. Jarvis 2007; Knapp and Wheeler 2009). The universal application of binomial nomenclature over 250 years remains a fundamental underpinning, providing names so necessary to organise biodiversity information and exchange ideas about the use, relevance and conservation of life on Earth.

Through his students, Linnaeus helped focus upon a global inventory of life as a key objective, still yet to be realised, but tantalizingly now within our grasp (Hopper 2007). At the same time, Linnaeus was a product of his time, seeing biodiversity as a collection of assets to be used for economic benefit for a struggling post-war nation. He advocated schemes for cultivating useful plants in Sweden often well beyond ecological and practical reality (bananas for example), but somehow managed to move effortlessly on to other ideas that won favour with Sweden's political elite when previous schemes did not live up to their early promise (Koerner 1999).

The Scandanavian lands traversed by Linnaeus are underlain by ancient granitic rocks, scraped bare by Quaternary glaciers, with soils rejuvenated through glacial grinding to a high level of fertility characteristic of much of those found on Eurasia and North America (Carlgren and Mattsson 2001; Vidal Romani and Twidale 2005; Fig. 1). Given that most people to the present day occupy these northern continents, including most biologists and conservation practitioners, it is perhaps not surprising that theory underpinning much of today's ecology and evolutionary and conservation biology arises from these relatively young, often disturbed, fertile landscapes (YODFELs).

Indeed, the much-celebrated Charles Darwin, born two centuries ago this year, was increasingly comfortable in comprehending evolutionary and ecological processes at work on the YODFELs of temperate South America, even though the biota was strange, species-rich and new to him (Keynes 1988, 2002; Thomson 2009). Concepts of natural selection and the origin of species crystallised through Darwin's observations on the volcanic YODFELs of the Galapagos Islands (Grant and Grant 2008). As reviewed elsewhere (Hopper and Lambers 2009), Darwin was less insightful, if not indifferent and disparaging, to the botanical wonders on the old, climatically buffered,

infertile landscapes (OCBILs) of the Southwest Australian Floristic Region (*sensu* Hopper and Gioia 2004), the Blue Mountains inland from Sydney, and the Greater Cape Floristic Region (Born et al. 2007). Of course, Darwin's view—'Since leaving England I do not think we have visited any one place so dull & uninteresting as K[ing] George's Sound'—was not shared by all early visitors. The normally restrained Robert Brown, in correspondence to Sir Joseph Banks regarding Flinders' *Investigator* expedition, enthused that southwest Australia 'would, I am convinc'd, amply repay a second examination.' (Vallance et al. 2001). Yet this region and the Greater Cape remain problematic to this day for theorists, defying, for example, the view that species-richness increases from the poles to the Equator (Cowling et al. 1996).

The Southwest Australian Floristic Region and Greater Cape continue to confound attempts to understand the origins of species richness and are usually ignored, overlooked or regarded as minor exceptions by global modellers (e.g. Dynesius and Jansson 2000; Jansson and Dynesius 2002; Jansson 2003; Ricklefs 2004; Wiens and Donoghue 2004; Lavers and Field 2006; Jansson and Davies 2008). This is of more than academic interest, as there are also significant conservation implications flowing from assumptions made in global models that may well be inappropriate for OCBILs (Hopper 1997, 2003; Hopper and Gioia 2004). Indeed, homogenizing the complex patterns of diversity in space and time of OCBIL biota to fit global analyses, even where focussed on mediterranean-climate regions (e.g. Underwood et al. 2009a, b), requires critical and close scrutiny before recommendations are accepted and implemented. This problem of scale, focus and approach is summarised in Murphy's (1989) succinct encapsulation regarding nascent theory in conservation biology: "wrong species, wrong scale, wrong conclusions".

As the biota of the more insular and ancient landscapes of the southern hemisphere have become better understood (Lusk and Bellingham 2004), ascertaining the limits to scientific generalization in evolutionary and conservation biology has become a significant challenge. The theory of island biogeography illustrates this well, having to be modified significantly as empirical testing has revealed greater complexity and less predictability than first hoped for (Gilbert 1980; Brown and Lomolino 2000; Whittaker et al. 2005). Some authors argue that there are few (if

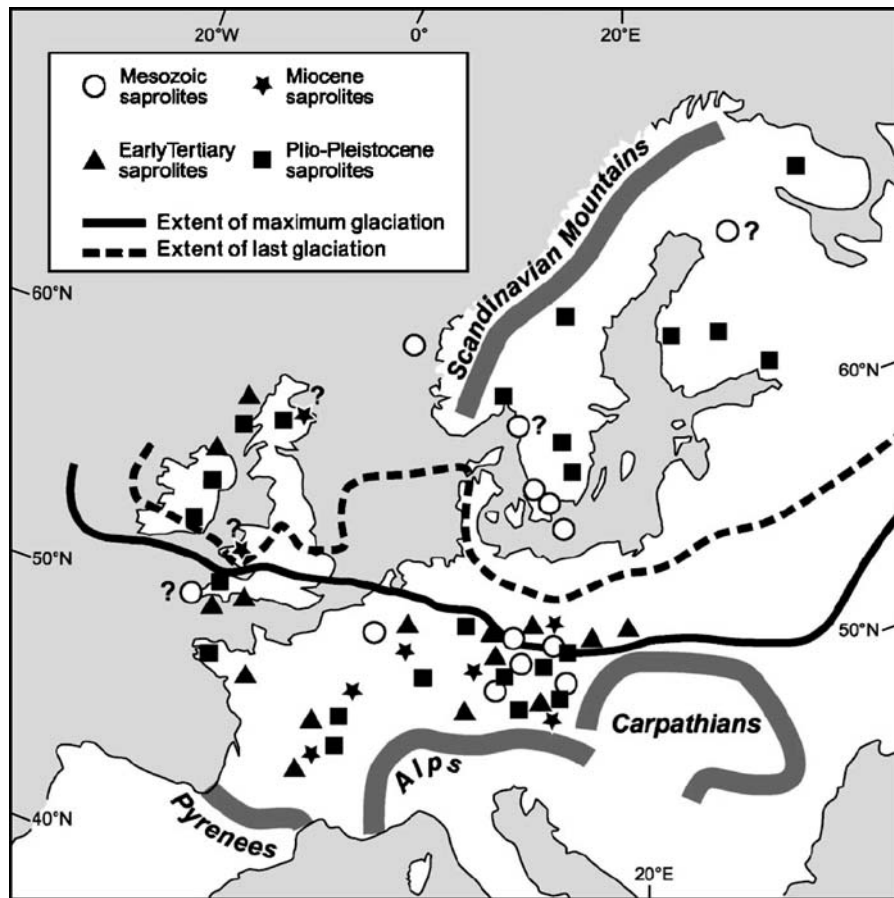


Fig. 1 European extent of maximum and last glaciation, and the distribution of relict weathering mantles (saprolites), with their most likely ages. *Question marks* indicate ages inferred from circumstantial evidence such as long-distance correlations with saprolites of known ages or morphostratigraphic dating. Excluding the Cretaceous, the Mesozoic (251–65.5 Ma) and Palaeogene or Early-Mid Tertiary (65.5–23 Ma) in Europe were generally characterised by ‘tectonic stability within low relief

surfaces’, perhaps identical to those characterizing today’s surviving OCBILs. Thus, saprolites mapped as Mesozoic or Early Tertiary with prolonged oceanic climatic buffering may well have constituted old climatically buffered infertile landscapes (OCBILs) prior to glaciation and the increased tectonism, marine inundation, uplift and extensive denudation on uplands of the Cretaceous (145.5–65.5 Ma) and Neogene (23–0 Ma). From Migoñ and Lidmar-Bergström (2002), with permission

any) general principles applicable globally to biodiversity, other than natural selection. Rare v/s common species, for example, seem to display idiosyncratic biological attributes (Fiedler 1986; Gitzendanner and Soltis 2000; Poot and Lambers 2003), as do fossil species (Willis and Niklas 2004). Attempts to generalise above the species-level in conservation biology may be futile (Ronce et al. 2000). Use of easily sampled groups of plants or animals as surrogates for others or for all biodiversity in conservation biogeography may or may not be fundamentally flawed (e.g. Keighery et al. 2004 v/s Sauberer et al. 2004). Whittaker et al. (2005) advocated cogently for renewed efforts in development of theory in conser-

vation biogeography given the obvious complexity, scale dependencies and uncertainties in predictive analysis evident in the literature.

The present paper proposes that some generalities for the theory of evolution, ecology and conservation biology arise from a consideration of landscape age, climatic buffering and soil fertility. The formation of landscapes on Earth is a process of continual renewal, intimately linked to plate tectonics and their consequences. However, rates of renewal vary significantly across the globe. Some landscapes—OCBILs—exhibit greater antiquity and stability, and their biota offer exciting challenges to evolutionary and conservation biologists, in every way as interesting as YODFELs where

evolution has occurred on new landscapes freshly exposed by volcanism, glacial retreat, mountain-building or altered sea levels.

My aim here is to explore a widely scattered literature and develop new theory pertinent to patterns and processes that characterise evolution, ecology and conservation on OCBILs as compared with YODFELs. Included among the more significant areas on Earth that have OCBILs are three: the Southwest Australian Floristic Region (Hopper and Gioia 2004), the Greater Cape Floristic Region of South Africa (comprising the fynbos dominated Cape Floristic Region and the Succulent Karoo Biome—Born et al. 2007), and the Pantepui region of the Guyana Shield in South America (Berry and Riina 2005).

Prior to Pleistocene glaciations, many other regions on Earth probably had landscapes similar to today's OCBILs (King 1962; Pillans 2007; Fig. 1), and the ghosts of evolutionary processes past may persist in taxa that survived in glacial or periglacial refuges (Knowles 2001; Migoń and Lidmar-Bergström 2002; Petit et al. 2003; Willis and Niklas 2004; Schonswetter et al. 2005; García 2008; Brundu et al. 2008). In northern Europe, for example (Fig. 1), and in North America (Swenson and Howard 2005; Soltis et al. 2006), postglacial lands have cryptic refugia or relictual saprolitic soils located in small microenvironmentally favourable sites. In these refugia, small populations persisted through glaciation. These populations included habitat generalist trees with small seeds and prone to vegetative propagation, and habitat generalist mammals (Rowe et al. 2004; Bhagwat and Willis 2008). Rare plants on Californian serpentine outcrops (Harrison et al. 2008) and elsewhere (Jansson and Dynesius 2002; Jansson 2003) persisted through the Quaternary where climate is most benign and has been stable. The existence of double the number of Chinese species in plant taxa compared with sisters in eastern North America has been correlated with greater topographic heterogeneity and therefore more local refugia in China (Qian and Ricklefs 2000).

In the three Mediterranean climate regions dominated by YODFELs (the Mediterranean, California and Chile), mesic refugial habitat is created through facilitation by other plant species for recruitment of drought-intolerant species rather than through favourable hydrogeomorphological factors (Valiente-Banuet et al. 2006). Woody, evergreen, resprouting, late-successional, Tertiary-relict species with fleshy fruits

and large seeds recruit far more commonly in localised, mesic, shaded refuges beneath nurse plants of early-succession, deciduous, dry-fruited species adapted to semi-arid conditions. While this ecological process is well-established, Valiente-Banuet et al.'s (2006) assertion that the woody, evergreen resprouters are recently-evolved following the Neogene onset of Mediterranean climate is not supported by fossil studies in California of the Eocene or earlier Madro-Tertiary flora (Raven and Axelrod 1978). Another example of refugia is seen in Australian deserts where multiple localised refugia occur that persisted over several Pleistocene glacial maxima (Byrne et al. 2008).

Large clonal stands of aspen (*Populus*) in North America and Eurasia (e.g. Brundu et al. 2008) could be the product of selective regimes in extensive past OCBILs rather than of the more recent YODFELs in which they are found growing today. Molecular phylogenetic studies on which are analysed ancestral ecological niches (e.g. Hardy and Linder 2005) would provide a useful test of such hypotheses. Hence the theory proposed herein for OCBILs may have wider applicability than for the biota of just the three regions of primary focus in this paper.

On first principles, prolonged opportunities for evolution to run its course should result in sophisticated, complex and ongoing biological adaptations for lineages able to persist on OCBILs. Also likely to be particularly evidenced in OCBILs is phylogenetic niche conservatism, the tendency of species to retain ancestral ecological characteristics (Harvey and Pagel 1991; Wiens and Graham 2005; Tiffney 2008; Crisp et al. 2009), a phenomenon used to help explain high species richness in tropical regions (Wiens and Donoghue 2004; Donoghue 2008), and the persistence of rare species in climatically stable refugia (Stebbins and Major 1965; Hopper 1979; Hopper et al. 1996; Goldblatt and Manning 2002; Jansson and Dynesius 2002; Jansson 2003; Harrison et al. 2008). Is this so? What special environmental attributes characterise these landscapes? How have components of their biota evolved in response? Are there special mechanisms and processes at work, or are they simply those by now well documented but developed and matured through time? Is what we see today much more the result of historical contingency (*sensu* Gould 1988; Herrera 1992) than adaptation to contemporary environments? What are the implications for conserving biota on old, climatically buffered landscapes?

As we shall see, such questions sometimes have been asked, usually in the context of theory developed elsewhere on biota from much younger northern landscapes (e.g. Dodson and Westoby 1985; the “Cape Special Feature” issue of *Diversity and Distributions*, volume 12, published in 2006). Perhaps an attempt to construct theory directly pertinent to OCBILs will open new research perspectives. It is certain that much remains to be explored before satisfying answers are in hand. However, a growing literature is not without its highlights and significant insights. In such an auspicious year, celebrating the bicentenary of the birth of Charles Darwin and the sesquicentenary of the publication of *The Origin of Species* (Darwin 1859), it is opportune to make a start on OCBIL theory and hopefully lay a foundation for future research.

The approach here to formulation of theory is based on qualitative reasoning in order to cover the breadth and depth of the subject succinctly. Ghiselin (1969, pg 21) outlines the scientific legitimacy of such an approach, so powerfully used by Darwin and others: ‘Scientific inferences should be accepted because the premises are true and because the conclusions follow logically. The truth does not derive from the jargon [such as mathematical equations] in which it is expressed’. Ghiselin cautions against the ‘superstition of numerology’—the belief that scientific work must employ mathematics and quantification. To quantify sometimes helps, as I have found in various studies (e.g. Hopper and Campbell 1977; Hopper 1978; Campbell et al. 2000; Hopper and Gioia 2004; Krauss et al. 2007; Hopper et al. 2009), but it may not make conclusions any closer an approximation to the truth than those drawn from qualitative logic. In this review, space does not allow for detailed quantitative modeling and statistical testing of each hypothesis proposed. Rather, the aim is to present a coherent overview and sufficient examples and literature citations to enable the reader to explore the subject further and devise appropriate field studies or experiments to test hypotheses of interest.

Identifying old, climatically buffered, infertile landscapes (OCBILs)

Applying the terms ‘old’ and ‘young’ to landscape age clearly alludes to relative positions along a quantitatively varying parameter. Hence, landscape

age cannot be defined in any absolute way. Boundaries will be fuzzy and some exclusions and inclusions will seem arbitrary. Still, as I hope to demonstrate, there is much of value conceptually and scientifically embodied in these terms. It is not too difficult to define OCBILs and YODFELs as end points in multivariate space and identify some regions that unequivocally fit such definitions.

How might very old landscapes be identified? The term ‘palaeosurface’ is pertinent here, defined by Widdowson (1997, pg 5) as “an identifiable topographic surface of either endogenic or exogenic origin, recognizable as part of the geological record or otherwise of demonstrable antiquity, which is, or was, originally of regional significance, and which as a consequence of its evolution, displays the effects of surface alteration resulting from a prolonged period of weathering, erosion, or non-deposition”. Hence, we are looking for landscapes that are regional in scale, with evidence of prolonged weathering and non-deposition, of demonstrable geological antiquity.

Weathering never stops; old soils erode and new soils form (e.g. Vitousek et al. 2003; Turkington et al. 2005; Lambers et al. 2008; Viles et al. 2008). Nonetheless there are places on Earth where these processes have slowed and the general form of the landscape has persisted for tens of millions of years. Good starting points are geological shields or orogens containing old crystalline rocks and mountain chains (Fig. 2). These are found on all continents and some larger islands, usually on passive plate margins well away from zones of plate collision where orogeny and vulcanism create new landscapes constantly (Twidale 1982; Vidal Romani and Twidale 2005).

The field of potentially oldest terrains narrows as other processes responsible for landscape rejuvenation are considered. Marine inundation, highest in the mid-Cretaceous (100–90 Ma—Miller et al. 2005), except for the anomalous earlier flooding of Australia at 110 Ma (Gurnis et al. 1998), covered many shield areas (Fig. 3). Similar high levels were attained again in the early Eocene (50 Ma—Miller et al. 2005). Flooding by rivers and inland lakes has continued to do so in lowlands, and most extensive of all have been the two monumental outcomes of Neogene climate change that transformed vast areas—glaciation and the formation of desert dune systems with associated dust storms (Chen and Barton 1991; Zachos et al. 2001; Hesse and McTainsh 2003; Jahn et al. 2003). Plants,

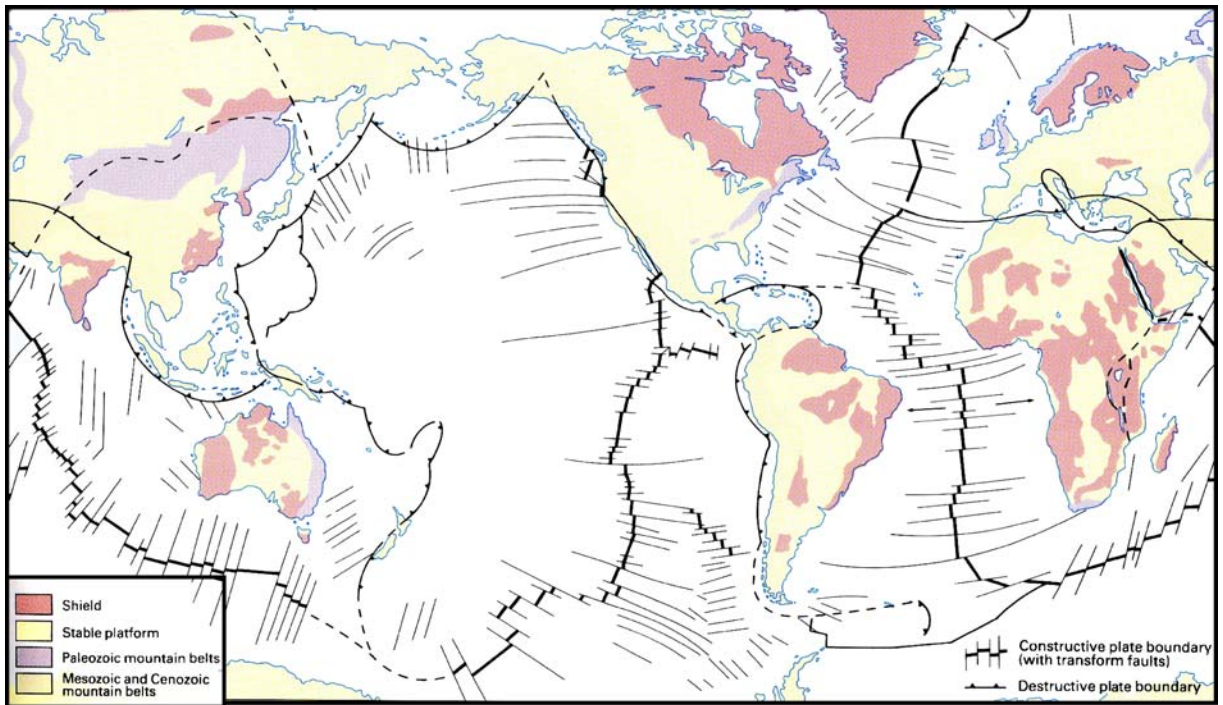


Fig. 2 Geological shields or orogens form the ancient stable cores of continents and large islands and therefore form the starting points in the search for OCBILs. However, their old

rocks are often overlain by younger sediments due to inundation, glaciation, dust storms, volcanism and other factors. From Smith (1989)

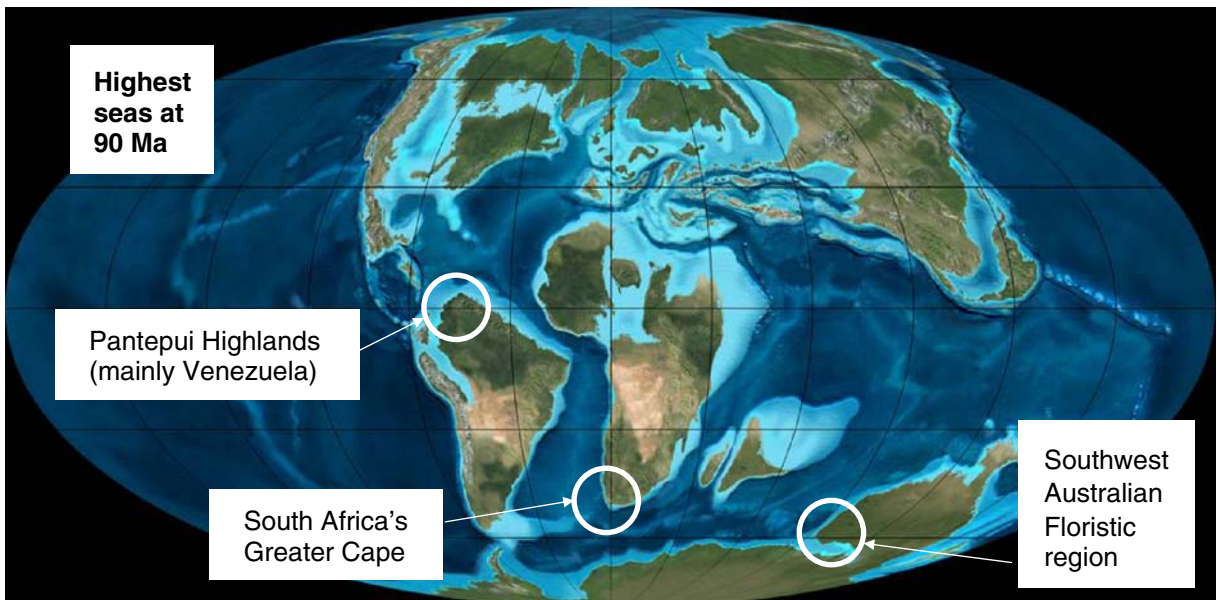


Fig. 3 At least three geologically stable, unglaciated regions persist today, as old landscapes with prolonged oceanically buffered climates since the early Cretaceous (140 Ma), from land that was above water when sea levels were close to the highest known 90 Ma. These three regions represent today's

OCBILs. Similar sea levels were attained in the early Eocene (50 Ma), further reducing the global extent of OCBILs. Late-Cretaceous reconstruction courtesy of Ronald C Blakey Northern Arizona University

cryptogamic soil crusts and bioturbation by animals add additional complexity to landscape change and rejuvenation (Viles et al. 2008).

We are left with a very small selection of old shield landscapes, fortuitously placed away from the poles continuously since the early Cretaceous, adjacent to oceans that buffered the land from climatic extremes since the Jurassic. Such old, stable, climatically buffered landscapes have endured weathering ever since, their soils rendered almost devoid of nutrients essential for plant and animal life (Lindsay 1985; Orians and Milewski 2007). They are phosphorus-limited systems (Lambers et al. 2008). OCBILs best meeting these criteria (Figs. 3, 4) are prominent and widespread in the Southwest Australian Floristic Region, South Africa's Greater Cape, and Venezuela's Pantepui Highlands (the inspiration for Conan Doyle's "The Lost World"). Other places could also be considered (King

1962; Pillans 2007), such as parts of Brazil, east and west Africa, Madagascar and New Caledonia, as well as many regions in Australia (Twidale 1976, 2007), but the first three listed above will suffice to draw out the evolutionary theory and conservation implications arising from a focus on OCBILs.

Within regions where OCBILs dominate, there will also be YODFELs. Floodplains and other wetland margins, coastlines, steep slopes, dune systems etc. are interspersed among classic OCBILs in complex mosaics. Similarly, on continents like Australia, where many old landscapes are evident (Twidale 1976; Gale 1992; Pillans 2007; Branagan 2008; Fig. 5), such old landscapes will vary in their relative age. As in northern Europe (Fig. 1) and parts of Australia (Twidale 1976, 2007), old landscapes may be overlain by younger landscapes and subsequently exhumed, adding further context-specific local complexity (Pillans 2007).

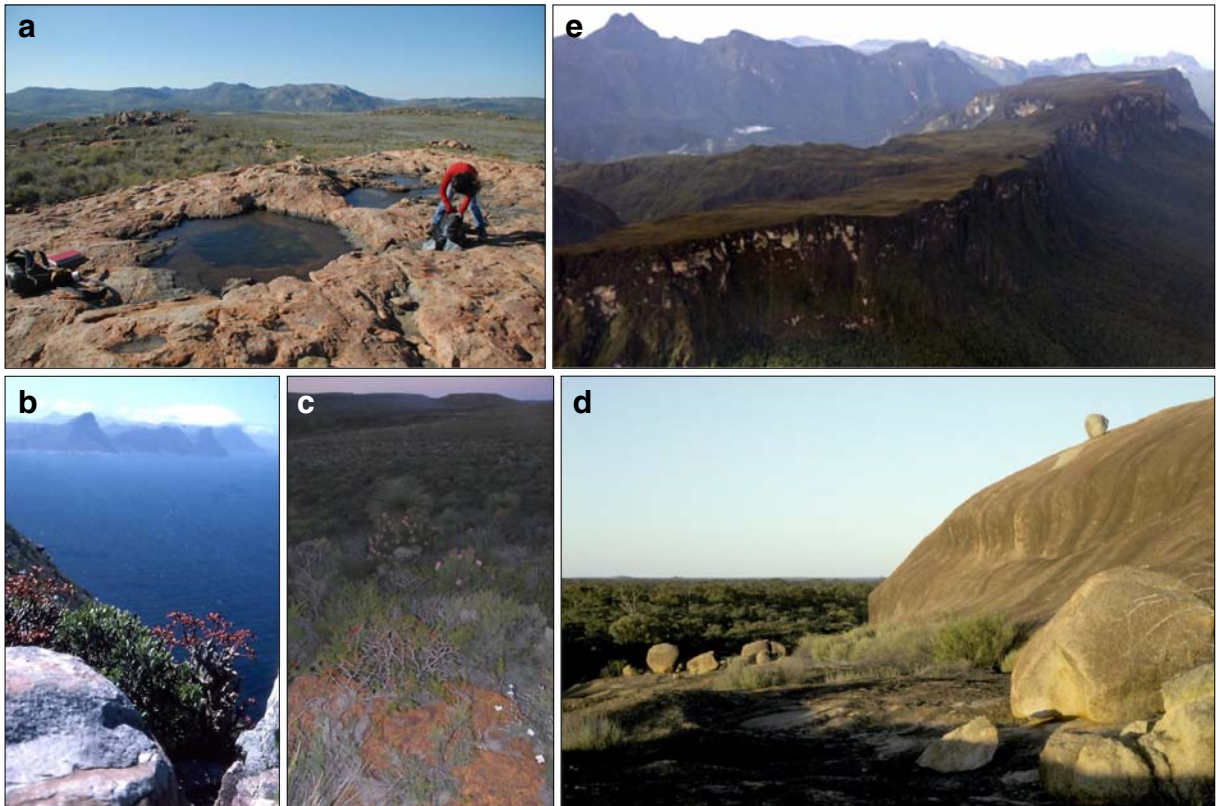


Fig. 4 OCBILs are confined primarily to three regions, although there are other possible candidates and OCBILs may have been more common prior to Quaternary glaciations (photos by the author unless otherwise stated): **a** high granite plateau of the Kamiesberg, Namaqualand, South Africa; **b** looking east from Cape Point across False Bay to the

Kogelberg World Heritage of the sandstone SW Cape Fold Mountains, South Africa; **c** Lesueur National Park lateritic uplands, Southwest Australian Floristic Region; **d** McDermid Rock and subdued granitic plain, inland Southwest Australian Floristic Region; **e** sandstone Cerro de la Neblina, Pantepui, Venezuela-Brazil border (photo D. Bruce Means)



Fig. 5 Australia, showing the boundary between inland areas of low relief, low denudation rates and ancient landscapes, and coastal areas of higher relief, higher denudation rates and more recent landscapes, where YODFELs predominate. OCBILs exist today primarily in southwest Australia, where prolonged maritime influence has buffered climate. Elsewhere in Australia, the mid-late Tertiary onset of aridity has rendered many past OCBILs ineffective, turning them into regions

dominated by YODFELs, where greater extinction rates have prevailed. The *Meckering Line* (Mulcahy 1967) distinguishes the significant drainage divide in the Southwest Australian Floristic Region between active westward-flowing river systems and inland unco-ordinated drainage associated with Tertiary palaeoriver valleys now occupied by extensive salt lakes that rarely link and flow. From Gale (1992), with permission

Hence the following account needs to be interpreted critically integrating landscape processes and relative age within regions when attempting to implement conservation management derived from OCBIL theory. Bierman (1994), Widdowson (1997), Twidale (1976, 1997, 2007), Duller (2000), Migoñ and Lidmar-Bergström (2002) and Reiners and Brandon (2006) provide useful introductions to the field of ascertaining relative landscape age.

Location of OCBILs within three regions

To help future workers ensure their research is appropriately located, a brief discussion of where OCBILs are to be found in the three regions of interest

is warranted. Gross comparisons of regions, though often done (e.g. Cowling et al. 1996; Hopper and Gioia 2004; Underwood et al. 2009a, b), are not strictly apt, as geomorphological and climatic histories differ, as does the dispersion of OCBILs and YODFELs within each region.

Southwest Australia

OCBILs in the Southwest Australian Floristic Region are most common inland of the Meckering Line (Mulcahy 1967; Fig. 5). OCBILs predominate on high points in the subdued topography of the region, such as on lateritic hilltops (Brown 1989), granite outcrops (Hopper et al. 1997; Barthlott and Porembski 2000; Nikulinsky and Hopper 2008), and high

sandplains. Salt lake systems lining palaeorivers are also of considerable antiquity and qualify as OCBILs. YODFELs occur within this matrix, on steep slopes (e.g. ‘breakaways’ on the escarpments of mesas) and in the form of alluvial sand and terraces or as aeolian dunes flanking salt lakes. West of the Meckering Line OCBILs are also to be found, e.g., in the lateritic hills and sandplains of the Darling Plateau, or on granite outcrops. Fluvial denudation is greater here, however, so that incised river valleys are clearly YODFELs, as are the richer slopes occupied by York gum (*Eucalyptus loxophleba*) and wandoo (*E. wandoo*).

The Greater Cape

Miocene-Pliocene uplift and Quaternary sea level changes reduced the extent of OCBILs in parts of the Greater Cape (Deacon et al. 1992; Cowling et al. 2009). However, OCBILs are prevalent on persisting African Surface plateaux and mountain regions such as the Kamiesberg in Namaqualand and in flatter reaches of the Cape Fold mountains (Fig. 4). The summits of classic flat-topped mountains including the Matsikamma and Table Mountain are obvious OCBILs. YODFELs are complexly interspersed on steep slopes, incised river valleys, renosterveld and coastal plains, as well as dune systems such as are found on the Knersvlakte of southern Namaqualand. Fluvial terraces and plains associated with wetlands also are seen as YODFELs in the region.

Pantepui

The summits of tepui are OCBILs edged by sheer-walled YODFELs and talus slopes. Flowing water also creates YODFELs on tepuis, whereas pools, seeps and peat-bogs with uncoordinated drainage are OCBILs. Shallow soils on persistent, flat to gently-sloping sandstone outcrops supporting herbfields and stunted shrublands dominated by species of *Bonnetia* are replete with organisms of OCBILs. Huber (1995a, 2006) summarised information on the non-gramineous broad-leaved herbaceous meadow communities on Pantepui OCBILs constituted by endemic genera of the Rapateaceae, Bromeliaceae, Xyridaceae, Eriocaulaceae and Cyperaceae. Huber (2006, pg 465), suggested that: “non-gramineous meadows representing ancient species pools of Guayana-centred families had evolved successful colonization strategies in occupying extremely nutrient poor sites at all altitudinal levels”. Hence, OCBILs may also

be found below the tepui summits in appropriate geomorphological contexts of low disturbance and deeply weathered soils.

YODFELs and conservation

It is evident that today, YODFELs dominate the Earth, and are the places where most humans live (Figs. 1, 2, 3). Sequestration of nutrients for living and reproduction is a fundamental challenge for all species. Ours has come to dominate the globe from this perspective (Wackernagel et al. 2002). Only the poorest people and/or those marginalised through military or cultural domination are pushed into occupying OCBILs. Noongar Aboriginal people occupied the relatively fertile and localised YODFELs of the Southwest Australian Floristic Region until usurped by colonial Europeans (Hallam 1975; Carter 2006), as did the Khoi-San and Nama in the Greater Cape of South Africa (Mountain 2003; Carstens 2007). In a few cases, as in the soldier-settlement schemes promoted after the two World Wars in southwest Australia (Beresford 2001), have reasonably affluent people come to occupy OCBILs. This occupation seems temporary, however, based on recent episodes of farmers struggling to make ends meet and abandonment of badly degraded and salinised land in favour of urban jobs (Allison and Hobbs 2004).

Those organisms able to rapidly occupy YODFELs inherit the Earth. Plants of YODFELs, for example, have many biological attributes regarded as characteristic of weedy organisms, or classic r-selected species (Table 1; Gadgil and Solbrig 1972). They exhibit attributes of the ‘ruderal strategy’ (Grimes 1977) or aspects of the ‘coloniser syndrome’ (Baker and Stebbins 1965), although such concepts should be used with considerable caution as their generality is

Table 1 Theoretical attributes of plants from young, often disturbed, fertile landscapes (YODFELs)

Good dispersal mechanisms
Good colonisers
Common and widespread
Recently evolved rather than relictual
Nutritional and biological generalists
Tolerant of human disturbance
Intolerant of prolonged fragmentation and rarity
Low or high population-genetic and species diversity

Table 2 Implications for land-use on YODFELs

Land-use practices are widely transferable
Native vegetation must be constantly suppressed to make way—old field succession theory
Within reason, Earth-moving, tilling, mining, logging, nutrient addition and removing groundwater are environmentally inconsequential
Introducing exotic organisms for human purposes is benign

questionable (Ronce et al. 2000). Usually, these organisms are able to disperse rapidly and widely, and therefore are successful colonisers of new territory (Petit et al. 2003; Lavergne et al. 2004). Consequently, given the abundance of YODFELs worldwide, successful colonisers tend to be common and widespread, unless the YODFELs are constrained geographically such as on volcanic islands (Carlquist 1974). Organisms on YODFELs are often from young lineages with many sister taxa, and tend to dominate in communities of low species richness (e.g. Darwin's finches on the Galapagos—Grant and Grant 2008).

Contrary to earlier hypotheses, widespread common species do not routinely exhibit higher intrapopulational genetic variability and relatively low divergence between populations compared with rarer congeners (Gitzendanner and Soltis 2000). They can exhibit either high or low variation. Being a generalist in terms of nutrition (especially in nitrogen-limited soils—Clark and Tilman 2008) and other biological attributes helps in occupying YODFELs, as does tolerance of ecological disturbance by humans (Lambers et al. 1998; Hill et al. 2002). Lastly, when their populations are fragmented and the species becomes rare, classic inbreeding effects and population decline to extinction become evident (Keller and Waller 2002; Ouborg et al. 2006), unless such local populations are located in refugial habitat favouring persistence (Jansson & Dynesius 2002; Jansson 2003; Harrison et al. 2008). Such an array of attributes has consequences in terms of land use and conservation management for species of YODFELs (Tables 2, 3).

The widespread and common occurrence of YODFELs, especially in the Northern Hemisphere, means that many land-use practices are widely transferable. As old-field succession theory predicts, agricultural and urbanized people have to suppress and clear native vegetation continuously, as it contains many species with weedy tendencies able to establish self-sustaining populations if given a chance (Cramer and Hobbs 2007). Human disturbances such as land clearing, tilling and the application of fertilizers that mimic the natural disturbance regimes of YODFELs will conserve native species. Furthermore introduction of most exotic organisms is relatively benign, because native species tend to be adapted to intense competition and can usually persist against exotics. Occasionally, this is not so, e.g., the hybrid/introgressed *Rhododendron ponticum* in Ireland has become a major weed that suppresses the growth of all native species (Erfmeier and Bruelheide 2004). Another example is seen with Californian YODFELs, where intensive grazing by cattle and sheep combined with reduced fire frequency and increased soil disturbance have drastically decreased the abundance of native herbaceous species and increased exotic invasives such as annual grasses from the Mediterranean (Minnich 2008).

An attempt to distil key conservation principles from the above theoretical consideration of YODFEL organisms leads to the conclusion that it is sufficient to provide space, preferably in large amounts, on lands that bear characteristic ongoing human disturbance. Significant opportunities for ecological restoration and reconciliation are effectively global, allowing the

Table 3 Conservation principles for plant diversity on YODFELs

Providing space for preserves is enough (plants will colonise lands left unused)
Individual remnants of wild vegetation are interchangeable due to low endemism
Bigger is better (Single Large Or Several Small nature reserves debate)
Ongoing forms of human disturbance are helpful (mimicking natural disturbances)
Connecting fragmented populations with corridors is desirable
Sourcing seeds from wide areas for restoration is fine

coexistence of native biodiversity and humans in YODFELs if disturbance regimes are appropriate (Whittaker et al. 2005; Miller 2006).

Do the same conservation principles apply to plant diversity as people move into marginal habitats that are old, geologically and climatically stable, much less regularly disturbed and relatively infertile? What can OCBIL theory tell us? Fundamental differences in natural selection for dispersal, conspicuous dominance and rarity in OCBILs exist compared with those observed in YODFELs.

OCBIL theory

OCBIL theory aims to develop an integrated series of hypotheses explaining the evolution and ecology of, and best conservation practices for, biota on globally very old landscapes. From first principles, the opportunity for continuous existence on ancient weathered infertile landscapes (Fig. 4) would be expected to select for biological traits that are in contrast to those favoured on YODFELs.

It is important to note in such a discussion that the evolution of biological traits is a complex process influenced by many factors. As Darwin (1862, 1875a, 1875b) so eloquently illustrated for orchids, carnivorous plants and climbing plants, the path towards similar structures may follow many convergent routes, where descent with modification builds upon existing frameworks through natural selection.

A significant trap for ecologists and evolutionary biologists is to infer adaptation where there has been none—to confuse an effect or correlation with evolutionary function (Williams 1966; Ghiselin 1969). For example, resprouting after fire is a common pattern observed in seasonally arid environments (Bellingham and Sparrow 2000; Bond and Midgley 2001), and therefore has been assumed to be an adaptation to fire regimes (Gill 1977; Wisheu et al. 2000; Orians and Milewski 2007). Yet rigorous tests of this hypothesis are difficult to devise, requiring the demonstration of function, heritability, natural selection and phylogenetic context (Ghiselin 1969; Whelan 1995; Mishler 2000; Horton 2000; Hopper 2003). Bond and Keeley (2005) surmised: ‘There are few studies of the evolution of fire-adaptive traits, and many plant traits have been uncritically labelled as ‘fire adaptations’ without any rigorous analysis either as to the functional importance

of the trait, or its phylogenetic origin.’ Indeed, resprouting could evolve in response to diverse processes other than fire that kill aerial plant parts, including drought, frost, grazing, flood damage, landslide and strong wind (Main 1996; Hopper 2003).

Gould and Vrba (1982) coined the term ‘exaptation’ to account for situations in which an obvious adapted state appears not to have evolved *in situ* through the action of natural selection, but rather to be the consequence of selection for another purpose in a separate environment. An exapted trait thus may have evolved, for example, in response to infertile soils that then confers survival value in a subsequent arid fire-prone environment. For example, on face value, tough fibrous foliage (sclerophylly) appears to function to conserve moisture in arid or semi-arid environments. However, there is a fundamental difference between sclerophylly and xerophylly, the latter alluding to specific adaptations for coping with drought such as sunken pores (stomata) for gas and moisture exchange (Seddon 1974). Sclerophylly appeared in many Australian plant families well before the onset of aridity from 30 Ma (Byrne et al. 2008) and its intensification over the past 10 Ma. This is evident by the presence of sclerophyllous fossil leaves aged at 50–60 Ma, covered in epiphyllous rainforest fungi (indicative of moist environments), lacking xerophyllous adaptations (Hill 1998; Hill and Brodribb 2001). Selection for sclerophylly occurred under mesic conditions, as a consequence of excessive accumulation of carbon from nutrient poor soils (Read et al. 2009). Only afterwards did sclerophylly become an exaptation to aridity. In this light, careful experiments and rigorous attempts at falsification are needed to ascertain the merits of the hypotheses on the evolution of traits elaborated below.

OCBIL theory proposes specific adaptations arising from multifactorial selective regimes on old, climatically-buffered infertile landscapes. Attempts to account for attributes of OCBIL biota from a single cause such as adaptation to soil types (Beard et al. 2000) or fire (see below) are fraught. Alternative hypotheses rarely are addressed in such narrowly focused approaches. Concurrent with recent literature (e.g. Cowling et al. 2009; van der Niet and Johnson 2009), OCBIL theory proposes a more complex interplay of contributing causes, varying in importance from taxon to taxon, but sufficiently tractable experimentally to enable falsification of competing hypotheses in any given case (e.g. James et al. 1999; Bussell et al. 2002; Yates et al.

2007a). Thus, seven pertinent predictions may be derived from OCBIL theory (Table 4).

1. Reduced dispersability, increased local endemism and common rarity

OCBIL organisms should exhibit reduced dispersability, high numbers of localised rare endemics and strongly differentiated population systems Effective dispersal involves transport of seeds or vegetative propagules some distance from the mother plant, followed by germination and successful establishment to form a breeding population at a new site (Carlquist 1974). One of the most significant discoveries revealed by dating molecular phylogenetic data through calibration with fossils has been confirmation of Darwin's hypothesis that long-distance transoceanic dispersal has been common in the history of plant life (e.g. Donoghue et al. 2001; Crisp et al. 2009). At a more local scale, it is evident from molecular phylogenetic studies that multiple dispersals have occurred to, from and within the Southwest Australian Floristic Region (Hopper and Gioia 2004).

However, dispersal from parental habitat has high risks on OCBILs, with few attendant rewards, as are found, for example, by those rapid dispersers able to first colonise YODFELs through long-distance dispersal, e.g., when glaciers, deserts, oceans, or floodwaters retreat or volcanic oceanic islands form (Carlquist 1974; Cain et al. 2000; Petit et al. 2003). A perusal of the seed morphology of Southwest Australian Floristic Region plant genera highlights how few have wings or fleshy arils to aid with wind or animal-mediated dispersal (Sweedman and Merritt 2006). This phenomenon does not apply so extensively in the Greater Cape, which is replete with local endemics, but also supports a greater component of fleshy-fruited Afrotropical rainforest elements intermixed with endemic fynbos

and succulent karoo taxa, and families with wind-dispersed seed like Asteraceae are more prominently represented (Goldblatt and Manning 2002). Exceptional of course are the mesembs (Aizoaceae), which have radiated extensively in semi-arid succulent karoo vegetation, and have seeds mostly dispersed short distances by rainwater (Klak et al. 2004; Ellis et al. 2006). The Pantepui flora remains to be investigated from the dispersal perspective.

One striking aspect of the majority of the Southwest Australian Floristic Region's 8000 native plant species is the absence of obvious means of seed dispersal. Except for orchids, daisies, some native grasses, *Banksia* (Fig. 6), *Hakea* (Proteaceae) and she-oaks (*Casuarina* and *Allocasuarina*, Casuarinaceae), few species have large wings or light-weight seeds for wind dispersal. The seeds of most eucalypts, kangaroo paws (*Anigozanthos*, Haemodoraceae), or most shrubs and perennial herbs that dominate Southwest Australian Floristic Region plant communities are unlikely to disperse from the maternal plant more than a few metres unless picked up by cyclonic winds, firestorms, sheet-flooding or animals (see He et al. (2004) for such an exception in *Banksia*). A typical example of limited dispersability emerged in a study of the confinement of hybrid kangaroo paws in a narrow ecotone between the habitats of the parental species (Hopper 1977).

Another significant deficiency in the southwest flora are berries, drupes and other fleshy fruits encasing seeds as an enticement for birds and mammals to consume and disperse seeds in their droppings. Exceptions are semi-parasitic quandongs and sandalwoods (*Santalum*, Santalaceae), mistletoes (Loranthaceae) and many southern heaths (Ericaceae—Calviño-Cancela et al. 2006). Legumes, including wattles (*Acacia*, Mimosaceae), may carry a fleshy aril or elaiosome attached to individual seeds (Sweedman and Merritt 2006). These seeds are usually gathered by ants and dispersed short

Table 4 Seven predictions derived from OCBIL theory

1.	Reduced dispersability, increased local endemism and common rarity
2.	Accentuated persistence—old lineages (Gondwanan Heritage Hypothesis), old individuals (Ultimate Self Hypothesis)
3.	The James Effect (pursuit of heterozygosity, e.g., bird pollination, genomic coalescence)
4.	Prolonged speciation at the margins (Semiarid Cradle Hypothesis)
5.	Adaptation to saline soils (only flat lands such as the Southwest Australian Floristic Region)
6.	Nutritional and other biological specialisation
7.	Special vulnerability (e.g. to soil removal) and enhanced resilience (e.g. to fragmentation)



Fig. 6 Examples of old lineages mentioned in the text that are extant in the Southwest Australian Floristic Region (photos by the author unless otherwise stated): **a** *Dasygogon hookeri* (Dasygogonaceae); **b** *Dasygogon bromeliifolius* (Dasygogonaceae) with honey possum

(*Tarsipes rostratus*); **c** *Calectasia narragara* (Dasygogonaceae—photo RL Barrett); **d** *Agonis flexuosa* (Myrtaceae); **e** *Banksia coccinea* (Proteaceae) with honey possum (*Tarsipes rostratus*); **f** *Cephalotus follicularis* (Cephalotaceae—photo AP Brown)

distances (averaging 1–2 m), often to underground caches (Berg 1975; Krauss and He 2006; Gomez and Espadaler 1998; He et al. 2009). In the Greater Cape, myrmecochory also is common (Bond et al. 1991; Cowling et al. 1994). In a few species, such as the coastal wattle *Acacia cyclops*, the aril is big and bright red, attracting birds as dispersal agents. However, the vast majority of Southwest Australian Floristic Region plants lack such enticements for dispersal.

Nevertheless, occasional long distance dispersal of myrmecochorous seeds by storms or secondary, free-ranging, generalists granivores has been documented over distances of a kilometre or two (e.g. *Daviesia triflora*, Fabaceae—He et al. 2009). However, such

long distance dispersal in these and other OCBIL species studied (He et al. 2004) applies to only 2–7% of seed, compared with estimated long distance dispersal for 18–40% of seeds for YODFEL species (He et al. 2009). It is therefore hypothesized that, in the Southwest Australian Floristic Region, staying close to the maternal plant has been the safest bet for most seeds and propagules for millions of years. In many situations, moving even tens of metres away increases the likelihood of germination on a different soil type or seral stage and therefore being at a competitive disadvantage to species of another soil preference or seral stage. A few recent studies explore this theme—e.g. granite inselberg populations of

Myrtaceae (*Verticordia staminosa*, Yates et al. 2007a; *Eucalyptus caesia*, Byrne and Hopper 2008; Fig. 7).

Contrast this with being a plant in a coniferous forest on the edge of a retreating ice-age glacier in North America, Eurasia or New Zealand (Willson et al. 1990; Petit et al. 2003; Willis and Niklas 2004; Bhagwat and Willis 2008). Vast areas of rejuvenated bare fertile soil are available to those species able to disperse their seeds long distances, albeit through occasional events rarely evident in contemporary ecological or genetic studies (e.g. Cain et al. 2000; Johansen and Latta 2003). It is little wonder that adaptations such as small-seededness, prominent wings on seeds or berry fruits are prevalent in these postglacial habitats (Brundu et al. 2008). For example, vertebrate dispersal ranges up to 60% of the flora in New Zealand forests, and wind dispersal ranges as high as 70% of the flora in Alaska (Willson et al. 1990).

Reduced dispersability also should encourage local genetic divergence and allopatric speciation, resulting in a proliferation of ancient population systems displaying unusually high levels of interpopulational genetic divergence. In turn, given the time involved to persist on OCBILs, prolonged interpopulational divergence should lead to the evolution of suites of local endemic species, assuming positive covariation of these two factors in response to selection (He et al. 2008). Studies of the population genetics, cytogenetics and phylogeography of Southwest Australian Floristic

Region species have indeed affirmed such pronounced interpopulational divergence patterns in many species (Coates 2000; James 2000; Hopper and Gioia 2004; Byrne 2007), with occasional exceptions (e.g. Swartz et al. 2009). In the Cape region, few detailed studies along these lines have been reported (but see Goldblatt's (1986) chromosomal work on *Moraea fugax*). Future studies for the Cape region are needed applying molecular analysis to population phylogeography, as well as traditional chromosome and breeding system work (Hopper et al. 2009). Similarly, the Pantepui biota remains virtually an open book for such work, although a promising start has been made in a few genera (e.g. Givnish et al. 2000).

The three OCBIL regions are rich in local endemic species as predicted (Table 5), extraordinarily so for continental areas (Carlquist 1974; Cowling et al. 1996; Hopper and Gioia 2004). Indeed, the anomaly of species-rich temperate regions in the Southwest Australian Floristic Region and Greater Cape continues to challenge global modellers focussed on latitudinal gradients in the world's biota (Dynesius and Jansson 2000; Jansson 2003; Ricklefs 2004; Wiens and Donoghue 2004; Lavers and Field 2006; Jansson and Davies 2008). Warm and wet environments are not the exclusive zones of high endemism and species richness. A comprehensive theory of diversity needs to embrace a historical perspective (Ricklefs 2004; Wiens and Donoghue 2004) if it is to help explain exceptional richness, especially in present-day low-

Fig. 7 *Eucalyptus caesia* (Myrtaceae), pollinated by birds such as the Brown Honeyeater (*Lichmera indistincta*, Meliphagidae), exemplifies a species with genetically isolated disjunct populations persistent for millions of years on OCBILs in the Southwest Australian Floristic Region (Boyagin Rock—photos by the author)



Table 5 Number of plant species and endemics in OCBIL floristic regions

Area (km ²)	OCBIL Region	# species present	# (%) species endemic	Authority
5,000	Pantepui	2,447	1034 (42%)	Berry and Riina (2005)
90,000	Cape	9,030	6208 (68.7)	Goldblatt and Manning (2000)
100,250	Succulent karoo	4,849	1954 (40.3)	Hilton-Taylor (1996)
302,630	Southwest Australian Floristic Region	6,759	3370 (49)	Hopper and Gioia (2004)

moisture and low-energy environments (Hopper 1979; Cowling 1992).

Besides exceptional local endemism and high species-richness, OCBILs also display extraordinarily high beta and gamma diversity (Cowling et al. 1996; Hopper and Gioia 2004). Rapid geographical replacement of taxa and vegetation types occurs to the point where useful sampling and predictive ecological approaches in YODFELS such as digital terrain modelling account for very little of the observed geographical pattern in OCBIL plant life (e.g. Dirnböck et al. 2002). Simplification of the complex geographical pattern of OCBIL biota with surrogates such as broad vegetation types (e.g. Underwood et al. 2009a, b) is similarly unhelpful, leading to conservation recommendations that ignore where the real major problems and priorities for biodiversity conservation lie (i.e. in the imperilled species-rich shrublands and herbfields of OCBILs rather than the more extensive relatively species-poor woodlands of YODFELS in the Southwest Australian Floristic Region). Apart from reduced dispersability, other plant traits and evolutionary processes contribute to the observed complexity in spatial patterning in OCBIL biota.

2. Accentuated persistence—old lineages (Gondwanan Heritage hypothesis), old individuals (Ultimate Self Hypothesis)

Based on the premise that natural selection has favoured limited dispersability of sedentary organisms (see 1 above), OCBILs should have elevated persistence of lineages and long-lived individuals Given that the three OCBIL regions have not been glaciated since at least the Permian, and they have been exposed to oceanic moderation of climate since the Jurassic, it is hypothesised that some lineages that arose during Gondwanan times or soon thereafter have had the opportunity to persist to the present day—a proposition known as the Gondwanan Heritage Hypothesis (Hopper et al. 1996). If the same

applies to northern continents, an equivalent Laurasian Heritage Hypothesis would pertain. For example, mid-Jurassic fossils of *Torreya* are known (Donoghue et al. 2001) and some Angiosperm families and orders endemic to the Northern Hemisphere have Cretaceous origins (Magallón and Castillo 2009).

Fortunately, we can test for old lineages using molecular phylogenies calibrated with fossils of known age or through the record of occupation of islands of known age. The three OCBIL regions do indeed have significant representation of ancient plant lineages (Table 6). Indeed, the Southwest Australian Floristic Region's Dasypogonales (APG II 2003; Janssen and Bremer 2004—both treat the Dasypogonaceae as an unplaced family) are the world's most localised plant order (one species of *Calectasia* is found in South Australia/Victoria but all other taxa are confined to the Southwest Australian Floristic Region; Fig. 6). The same applies to some animal groups (e.g. the marsupial *Tarsipes rostratus* (Tarsipideae), endemic to the Southwest Australian Floristic Region—Nilsson et al. 2004; Fig. 6). The fossil record in the Southwest Australian Floristic Region affirms the prolonged persistence of some plant genera such as *Banksia* (Proteaceae, 40 Ma) and *Agonis* (Myrtaceae, 30 Ma—Hopper and Gioia 2004; Fig. 6).

Recent attention to such phylogenetic information has been drawn by Forest et al. (2007), who demonstrated that it is now possible to assess phylogenetic diversity at generic level across the Cape flora using molecular tools, and to show that different conservation priorities for regions within the Cape emerge from a consideration of raw species richness alone. Research currently is underway to ascertain if a similar pattern applies to the Southwest Australian Floristic Region (Forest et al., unpublished).

Ancient population systems also are evident in OCBILs, especially the Southwest Australian Floristic Region (Coates 2000; Yates et al. 2007a). For example, the Chiddarcooping population of *Eucalyptus caesia*

Table 6 Persistence exemplified by endemic plant families and the Order Dasypogonales in OCBIL floristic regions

OCBIL Region (data source)	Area (km ²)	# families present	# (%) families endemic	Endemic family and Order names	Authority
Pantepui	5,000	158	1 (0.5)	Tepuianthaceae	Berry and Riina (2005)
Cape	90,000	173	4 (3)	Penaeaceae Grubbiaceae Roridulaceae Geissolomataceae	Goldblatt and Manning (2002)
Succulent karoo	100,250	n.a.	0 (0)	n.a.	Hilton-Taylor (1996)
Southwest Australian Floristic Region	302,630	143	6 (4)	Cephalotaceae Eremosynaceae Emblingiaceae Dasypogonales Anarthriaceae Ecdeiocoleaceae	Hopper and Gioia (2004)

(Fig. 7), characterised by a highly divergent chloroplast haplotype of 10 unique mutations, has an estimated late Pliocene age of 1.76 My (Byrne and Hopper 2008). Similarly, two allopatric population clusters of the endangered shrub *Lambertia orbifolia* (Proteaceae) are estimated to have diverged more than two million years ago (Byrne et al. 1999), and an isolated population of *Acacia verrucula* (Mimosaceae) in the Ravensthorpe Range of southern southwest Australia diverged from its sisters about 900 Ka (Byrne 2007).

Concerning individual organisms, long-term survival on old, stable, infertile environments places strong selection pressures on strategies for persistence. Acquisition of biomass is so difficult that all sorts of mechanisms to retain it should evolve (Orians and Milewski 2007; Read et al. 2009). It is no coincidence that the concept of the persistence niche arose from workers based in the Greater Cape (Bond and Midgley 2001). Extreme clonality and the virtual abandonment of genetic variation, as seen in the Wollemi pine *Wollemia nobilis* (Peakall et al. 2003), a rare endemic of the old landscapes of Sydney's Blue Mountains, were an interest of the University of Western Australia's Sid James, who coined the 'Ultimate Self Hypothesis' to describe this phenomenon (Hopper and Barlow 2000). James' idea is that persistent lineages are 'recombinationally capable with low allelic diversity' (James 2000, pg 341). In some taxa a genotype evolves (the ultimate self) that is eminently suited to all challenges that environments through time pose for them. Therefore, they have no need for genetic variation to cope

with and evolve through environmental change as conventional theory proposes. Hence, the Ultimate Self Hypothesis is the OCBIL equivalent of, and therefore complements, Baker's (1965) 'general-purpose genotype' hypothesis proposed for invasive weeds of and from YODFELs (Lynch 1984). In developing the Ultimate Self Hypothesis, James explored clonality in taxa in southwest Australia ranging from *Drosera* (Chen et al. 1997) to *Eucalyptus* (Kennington and James 1997) and seagrasses (Waycott et al. 1996). Extending the ultimate self through parthenogenesis (Hörandl 2006) might also be expected in OCBILs but, as yet, little detailed information exists on asexual reproduction in our areas of interest.

Various molecular tools and age estimates enable James' predictions to be tested. In the case of mallee eucalypts in the Southwest Australian Floristic Region, estimates for the single known clone of *Eucalyptus phylacis* place it as ca. 6,380 years old (Rossetto et al. 1997). Clonality in other mallee eucalypts is increasingly evident (e.g. Byrne and Hopper 2008). Persistence through resprouting from underground structures is a noteworthy feature of plants in OCBIL regions (Bellingham and Sparrow 2000; Bond and Midgley 2001). Persistence of long-lived adult plants was regarded by Yates et al. (2007a) as fundamental to the prolonged presence of the rare subshrub *Verticordia staminosa* (Myrtaceae) on isolated granite outcrops in the Southwest Australian Floristic Region.

The southwest flora today is dominated by families rich in woody long-lived perennials (Hopper and Gioia

2004) such as Myrtaceae (1,283 species/subspecies), Proteaceae (859), Fabaceae (540), Mimosaceae (503), and Ericaceae (297). Resprouting shrubs and trees dominate many communities, perhaps in response to recurrent fire, but the origins of their persistent perennial habit may have predated modern fire regimes and arisen from one or more multiple causes that damage above-ground parts (Main 1996; Hopper 2003). Photographic evidence is accumulating of long-term persistence of woody individuals in the South West Australian Floristic Region (e.g. Gibson 2007). Of course, shorter-lived, non-sprouting woody plants are also to be found in OCBILs, especially where appropriate fire regimes prevail (Cowling 1987, 1992; Hopper et al. 1990).

3. The James Effect (selection for heterozygosity in small populations, e.g., through 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 due to small population size This process is named for Associate Professor Sid James (1933–1998) of The University of Western Australia, who devoted his research career to exploring hypotheses in the field of genetic system responses to small population size and inbreeding (James 1992, 2000; Hopper and Barlow 2000). If selection favours ‘staying put’ in OCBILs, inbreeding through small population size is likely. Various adaptations enable an escape from the debilitating effects of inbreeding, as the pioneering work of Darwin (1862, 1876) demonstrated.

While seed may not disperse often or widely, pollen might through the help of strong-flying animals, notably birds (Byrne et al. 2007; Yates et al. 2007b; Phillips et al. in press; Krauss et al. 2009). The Southwest Australian Floristic Region has the highest proportion of vertebrate-pollinated plants in the world (15%), a figure that escalates to 40% when only the rarest component of the flora is considered (Hopper et al. 1990, Hopper and Gioia 2004). Vertebrate pollination also features in the Greater Cape, although proportionately less so than for the Southwest Australian Floristic Region (Rebello 1987). Similarly, there are certainly hummingbird-pollinated plants on the Pantepui, but an analysis of reproductive biology of plants of the Gran Sabana suggests that bird-pollinated

species are likely to account for less than 10% of the flora (Ramirez 1993). Perhaps strong flying insects, which account for most pollinator activity in all three OCBILs, play the main role in the Pantepui (e.g. Renner 1989). Some remarkable insect-pollinated systems have evolved in the Greater Cape, including the suite of genera that have adapted to pollination by strong-flying long-tongued flies, oil-collecting bees, butterflies and hopliine beetles (Goldblatt and Manning 2000; Johnson and Steiner 2003; Pauw 2007). Similarly in the Southwest Australian Floristic Region, the evolution of terrestrial orchids has involved multiple shifts from food-rewarding pollination to pollination by sexual deception of male wasps, followed by speciation within clades so-adapted (Hopper and Brown 2007; Brown et al. 2008).

Alternatively, various cytogenetic processes have the effect of conserving heterozygosity despite inbreeding, embraced in the concept of genomic coalescence (James 1992, 2000). James (1992) argued that strong selection for genic and chromosomal mechanisms that prevent loss of genetic variation or adapted gene complexes occurred in small inbred populations. These genetic mechanisms include translocation heterozygosity, dysploidy, polyploidy (Leitch and Leitch 2008) and the evolution of B chromosome systems. An increase in genome size, known to be correlated positively with rarity (Vinogradov 2003; Knight et al. 2005), is hypothesized to reflect the acquisition of increasingly complex genetic system control mechanisms associated with such cytoevolution. Larger genomes are therefore predicted to be evident in OCBIL biota.

The evolution of sex-forms may achieve the same outcome, although evidence for enhanced dioecy is not apparent for OCBILs—‘geographic distribution has no strong effect on the presence or absence of dioecy’ (Renner and Ricklefs 1995, pg 605). About 6% of angiosperms are dioecious, and this mating system is positively correlated with money, abiotic pollination and climbing habit (Renner and Ricklefs 1995). In the Southwest Australian Floristic Region, 4% of flowering plants are dioecious (McComb 1966). A similar proportion has been recorded for the Gran Sabana of the Pantepui (Ramirez 1993). In the Cape Flora dioecy is 6.6%, with the Proteaceae and Restionaceae disproportionately represented among dioecious species (Steiner 1987). Countries dominated by YODFELs vary in the proportion of

dioecious species, from 4–6% for the British Isles, northeast USA and Alaska, to 12% in New Zealand and as high as 28% for the tropical volcanics of Hawaii (references in Steiner 1987).

Some lineages may be able to purge deleterious recessive genes and thereafter not endure the effects of deleterious recessives in inbred populations that persist for long periods of time. The Wollemi pine, occupying the ancient landscapes of the Blue Mountains near Sydney (Twidale 2007), provides such an example (Peakall et al. 2003). Similarly, a few taxa in the Southwest Australian Floristic Region display surprisingly little or no detectable genetic divergence among populations, yet persist in healthy populations of considerable antiquity, e.g. the seagrass *Amphibolus antarcticus* (Waycott et al. 1996). Small populations of *Eucalyptus caesia* (Fig. 7) persisting on isolated granite outcrops for millions of years do not display the effects of inbreeding depression, suggesting that deleterious recessives have been purged by natural selection (Byrne and Hopper 2008). This aspect of the population genetic architecture of plants in the Greater Cape and Pantepui awaits investigation.

A significant consequence of the James Effect, especially when cytogenetic responses to inbreeding are involved, is the incidental evolution of reproductive barriers between daughter and parental populations—speciation. OCBIL theory predicts that such modes of speciation are more common than previously appreciated, and account for species flocks (Cowling and Lamont 1998) much more so than ecological modes of speciation. Indeed, phylogenetic niche conservatism is very common, and biome shifts are rare among sister species (Crisp et al. 2009). Modes of speciation involving genetic system change need more attention, especially in the Greater Cape and Pantepui, where hitherto they remain largely uninvestigated.

Geitonogamous pollination is the most common mating event in hermaphroditic plants, given that pollinators usually work several flowers within a plant before moving to another. As James (2000) emphasized, apparent outbreeders in such cases are habitual inbreeders in terms of pollen flow. Conservation of heterozygosity becomes a powerful target of selection in such circumstances, and the James Effect brings in to focus that an especially diverse array of compensating genetic system responses is likely to be evident in OCBILs.

4. Prolonged speciation at the margins (Semiarid Cradle Hypothesis)

The relative climatic stability of OCBILs should be paralleled by variable climate in adjacent semi-arid areas enhancing prolonged speciation This idea received early attention from Californian plant evolutionary biologists (Stebbins 1952; Stebbins and Major 1965; Axelrod 1967, 1972) and was recently named the Semiarid Cradle Hypothesis (Hopper 2005). It has been embraced for the Southwest Australian Floristic Region (Hopper 1979; Hopper and Gioia 2004) but, interestingly, less so for the Greater Cape Region until recently (e.g. Verboom et al. 2009). The evidence from molecular systematics is now beginning to support the hypothesis in a range of genera. It is rather early to offer comment for the Pantepui, but some promising work on plant speciation is underway (Givnish et al. 2000).

Where in the Greater Cape region have recurrent episodes of speciation occurred? Several genera in the Cape flora have remarkable numbers of species—*Erica* (Ericaceae) with 658, *Aspalathus* (Fabaceae) with 272, *Moraea* (Iridaceae) with 250, *Pelargonium* (Geraniaceae) with 148 etc (Goldblatt and Manning 2002). Large genera of Aizoaceae in the adjacent succulent karoo include *Lampranthus* with 227 species and *Ruschia* with 220 (Klak et al. 2004).

It is becoming clear that, as in California and the Southwest Australian Floristic Region, speciation has been pronounced in the transitional rainfall zone between mesic refugia in the Cape Fold mountains and adjacent semi-arid slopes and lowlands extending inland, to the Eastern Cape and northwards to the Namib Desert. Recent species-level molecular analysis of *Pelargonium* (Bakker et al. 1998; 2005), *Moraea* (Goldblatt et al. 2002), and *Ehrharta* (Poaceae—Verboom et al. 2003) all demonstrate the importance of the semi-arid transitional rainfall belt, ranging from the drier slopes of the Cape Fold mountains up the west coast lowlands of the Cape region and adjacent Namaqualand, as a centre of accentuated species richness and diversification. Molecular phylogenetics of large genera of the 4,750 species of the succulent karoo, especially of Aizoaceae (Klak et al. 2004; Ellis et al. 2006) and daisies (Asteraceae), has revealed extraordinary speciation rates (Verboom et al. 2009).

These two families together comprise the two largest in this spectacularly rich succulent flora.

The Namib is estimated to be of Cretaceous age (Goudie and Eckardt 1999), and, save for some Neogene uplift (Cowling et al. 2009), the Cape Fold mountains have been geologically stable and climatically buffered by adjacent oceans since the Jurassic. Only the subdued flat landscape of the Southwest Australian Floristic Region is of comparable age and greater climatic stability (Cowling et al. 2005a) and also has experienced prolonged absence of glaciation, but the Australian deserts are of mid-late Tertiary age (Hopper 2005; Byrne et al. 2008), considerably younger than the Namib. Hence there has been a much longer period available for speciation in the semiarid cradle of the Greater Cape than in the Southwest Australian Floristic Region. Indeed, the oldest lineages in the Namib speciating southwards through semiarid Namaqualand (Fig. 4) to the Cape are evident in recent studies of insect groups such as the remarkable new order of Heelwalkers (Mantophasmatodea; Damgaard et al. 2008) and in lizards (e.g. Southern Rock Agama—Swart et al. 2009). Similar arguments apply to the semiarid Little Karoo and eastern Cape regions, the latter in particular renowned for its rich subtropical thicket flora with pronounced phylogenetic diversity (Cowling et al. 2005b; Forest et al. 2007).

The contrary conclusion that the Namaqualand region is a site of more recent speciation than the Cape is correct for a number of species-rich genera (Verboom et al. 2009). However, these authors did not distinguish mesic refugia in the Cape from semiarid slopes. Such a distinction is needed to test the Semiarid Cradle Hypothesis. Moreover, sampling of taxa was directed at species-rich genera. A random sample of clades across the flora is needed to ascertain whether or not older lineages are to be found commonly in the semiarid cradle habitats. Forest et al. (2007) did not sample Namaqualand in their study of phylogenetic diversity. OCBIL theory predicts an approximately even dispersion of phylogenetic richness from the mesic refugia of the Cape to the semiarid transitional areas adjacent on slopes and north into Namaqualand. A test for even phylogenetic diversity pattern across similar mesic to transitional areas in the Southwest Australian Floristic Region is underway currently (Forest et al., in prep.).

Knowledge of modes of speciation in the Greater Cape flora remains fragmentary and speculative. One

focus is on ecological modes. Contemporary authors (e.g. Linder 2005) emphasize divergence due to aridification, edaphic and topographic complexity, fire-created niches and pollinator shifts. Many other comparable areas of the world characterised by these environmental attributes do not approach the species richness of the Greater Cape, especially three of the four with a mediterranean climate (the Southwest Australian Floristic Region, of course, lacks significant mountains). Consequently, other factors must be central to explain the Greater Cape's extraordinary floristic richness (Hopper and Gioia 2004; Cowling et al. 2009).

If recurrent speciation among old lineages has occurred in the semiarid cradle of the Greater Cape, new environmental factors emerge as significant—those emphasised in OCBIL theory—including unparalleled opportunities for population persistence, isolation, and highly tuned adaptation to local circumstances (see also Cowling et al. 2009). However, ecological factors alone do not necessarily lead to speciation, as is evident in many countries where widespread generalists occupy a broad range of soil types, topographies and climatic zones (e.g. species of boreal conifer forests—Petit et al. 2003). Of equal relevance is evidence highlighted above that phylogenetic niche conservatism is much more common than previously understood, indicating that ecological speciation may not be as important as given recent credence.

Alternatively, then, contemporary theory outlined in the preceding section indicates the importance of genetic and cytogenetic processes that ultimately result in the fixation of reproductive or ecological isolating barriers with speciation as an incidental byproduct. Chromosomal change is one of the more obvious adaptive genetic system responses in such circumstances. In the Greater Cape region, OCBIL theory brings sharply into focus the need for future studies to apply molecular analysis, as well as traditional chromosome and breeding system work to population phylogeography. The power of this approach to help unravel evolutionary processes at the population level has been demonstrated for taxa of the Southwest Australian Floristic Region (e.g. James 1992, 2000; James et al. 1999; Bussell et al. 2002; Coates et al. 2003; Watanabe et al. 2006).

5. Nutritional and other biological specialisation

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 and parasitism etc (e.g. Pate 1989; Pate et al. 1984; Cowling and Richardson 1995; Cowling and Pierce 1999; Lambers and Shane 2007; Orians and Milewski 2007; Phillips et al. *in press*).

The nutritional challenge posed by deeply weathered, highly infertile soils will have pervasive biological outcomes, especially given the tens of millions of years that OCBIL organisms have had to evolve *in situ*. Accentuated development of ecophysiological adaptations in roots and other underground structures is evident (Lamont 1982). Cluster roots (Shane and Lambers 2005), dauciform roots (Shane et al. 2005), geophytism (Parsons and Hopper 2003; Proches et al. 2005a) and extensive water-foraging strategies (Poot and Lambers 2008) are evident in the Southwest Australian Floristic Region and the Greater Cape. Removal of perennial native vegetation in these regions has required massive importation of nutrients to sustain cereal agriculture (Cordell et al. 2009). Superphosphate is spread annually on paddocks, often aerially, where wind drift into adjacent remnants of native vegetation causes phosphate poisoning of native plants and invasion of YODFELs and OCBILs alike by non-native weedy species (Hobbs and Atkins 1991). Aerial deposition of nutrient-enriched dust storms is an additional background factor that may have enhanced Greater Cape soils historically (Soderberg and Compton 2007). The more impoverished soils of the Southwest Australian Floristic Region appear not to have received such geologically exogenous enrichment due to prevailing oceanic westerly winds (Hesse and McTainsh 2003).

Mycorrhizal and bacterial symbioses are found in the Southwest Australian Floristic Region and the Greater Cape, though usually in taxa common on less infertile soils than those of OCBILs (Lamont 1982; Brundrett 2004, 2009; Lambers et al. 2008). In southwest Australia, ectomycorrhizal partnerships are five times more frequent than expected, associated in particular with Myrtaceae and Fabaceae (Brundrett 2009). Microbial symbioses also are seen among marsupial herbivores and termites in these two

regions (Kinnear et al. 1979; Kinnear and Main 1979; Douglas 2009).

Sophisticated mechanisms for mining and remobilisation of P are especially marked on OCBILs, for example, in *Banksia* (Denton et al. 2007; Lambers et al. 2008). Intriguingly, such adaptations have been hypothesised as phytotaria—agents of soil bioengineering leading to ‘the formation of silicon- or iron-based linings of vertical channels and pores, binding of sand on roots, generation of organically derived hydrophobicity, development of clay-based hardpans and texture-contrast seals, precipitation of silcrete, calcrete and ferricrete pavements, effective accessing and conservation of P resources, including mining by microbes and the biological cycling of Si and Al via plants and micro-organisms’ which create phytotaria ... ‘the collective outcomes of the above biotic influences in construction and maintenance of niches peculiar to specific vegetation types (Verboom and Pate 2006a, pg 71; see also Pate et al. 2001; Verboom and Pate 2003, 2006b; Pate and Verboom 2009). Thus, plants with traits conducive to long-term persistence in OCBILs have modified their edaphic environment to further enhance their persistence and keep competitors at bay.

A range of other biological adaptations may be predicted for OCBILs. For example, mechanical and chemical defences of plant parts will be accentuated in OCBILs, given the scarcity of essential nutrients in impoverished soils (Orians and Milewski 2007; Read et al. 2009). Deciduous leaves are rarely seen for the same reason in the Southwest Australian Floristic Region, where infertility is greatest (Dallman 1998). Deciduous shrubs are more evident in the Greater Cape, especially in the succulent karoo vegetation of Namaqualand where soils are less infertile.

As discussed earlier, an accentuated degree of myrmecochory and seed burial will be evident. Underground caching of seeds by animals other than ants has been documented, though this is a process at great threat due to local extinction of relevant marsupials in the Southwest Australian Floristic Region and beyond (Murphy et al. 2005).

Parasitism (Press and Graves 1995; Nickrent et al. 1998) would be expected to be highly developed in OCBIL plants, providing an alternative to evolving direct nutrient scavenging adaptations in highly infertile soils. Curiously, this does not seem to be the case, at least in terms of numbers of species of parasitic plants in the South West Australian Floristic

Region (Brundrett 2009). However, generic diversity of parasites and hemiparasites is high, indicating that persistence of old clades has been favoured. *Nuytsia floribunda*, for example, an arborescent monotypic genus endemic to the Southwest Australian Floristic Region, is sister to all other Loranthaceae (Wilson and Calvin 2007). The Greater Cape is similarly rich in parasitic plants at generic level, though species-poor relative to tropical regions (Visser 1981; Polhill and Wiens 1998).

Adaptations for long distance pollination by strong flying animals is another prediction for OCBILs discussed above (see the James Effect). Nectar is energetically inexpensive for plants to produce in environments impoverished of nutrients. Discovery of new adaptive traits in pollination ecology has been especially prominent and ongoing for OCBIL biotas (Johnson 2006; Phillips et al. 2009). Intriguingly, some species in Namaqualand have diverged in floral morphology without obvious differences in pollination ecology, revealing a level of complexity in trait evolution hitherto unsuspected (Ellis and Johnson 2009). A rich field for future enquiry undoubtedly exists in the pollination ecology of OCBIL plants.

The world's greatest diversity of carnivorous plant genera (Ellison and Gotelli 2009) is seen in the Pantepui (Givnish et al. 2000), whereas explosive radiation of sundews (*Drosera*) and an unexpectedly high proportion of carnivorous plants is evident in the Southwest Australian Floristic Region (Chen et al. 1997; Rivadavia et al. 2003; Heubl et al. 2006; Brundrett 2009). That this is an ancient solution to the nutritional challenges of OCBILs is seen in the presence of the Albany pitcher plant, *Cephalotus folliularis* (Cephalotaceae—Fig. 6f), a monotypic relict family of carnivores endemic to the high rainfall swamps of the Southwest Australian Floristic Region (Hopper and Gioia 2004; Ellison and Gotelli 2009).

6. Adaptation to saline soils (only on flat inland topography such as in the Southwest Australian Floristic Region)

The uniquely flat landscapes of the Southwest Australian Floristic Region have had prolonged presence of saline palaeoriver systems favouring evolution of accentuated tolerance to salinity (George et al. 2006) Halophyte diversity is extraordinary in the Southwest Australian Floristic Region, evolving

in many phylogenetically independent lineages, from the usual and expected families such as Chenopodiaceae (Shepherd et al. 2004) to the most dominant trees, such as individual species and series of eucalypts (Brooker and Hopper 1989). Such radiations date back at least to the late Miocene, with subsequent acceleration associated with increasing aridity (Martin 2006). The more mountainous OCBIL terrains of the Greater Cape and Pantepui have resulted in better flushing of salts from the landscape by rainfall, and special salt tolerance consequently is found rarely.

A suite of plants has evolved that are endemic to slightly elevated sandy rises embedded within southwest Australian salt lakes. These plants derive moisture from fresh water lenses narrowly perched above saline groundwater, and are especially vulnerable to landscape salinisation (Beresford 2001; George et al. 2006). *Tribonanthes minor*, for example, appears to have originated some 10 my ago (Hopper et al. 2009). *Caladenia drakeoides* is a critically endangered species with a similar ecology (Hopper et al. 1990; Brown et al. 1998). These examples bring us to a consideration of other special conservation challenges and opportunities predicted from OCBIL theory.

7. Special vulnerability (e.g. to soil removal) and enhanced resilience (e.g. to fragmentation)

Unusual resiliences and vulnerabilities might be evident among OCBIL organisms, such as enhanced abilities to persist in small fragmented populations but great susceptibility to major soil disturbances The biological responses arising from evolution in localised places subjected to minor soil disturbance and oceanically modulated stable climatic buffering will be profound. Organisms that have evolved for millions of years in fragmented population systems may well display unexpected persistence and resilience to modern fragmentation caused by human habitat clearance for agriculture, urbanisation and industry. Persistence of small populations on isolated granite outcrops in the Southwest Australian Floristic Region has been mentioned above. In the Greater Cape the principle of retaining small remnants of OCBIL vegetation is well established (Bond et al. 1988; Cowling and Bond 1991; Kemper et al. 1999; Cowling et al. 2003; Pressey et al. 2003). An interesting example concerns several orchids, including the common but disjunct populations of *Pterygodium*

catholicum, specialized for pollination by the oil collecting mellitid bee *Rediviva peringueyi* (Pauw 2007). Small nature reserves averaging 30 ha (ranging from 4 ha to 609 ha) supported high capsule set in *P. catholicum* in rural areas, even where fragmented by agriculture. Only in small urban areas where most indigenous vegetation in the surrounding landscape matrix had been removed was capsule set significantly depressed, and the pollinators presumably were rendered locally extinct. This study also demonstrated in early postfire successional vegetation almost complete reproductive impairment for populations of *P. catholicum* on sandy soils occupied by fynbos, irrespective of reserve size, compared with 25–100% capsule set for populations on clay-based soils occupied by renosterveld. Natural selection favouring disjunct populations confined to specific soils mixed in fine-scale mosaics with other soil types underlies the natural fragmentation of many OCBIL organisms.

Because wholesale topsoil removal or replacement by glaciation, inundation, volcanism, orogeny, dust storms etc has not occurred frequently on OCBILs, unusual vulnerability to soil removal and/or even minor forms of disturbance is to be expected. Work by Rokich et al. (2000) has demonstrated that the top 5 cm of soil in Southwest Australian Floristic Region *Banksia* woodlands contains 90% of all seed and micro-organisms that sustain the above ground vascular plant communities. The next 5 cm deeper contains a further 5%. Removal of this thin layer of topsoil compromises the ability of the community to persist and recover from other disturbances for very long periods of time. The opportunity in space and time is opened for invasive organisms, usually from YODFEL regions, to colonise the bare depleted soil.

This soil phenomenon leads to a prediction that OCBIL regions should display high levels of invasibility. A test of this hypothesis in a global inventory of the proportion of non-native weed species on granite outcrops provides some support (Fig. 8). Regions of eastern Australia, South Africa and the USA where glacial activity, orogeny, marine inundation or prolonged soil disturbance by animals have occurred support resilient native floras able to compete with exotic species under ongoing soil disturbance regimes. In contrast, native plant species on the ancient Australian landscapes unaffected by glacial, eustatic, orogenic or extensive soil disturbance by animals, such as the Southwest Australian

Floristic Region or South Australia's Eyre Peninsula, are much less resilient to non-native species' invasion, particularly where contemporary disturbance coincides with artificially elevated soil fertility causing P toxicity and other effects (Cramer and Hobbs 2007).

Invasibility of Cape plant communities by species of *Hakea*, *Acacia*, *Eucalyptus* and *Pinus* is exacerbated by fire regimes (e.g. Holmes et al. 2000). Reciprocally, Greater Cape geophytes and grasses such as *Ehrharta calycina* and *Eragrostis curvula* invade nutrient-enriched and frequently burnt Southwest Australian Floristic Region plant communities (e.g. Fisher et al. 2006). However, interpreting the evolutionary significance of fire in OCBILs is challenging indeed, and deserves brief comment.

The evolutionary conundrum of fire

Fire today is a common agent of disturbance in the Southwest Australian Floristic Region and in the Greater Cape, producing complex ecological outcomes because of the great variability in components of the fire regime such as frequency, intensity, seasonality and areal extent (Cowling 1992; Whelan 1995; Bond and van Wilgen 1996; Abbott and Burrows 2003; Hopper 2003). Its role in the Pantepui is less conspicuous and somewhat controversial, although occasional fire does occur (Givnish et al. 1986; Huber 1995b, 2006; Rull 1999).

There is a need for caution in reference to fire as a major evolutionary force in OCBILs, primarily because current evidence supporting such a hypothesis is equivocal at best. Many authors hold an alternative view, arguing for a central role of fire on the evolution of OCBIL biota (e.g. Cowling 1987, 1992; Wisheu et al. 2000; Orians and Milewski 2007). As explained earlier, the literature on plant traits inferred to be adaptations to fire (or fire regimes) is replete with confusion between adaptations and exaptations (Whelan 1995; Hopper 2003). Multiple evolutionary selective forces other than fire may be invoked as causes of traits that function today in coping with fire, including such traits as resprouting, obligate seed regeneration, brady-spory (less precisely named 'serotiny' by many), ethylene-induced post-fire flowering, hard-seededness, smoke-stimulated germination, myrmecochory and flammability of plant parts. Of course, increases in fitness and response to fire regimes for such traits

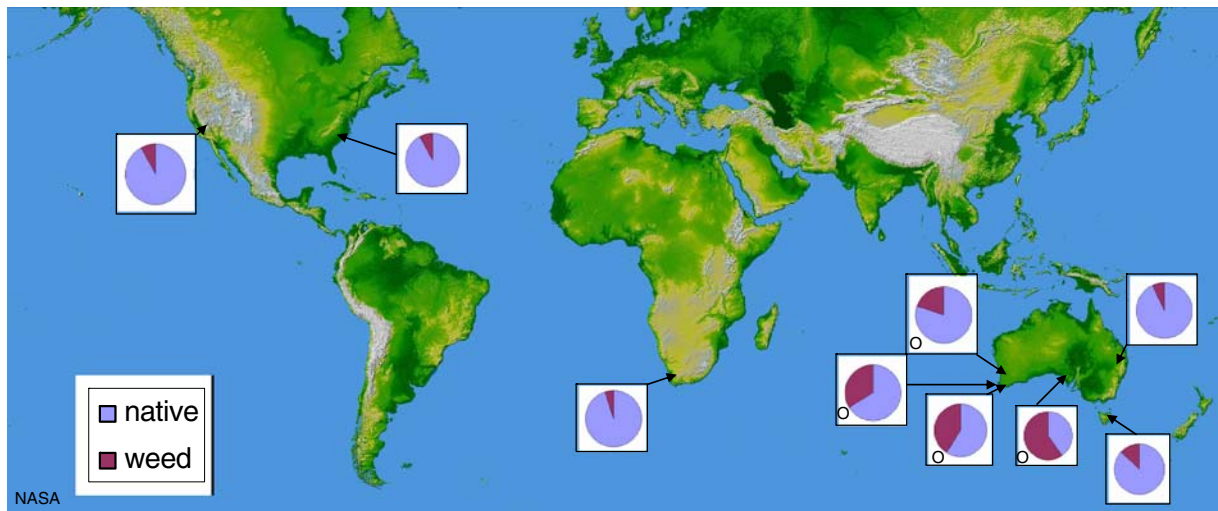


Fig. 8 The proportions of native plants versus exotic invasive non-native weeds on granite outcrop systems in selected OCBILs (*piecharts labelled O*) and YODFELs (Hopper

might exist. However, there is a need for a more critical approach to the question of adaptation in relation to fire regimes. Careful experimentation demonstrating function, inheritance, natural selection and phylogenetic context would furnish convincing evidence testing the evolutionary importance of fire regimes in OCBILs as a selective force on plant traits.

Conservation implications for biodiversity of OCBILS

The above attempt to achieve an integration of ideas pertaining to OCBIL theory leads to a series of hypotheses about conservation strategies, several of which are the converse of what conservation theory developed from studies of YODFEL organisms has proposed (Table 7). These are discussed briefly in the following text.

Providing space—small and isolated may be sufficient for persistence, edge-effects aside

Every remnant of native vegetation, no matter how small, is worth retaining. Remnants will have populations of some OCBIL organisms exhibiting unexpected persistence and enhanced resilience, despite massive fragmentation and loss of surrounding vegetation. In short, OCBIL biota can and do persist in unusually small fragments for longer than YODFEL biota would

2002). Outcrops in South Africa's Greater Cape are embedded in landscapes of variable age, from old to young

last under similar circumstances. Work on fragmentation effects in the Cape best illustrate the principle of not discounting small remnants of OCBIL vegetation (Bond et al. 1988; Cowling and Bond 1991; Kemper et al. 1999; Cowling et al. 2003; Pressey et al. 2003; Pauw 2007). Similar evidence exists in studies within the Southwest Australian Floristic Region (e.g. Yates et al. 2007c).

The above conclusion regarding the value of small remnants goes against the grain of conventional conservation theory, and brings into sharp focus the need for caution in applying methodological approaches and theory developed primarily on YODFELs to OCBIL biota. For example, the so-called SLOSS debate (single large versus several small) on nature reserve design reasonably concluded that larger was better in most cases studied (usually YODFELs, or on mobile components of OCBIL biota—Murphy 1989; Whittaker et al. 2005). Murphy (1989, pg 83) asserted: "... no competent biologist has ever suggested that reserves should not be as large as possible. Statements that small reserves could be designed that would protect more species than certain single large reserves led to the illogical suggestion that the fragmentation of intact habitat areas could be beneficial ... their conclusions are what every land developer and every timber industry representative wants to hear—chopping up natural habitats does not really put species at risk." Yet, for OCBILs, there is a converse to Murphy's line of argument. Fragmentation of the broader matrix of

Table 7 Conserving OCBIL biodiversity—hypotheses and strategies

- Every native vegetation remnant on OCBILs is valuable, no matter how small, and may have unique persisting communities—they are not interchangeable as often are those of YODFELS
- Small insular areas are often as good as large connected areas for OCBIL biota, edge-effects aside
- Connecting isolated OCBIL communities through revegetated corridors is often unnecessary and might foster weed, feral animal and disease invasions
- Human disturbance is often detrimental. There is a need in OCBILs to:
 - Focus human disturbance on YODFELS, away from OCBILs—e.g. on less infertile soils along coastal/wetland margins
 - Provide space for the biodiversity of OCBILs
 - Minimise soil removal via bulldozing etc
 - Minimise importation of nutrients
 - Minimise pollution causing climate change
 - Minimise importation of alien plants, animals and diseases, and control where possible
 - Minimise groundwater extraction
 - Minimise logging and removal of long-lived adult plants
 - Store seeds and other propagules
- In restoration of OCBIL vegetation, plant local seeds or cuttings

intact vegetation, threatening as it is, may have little impact on naturally disjunct OCBIL biota if their population systems remain intact and provided edge effects are minimal. Significant edge effects from invasive species, altered hydrogeomorphological processes, wind-drift of fertilizers, increased human access and disturbance etc. clearly will negate this statement. However, of greatest risk to OCBIL biota is the conclusion that because fragments are small, they are worthless for conservation. The same threat also applies for some YODFEL fragments of great conservation value—Arroyo-Rodriguez et al. (2009).

All remnants provide invaluable and irreplaceable nuclei for the future repair and restoration of OCBIL biota. We should certainly be wary of views that remnants are ‘too small to be viable’. Such statements are drawn from theory pertinent to YODFEL organisms, which would not have enough space (resources) to persist in the small remnants that are possible for OCBIL organisms to occupy and continue in their accentuated persistence. In a world where a fifth of carbon emissions still arise from ongoing destruction and burning of remaining wild vegetation (Houghton 2004), retaining remnants is especially critical in OCBIL regions, where the chances of repair and restoration are significantly more challenging than they are for YODFEL regions.

Providing space for organisms on OCBILs is as fundamental as it is for organisms on YODFELS. The major difference is that organisms of OCBILs rarely

will colonise space previously cleared of native vegetation of their own accord (Cramer and Hobbs 2007). Attempts at restoration and repair of disturbed and depleted OCBIL communities are in their infancy (Rokich et al. 2000), with the exception of more than three decades’ work on post-mining restoration in jarrah (*Eucalyptus marginata*) forest occupying OCBILs of the Darling Range near Perth (Koch and Hobbs 2007). Much more success has occurred with restoration of YODFEL communities, given that they are full of good dispersers and colonisers that can largely regenerate producing self-sustaining populations if space is provided.

Linking fragmented remnants of native vegetation with revegetated corridors is a perfectly appropriate strategy in YODFELS, but something we should be wary of for OCBILs. This conservation strategy, driven from a focus on mobile mammals and birds of YODFELS (Saunders et al. 1990), has significant drawbacks with OCBIL biota. The natural fragmentation and insularity of OCBIL communities should be understood and respected when devising revegetation strategies. At worst, revegetated corridors linking OCBIL communities become invasion portals for weeds (Proches et al. 2005b), feral animals and exotic diseases such as dieback due to root-rot (Shearer et al. 2004). The controversial suggestion that: ‘many native species of conservation concern have limited dispersal abilities and therefore would be more likely to benefit from corridors’ (Levy et al. 2005, pg 780)

as a counter to concerns about corridors as portals for invasives raised by Greater Cape botanists (Proches et al. 2005b) illustrates how contrasting perspectives have developed from foci on YODFEL v/s OCBIL biota.

The criticality of leaving topsoil intact

Bulldozing and removal of the thin layer of topsoil covering OCBILs has major negative consequences, whereas on YODFELs it is arguably little different from other erosional or depositional forces of nature arising from glaciation, flooding, wind storms, volcanism or orogeny. There are, of course, exceptions on YODFELs, but many species can survive such disturbances (Whittaker et al. 2005). Destruction of native biota on OCBILs followed the rapid and extensive clearance of native vegetation for cereal agriculture by bulldozers since World War II in the Southwest Australian Floristic Region (Beresford 2001). The flat subdued landscape has been relatively easy to work with heavy machinery, despite the rich covering of hardwood forest and shrubby vegetation. Removal of this perennial vegetation has required massive importation of readily available nutrients (superphosphate and trace elements) to sustain cereal agriculture. Moreover, the saline water-tables kept deep below the surface by water use of the native perennial vegetation have risen, extending ancient natural salt lake systems outwards and upwards across the landscape. Loss of a third of the current productive agricultural land due to rising salinity, as well as extensive damage to town and farm buildings, roads and other infrastructure in vulnerable parts of the landscape are increasingly evident or predicted (George et al. 2006). Replacing annual crops with deep-rooted perennials will be part of the solution to this significant environmental challenge.

Some segments of the Southwest Australian Floristic Region OCBILs have been so unattractive or impossible to work for agriculture that they have been spared from conversion by heavy machinery (e.g. rock outcrops and other hills, salt lake systems). These segments retain invaluable remnants of the native biota that will be of use in future repair and restoration. Similarly, OCBILs of the Greater Cape and Pantepui have been protected from the worst excesses of human disturbance because of their mountainous terrain. OCBIL communities in these regions are more intact comparatively, with a few

exceptions (e.g. the Cape Flats and renosterveld), than those in the Southwest Australian Floristic Region.

Sensitivity to soil removal is less pronounced in YODFELs embedded within OCBIL regions. Given the extensive Neogene uplift of mountains in the Greater Cape (Cowling et al. 2009), the area of YODFELs is greater than in the Southwest Australian Floristic Region and Pantepui. Nevertheless, the extensive occurrence of geophytes (Proches et al. 2005a) and resprouting shrubs in YODFELs occupied by fynbos, renosterveld and succulent karoo suggests that wholesale topsoil removal would be detrimental even for these landscapes so regularly disturbed by erosional and other processes.

Climate change and OCBILs

Given that climatic buffering over tens of millions of years has been important to the persistence of OCBIL communities, the spectre of rapid global warming in our time is particularly worrying for the world's OCBIL regions (Malcolm et al. 2006; Midgley and Thuiller 2005; Rull and Vegas-Vilarrubia 2006). However, present modeling based on climatic envelope approaches does not take account of the fundamental biological differences between organisms of OCBILs and YODFELs. Climatic envelope modeling seems more appropriate for easily-dispersed YODFEL biota than for that of OCBILs, but even with such YODFEL biota some caution is also needed in applying climatic envelope analysis (Hampe 2004; Whittaker et al. 2005; Ohlemüller et al. 2006; Millar et al. 2007).

An appreciation of the limited seed dispersal capabilities of most Southwest Australian Floristic Region plants suggests that tracking climate change by organisms is an unlikely option. Some dispersal might occur along local YODFELs such as coastal dunes, drainage lines and relatively fertile gentle slopes. The converse seems likely for plants of most other habitats, however. Much more likely for OCBIL plants under a drying climate scenario is that populations would die out in marginal habitat and persist only in refugial wetter habitat in the landscape. Evidence for historical contraction to small disjunct refugial sites is conspicuous in the Southwest Australian Floristic Region and in the adjacent arid zone (Hopper 1979; Hopper and Gioia 2004; Byrne et al. 2008). Many rare relictual species are found in locally wet

habitat such as on granite outcrops (e.g. Byrne and Hopper 2008; Fig. 7), on the southern slopes of breakaways (escarpments flanking mesas), on seeps and in ephemeral swamps (Brown et al. 1998). Conservation of such seasonally wet habitats will be a key strategy as the climate warms (Horwitz et al. 2008).

It is biologically naïve to assume in climatic modelling that OCBIL species are capable of colonising most patches of preferred soil within a given climatic envelope. Decades of searching for rare and poorly known plant species in the Southwest Australian Floristic Region (Hopper et al. 1990) has impressed upon me that occupation of all or even most of the available preferred soil patches occurs rarely. It is far more common for species to occur sporadically in localised patches even if their preferred soil is quite abundant and continuous over many kilometres. This reflects millions of years of population flux, local adaptation and local extinction, superbly illustrated recently for the granite outcrop shrub *Verticordia staminosa* (Yates et al. 2007a).

One only has to reflect upon the recent death of many plants on shallow soils adjacent to granite outcrops in the jarrah forest, wheatbelt and goldfields during summer heatwaves (Hopper unpublished; Yates et al. 2003) to appreciate that persistent global warming will have immediate and dramatic impact locally. It is the accelerated pace of present climate change, unprecedented in geological time, that poses such a significant threat to OCBIL floras that have persisted in climatically buffered regions for tens of millions of years. Moreover, given the severe limitations on seed dispersal of most native plants and relatively high proportion of non-native weeds now in disturbed and fertilised sites in the Southwest Australian Floristic Region, plant deaths associated with global warming may well exacerbate weed invasion and establishment.

Invasion biology

Left undisturbed, OCBILs are exceptionally resilient to invasion by non-native exotic organisms. However, this resilience tips over to extreme vulnerability when disturbance regimes are altered. A classic example is seen with clearing of native vegetation followed by application of fertilisers or altered hydrological regimes

for cereal agriculture, pasture production or horticulture. Then the impacts of importation of alien plants, animals and diseases are profound. Vast areas of OCBILs in the Southwest Australian Floristic Region have been occupied by European and South African non-native exotic weeds associated with agricultural and related landscape disturbances (Hussey et al. 2007). The sheer diversity of invasive weeds and numerical abundance of the most pernicious species in the Region (e.g. the grasses *Briza maxima* and *Avena fatua* from the Mediterranean or *Ehrharta longiflora* from South Africa) indicate an unusual level of vulnerability for OCBILs v/s YODFELs). Strict controls are needed, both with importation and in dealing with those invasives that already have become established.

Groves (1991) and Groves and Kilby (1993) considered the non-native floras of California, South Australia, Chile and South Africa, noting close to an order of magnitude more weed species recorded for the former two regions compared with those recorded for the latter two. No explanatory hypothesis for this striking difference in invasive floras was offered. However, it was noted for all four mediterranean climate regions that the majority of weed species had European origins, were either grasses or composites, were annuals or biennials and had been introduced deliberately as ornamental plants. Pre-adaptation to fire, low nutrients and grazing were suggested as attributes favouring establishment of weeds in the four regions. Of these factors, low nutrients are a hallmark of South African fynbos and South Australian mallee-heath weathered soils, but the younger soils of California and Chile are much richer.

In an attempt to control for geological variation across some of these regions, a cross-continental study of native v/s non-native exotic weeds on granite outcrops established that: 'Regions of eastern Australia, South Africa and the USA where glacial activity, orogeny, marine inundation or prolonged soil disturbance by animals have occurred have resilient native floras able to compete with exotics under ongoing soil disturbance regimes. In contrast, native plants on the ancient Australian landscapes unaffected by glacial, eustatic, orogenic or extensive soil disturbance by animals, such as southern WA or Eyre Peninsula, are much less resilient to weed invasion, particularly where contemporary disturbance coin-

cides with elevated soil fertility.’ (Hopper 2002, pg 96; see Fig. 8).

Repair and restoration of OCBIL communities should include control of exotics to have any chance of success (Cramer and Hobbs 2007). Major programmes for fox control and veld grass (*Ehrharta calycina*) control in the Southwest Australian Floristic Region have yielded extraordinary conservation benefits (Fisher et al. 2006; Kinnear et al. 1998). In the Greater Cape, the Working for Water Programme has achieved similar outcomes, creating jobs and delivering improved water supplies for human consumption as well as sources of fuelwood for impoverished people through the removal of invasive woody plants (van Wilgen et al. 1998). Fortunately thus far, the inaccessibility of the Pantepui has obviated the need for control of exotic species as few exotics have gained a foothold (Huber 1995b).

Minimising human disturbance

An overarching strategy is wherever possible to contain and minimise human disturbance of OCBILs and their rich endemic biota (Table 7). First peoples in the Southwest Australian Floristic Region and Greater Cape did just that, focussing on the more fertile and productive YODFELs embedded in these regions. Their numbers and impact remained low over long periods of time, at least 45,000 years in the Southwest Australian Floristic Region (Allen and O’Connell 2003), and more than double that for early modern humans in the Greater Cape (Parkington 2006). The remaining biota of OCBILs that persist are the legacy of the relatively sustainable life styles of Aboriginal people. The Pantepui appear not to have been colonised by first peoples because of inaccessibility as well as the lack of sizable game and few edible plants (Huber 1995b).

Today, despite vastly increased populations and consumption levels, the focus of human land-use remains much the same, with most cities, towns and agriculture located on YODFELs embedded within the Southwest Australian Floristic Region and Greater Cape—i.e. fertile valley floors and slopes, along the margins of wetlands and the coast. However, other human-mediated activities show no such localisation, intruding extensively into OCBILs—grazing, urbanization, infrastructure corridors for transport and

energy transmission, logging, fire, some forms of intensive agriculture, wildflower picking for cutflower sales, and the increasingly demanding search for fresh water and mineral resources to support contemporary economies.

The fundamental importance of minimising human impact can be illustrated with the extensive investigation into the causes of rarity of *Verticordia staminosa* subsp. *staminosa* (Yates et al. 2007a). It was discovered that removal of long-lived adult plants was the single most significant threat facing this rare endemic known from a thriving but highly localised population on a single granite inselberg in the Southwest Australian Floristic Region. We would do well to leave such global treasures alone, to carry on as they have done for millions of years (Byrne and Hopper 2008), and reduce our impact to opportunities for minimal-impact research and tourism. When resources are so rare and essential for local human quality of life, some additional disturbance may be required.

Repair and restoration of OCBILS—an infant science and practice

The extraordinary limitations on seed dispersal for most Southwest Australian Floristic Region, Greater Cape and Pantepui plant species indicate that using local seed and planting to soil type for revegetation are critical—more so than anywhere else on Earth (Hopper 1997; Holmes and Richardson 1999). These two practices will ensure the conservation of the full range of biodiversity, including all the local animals that track floristic differences over short distances.

Naturally there will be differences in what constitutes local seed depending upon the species of concern. Research currently is underway in the Southwest Australian Floristic Region to help put some provenance figures for local gene pools on a range of plant species of different biology and life-form (Bussell et al. 2006; Krauss and He 2006). Already we know that forest and major woodland trees in the Southwest Australian Floristic Region having continuous large populations are more genetically uniform across their geographical range than their understorey plants such as triggerplants (*Stylidium*, Stylidiaceae), kangaroo paws (*Anigozanthos*, Haemodoraceae), or mallee eucalypt species distributed on isolated granite outcrops. Until such research is well advanced, however,

the precautionary approach is to stay as local as possible in seed collecting within the soil type being revegetated. A similar strategy would seem desirable for repairing OCBIL vegetation in the Greater Cape (Holmes and Richardson 1999), but knowledge there of population genetic architecture and seed provenance needs much more research.

A recent review of sourcing seed for broadscale restoration argues against the wisdom of applying the precautionary principle to seed provenance (Broadhurst et al. 2008). It is proposed that local seed are often difficult or impossible to source in quantity in a reasonable time, that they are often inbred, that the scientific evidence for local adaptation is rarely available and, even if it were, climate change would render local adaptation meaningless in a rapidly warming world. As suggested above, there may well be greater latitude for sourcing seeds of species of YODFELs or for certain plant life histories generally, but to apply the same logic to all species of OCBILs poses grave risks indeed of creating genetically homogenised populations doomed to reproductive failure for many taxa (see also James 2000; Krauss and He 2006). There is mounting evidence that evolutionary responses of plant species to past (Cenozoic) climate change have involved contracting to local disjunct refugia both in peri-glacial environments and in aridifying environments (references above). Such local refugial populations are fundamentally important sources of seed or germplasm for restoration in OCBILs at least, and perhaps should not be ignored or homogenised. This debate exemplifies the pitfalls of attempts at global prescriptions in restoration ecology. As I have proposed above, echoing James (1992, 2000) and Main (1996), OCBIL biota may have biological attributes contrary to mainstream thinking in population genetics developed primarily from studies on YODFEL organisms. This view is reinforced by some surprising discoveries recently regarding the ability of myrtaceous trees such as eucalypts and shrubs to produce high quality seeds, albeit in reduced quantity, in very small populations (Krauss et al. 2007; Yates et al. 2007b; Ottewell et al. 2009).

There is similarly a fundamental need for caution and to rethink how agriculture is conducted on OCBILs if sustainability is a goal (Walker et al.

2001; Cramer and Hobbs 2007). It is evident that mainstream agricultural practice on OCBILs leads to desertification, salinization, soil acidification, non-native weed invasion and extensive loss of valuable topsoil through erosion and wind storms. Farmers from OCBIL regions are learning from each other through comparative studies and communication. For example, strip farming as practised by Nama people and others in the Greater Cape provides an example of an agricultural system that has lasted at least 2000 years (Fig. 9). Strip farming or alley cropping thus enables persistence of native biota in narrow bands interspersed with cereal crops. In contrast, extensive clearing of native vegetation for cereal or horticultural crops has been widely and rapidly practised in the Southwest Australian Floristic Region (Beresford 2001), except recently where greater attention to leaving vegetated buffers along drainage lines has become common (Watson 1991). Researchers and farmers have developed appropriate concepts for OCBILs such as minimum tillage to retain the fragile structure of top soil (Hobbs et al. 2008). In the Cape, protocols developed for restoration of fynbos illustrate many of the above principles (Holmes and Richardson 1999).

Where decisions are taken to abandon agricultural land in favour of local biodiversity, it is clear that old field succession theory developed primarily for YODFELs has limitations in regions dominated by OCBILs (Walker and Reddell 2007; Cramer et al. 2008). Aspects of community dynamics may differ fundamentally. In cases of self-recovering YODFELs with relatively intact biogeochemical attributes, virtually no management of old fields would be required. Old fields in fragmented native vegetation or whose hydrogeomorphological circumstances have been altered may need greater intervention to secure restoration of native biodiversity.

Much more problematic are old fields of OCBILs, to the point that recent reviewers have advocated abandonment of the concept of full restoration: 'The restoration of old fields stuck in a persistent, degraded state poses an ecological, philosophical and policy challenge. The most appropriate and achievable goal for these old fields will be the restoration of a plant community that fulfils some biodiversity goals, but which is largely focused on the provision of ecosystem services. If the ecological future is to be one



Fig. 9 Aerial photo illustrating alternative approaches to agricultural land use in the Greater Cape of South Africa, from more sustainable traditional strip or alley farming retaining darker strands of native vegetation, to paler areas where unsustainable wholesale clearing and transformation of the

native vegetation has occurred. Circular clearings are of irrigated horticulture (potato farming). Inset shows seasonal annual wildflowers on a strip left fallow between wheat crop strips in Namaqualand. Photos by the author

without an analog in the past, then restoration of old fields will incorporate novel elements of species composition and vegetation structure, so that ecological function can be restored. Approaching old-field restoration from this perspective will probably be challenging for restoration ecologists and local communities who have a strong preference for historical vegetation states.’ Cramer et al. (2008, pg 110).

I prefer a more optimistic view—that restoration on OCBILs is indeed possible, as evidenced, for example, by work on post-mining sites in the Southwest Australian Floristic Region’s jarrah forest (Koch and Hobbs 2007). It could be argued that Cramer et al. (2008) are overly pessimistic. It may be more possible than seems likely now that a step change upwards will occur in the future globally in the scale of resources that will be applied to address the present decline of carbon sinks and loss of biodiversity. If so, understanding the fundamental differences in biota and processes involved in restoration between OCBILs and YODFELs will be of considerable significance indeed.

Conclusion

While evidence exists to support several of the above predictions for evolution and conservation of OCBIL biodiversity, much remains to be done before understanding of processes approaches that for the much more common YODFELs in which most people live. The overarching thesis explored herein is embodied, with a twist, in a contemporary environmental mantra—*act globally, think locally*. We all have just one planet on which to live and we desperately need to devise new ways of living to ensure a sustainable and reasonable future quality of life. If we are to continue to share the Earth with the biodiversity so much celebrated and studied through Linnean collections over three centuries, conservation biology and restoration ecology need to mature and develop a firm theoretical underpinning with as much predictive power as is possible given the wonderful complexity of life and its evolution. It is hoped that the present contribution, in a small way, will stimulate further research and improvements to theory pertaining to

evolution, ecology and conservation of OCBIL and YODFEL biota.

Acknowledgements This paper is the culmination of four decades of wondering about and exploring the exceptionally rich endemic biota of the Southwest Australian Floristic Region and, more recently, that of the Greater Cape. I owe much to my teachers, especially Sid James, Bert Main, Hugh Paterson, George Seddon, Rowl Twidale and the many research collaborators, students and friends who have so warmly discussed ideas and pursued lines of research with me that collectively led to the present paper. I owe a special thanks to colleagues in South Africa who taught a complete novice so much in the field about the world's richest temperate flora—John Manning, John Rourke, Richard Cowling, Dee Snijman, Colin Paterson-Jones, Koos Roux, Peter Goldblatt and others. My understanding of YODFEL biota in the Northern Hemisphere similarly has been enhanced through the privilege of working with fine colleagues at the Royal Botanic Gardens, Kew and with its global collaborators. The realisation that things were different in the Southwest Australian Floristic Region and Greater Cape compared to what was mainstream in the literature from the Northern Hemisphere and eastern Australia was slow in coming (see Hopper (1979) for an early synthesis), but benefited from a degree of thinking and field exploration that few have the luxury or time to enjoy in this increasingly frenetic world. The ideas developed embryonically while I was a postgraduate student at The University of Western Australia, and then during employment with the Western Australian Herbarium, Department of Fisheries and Wildlife, Department of Conservation and Land Management, Kings Park and Botanic Garden, Botanic Gardens and Parks Authority, and The University of Western Australia. It was over two years (2004–2006) at the last institution that the concepts of OCBILs and YODFELs crystallised, and I was able to present to several audiences seminars underpinning the present paper. I am grateful for invitations to deliver addresses on these ideas subsequently in 2007 at the 3rd Global Botanic Gardens Congress in Wuhan, China, at the Linnean Society's Tercentenary celebratory conference in London on Unlocking the Past—Linnaean Collections past, present and future, at The Botanical Society of America's Botany 2007 conference in Chicago, and at MEDECOS 2007 in Perth. In 2008, aspects of this paper were included in lectures on Haemodoraceae delivered to the Cape Biota Symposium at Drakensville, Kwa-zulu Natal, on OCBIL theory at the University of Texas at Austin, and in the Nancy T. Burbidge Memorial Lecture (entitled *Old Australian landscapes yield new perspectives on biodiversity evolution and conservation*) to the Australian Systematic Botany Society's National Conference in Adelaide. In 2009 the theory was presented in a lecture to the University of Vienna's Institute of Biodiversity. I have benefitted from many discussions with colleagues at these venues. Hans Lambers, Colin Yates, Mark Chase, Don Bradshaw, Pieter Poot, Rhian Smith and ten anonymous referees for three journals commented on previous drafts and materially helped improve the final paper. Peggy Fiedler's thorough editing and critique were especially valuable. In having to consider such wide and generous input, the responsibility for ideas published herein nevertheless is mine alone.

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