Plant Soil (2009) 322:49–86
DOI 10.1007/s11104-009-0068-0

REVIEW ARTICLE

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

**Stephen D. Hopper**

Received: 16 March 2009 / Accepted: 8 June 2009 / Published online: 14 July 2009

**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 south-western 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.

**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

---

Responsible Editor: Hans Lambers.

S. D. Hopper (✉)
Directorate, Royal Botanic Gardens, Kew,
Richmond, Surrey TW9 3AB, UK
e-mail: s.hopper@kew.org

S. D. Hopper
School of Plant Biology,
The University of Western Australia,
Crawley, Western Australia, Australia 6009

## 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

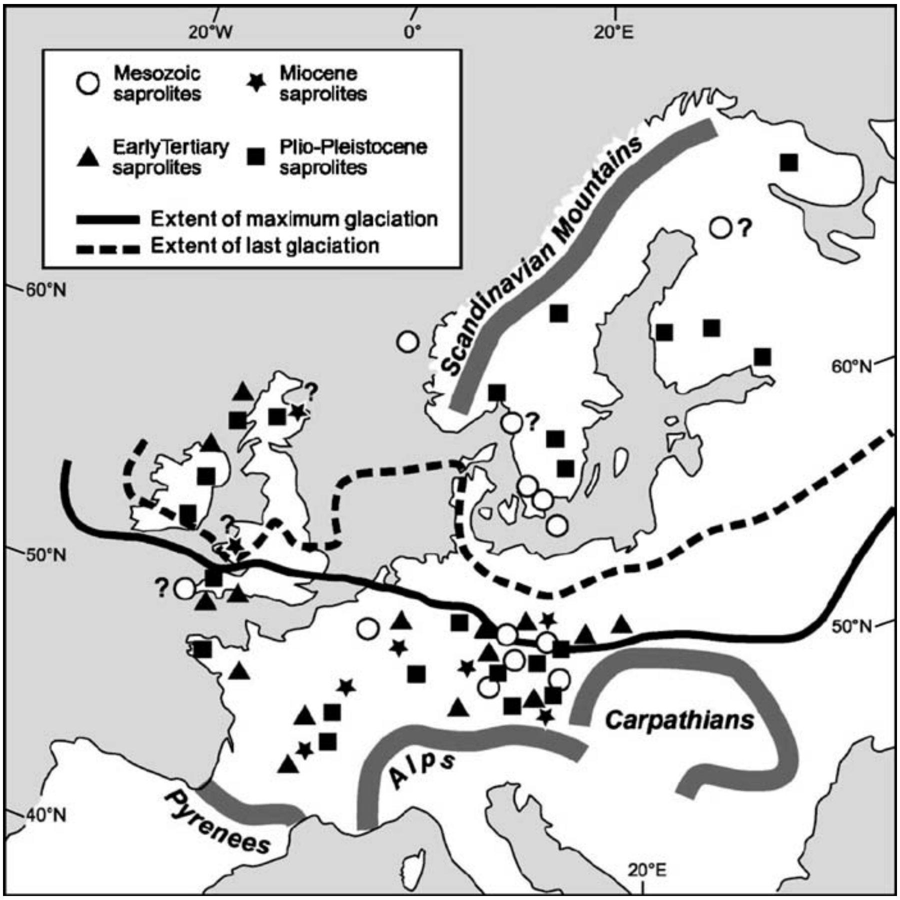

**Fig. 1** European extent of maximum and last glaciation, and the distribution of relict weathering mantles (saprolites), with their most likely ages. *Question marks* indicate ages inferred from circumstantial evidence such as long-distance correlations with saprolites of known ages or morphostratigraphic 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 Migoń 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 conservation 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 Axlerod (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,

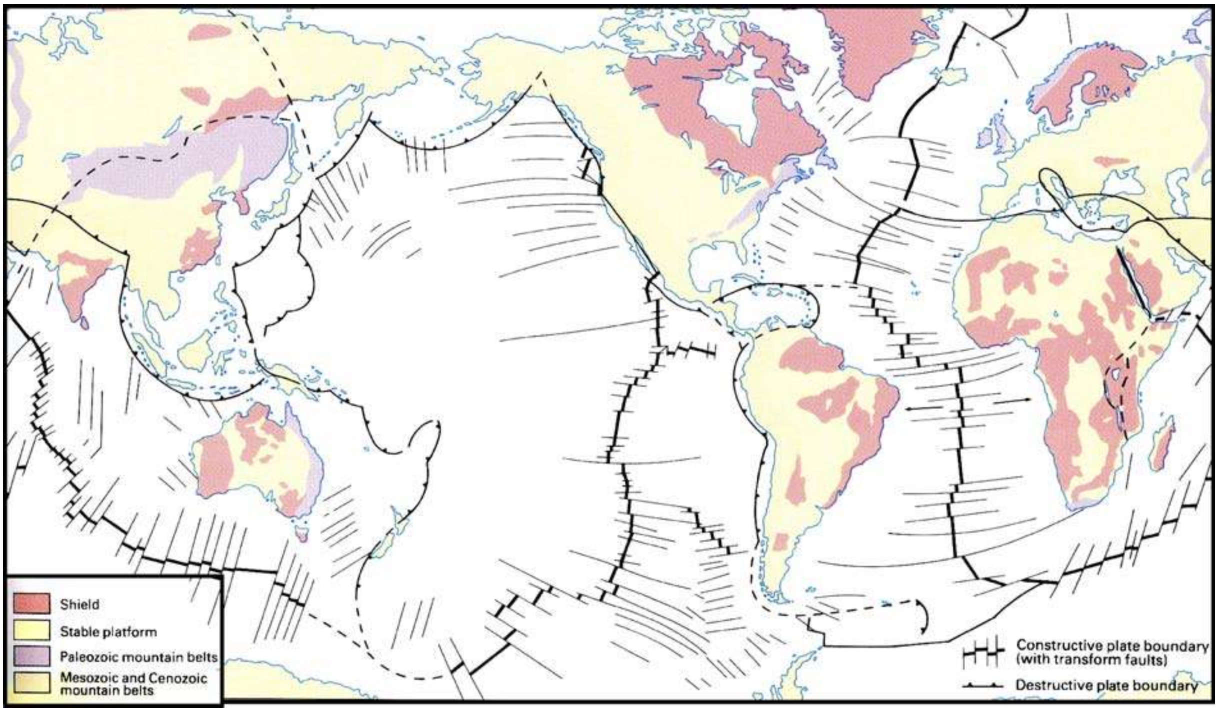

**Fig. 2** Geological shields or orogens form the ancient stable cores of continents and large islands and therefore form the starting points in the search for OCBILs. However, their old rocks are often overlain by younger sediments due to inundation, glaciation, dust storms, volcanism and other factors. From Smith (1989)

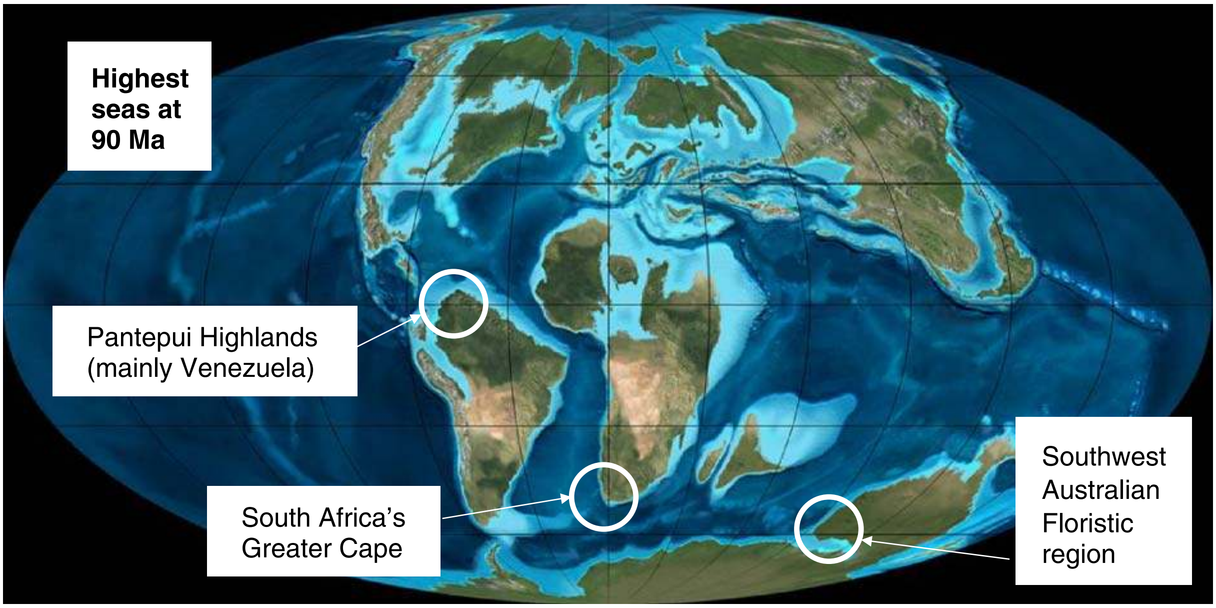

**Fig. 3** At least three geologically stable, unglaciated regions persist today, as old landscapes with prolonged oceanically buffered climates since the early Cretaceous (140 Ma), from land that was above water when sea levels were close to the highest known 90 Ma. These three regions represent today's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

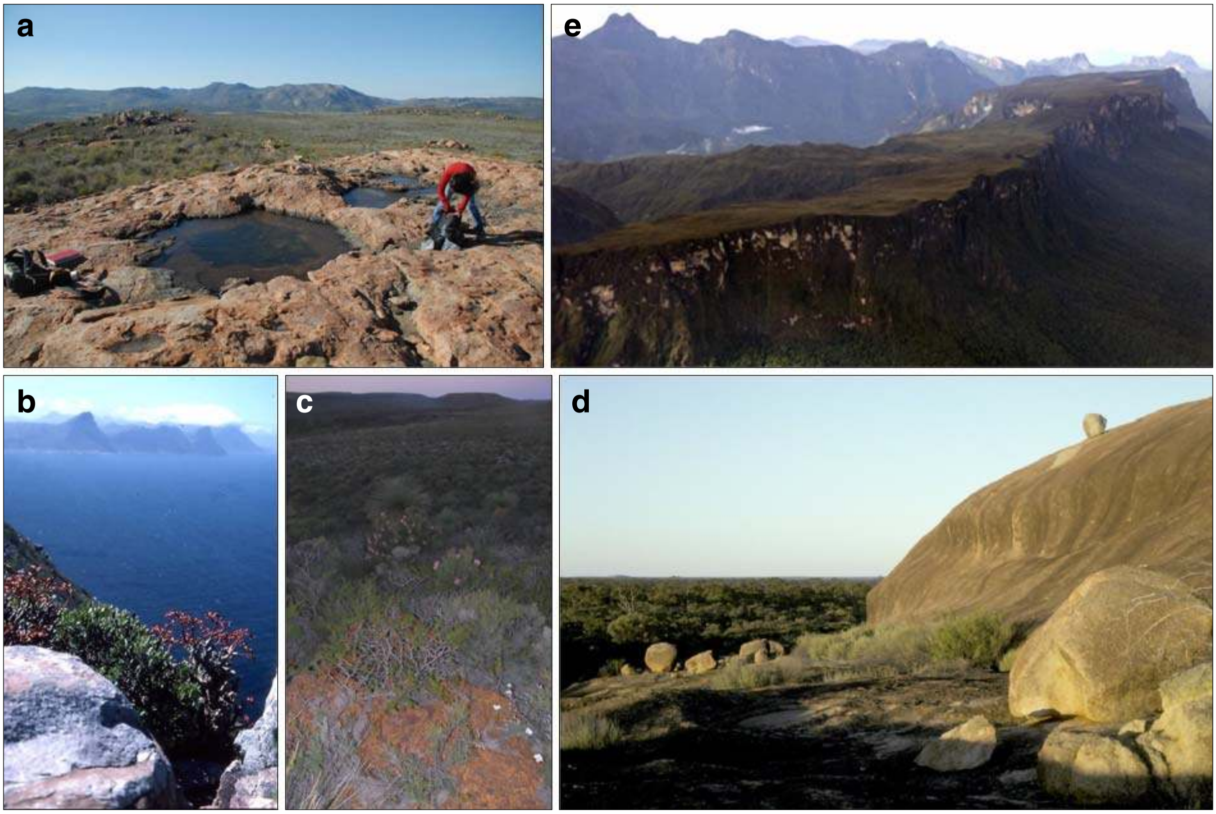

**Fig. 4** OCBILs are confined primarily to three regions, although there are other possible candidates and OCBILs may have been more common prior to Quaternary glaciations (photos by the author unless otherwise stated): **a** high granite plateau of the Kamiesberg, Namaqualand, South Africa; **b** looking 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 landsurfaces, 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), Migoń 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 Merrit 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 Afromontane 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** *Dasypogon hookeri* (Dasypogonaceae); **b** *Dasypogon bromeliifolius* (Dasypogonaceae) with honey possum (*Tarsipes rostratus*); **c** *Calectasia narragara* (Dasypogonaceae—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. Swarts 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; Rickleffs 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<br>Grubbiaceae<br>Roridulaceae<br>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<br>Eremosynaceae<br>Emblingiaceae<br>Dasypogonales<br>Anarthriaceae<br>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 verricula* (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 (Rebelo 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 monecy, 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 reknown 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 hemiparisites 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, bradyspory (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

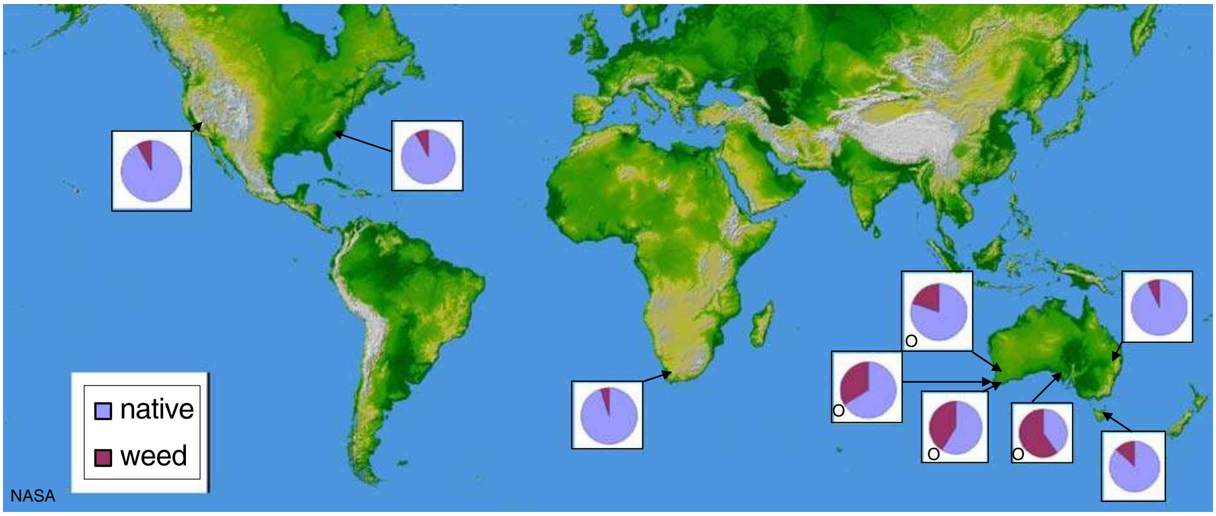

**Fig. 8** The proportions of native plants versus exotic invasive non-native weeds on granite outcrop systems in selected OCBILs (*piecharts labelled O*) and YODFELs (Hopper 2002). Outcrops in South Africa's Greater Cape are embedded in landscapes of variable age, from old to young

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 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 coventional 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 coincides 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 wih 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.

## References

Abbott I, Burrows N (eds) (2003) Fire in ecosystems of South-west Western Australia: impacts and management. Backhuys, Leiden

Allen J, O'Connell JF (2003) The long and the short of it: archaelogical approaches to determining when humans first colonised Australia and New Guinea. Austral Archaeol 57:5–10

Allison HE and Hobbs RJ (2004) Resilience, adaptive capacity, and the "Lock-in Trap" of the Western Australian agricultural region. *Ecol Soc* 9, 3. Available online. http://www.ecologyandsociety.org/vol9/iss1/art3/

Angiosperm Phylogeny Group (APG II) (2003) An update of the angiosperm phylogeny group classification for the orders and families of flowering plants: APG II. Bot J Linn Soc 141:399–436

Arroyo-Rodriguez V, Pineda E, Escobar F, Ben'Itez-Malvido J (2009) Value of small patches in the conservation of plant-species diversity in highly fragmented rainforest. Conserv Biol 23:729–739

Axelrod DI (1967) Drought, diastrophism and quantum evolution. Evolution 21:201–209

Axelrod DI (1972) Edaphic aridity as a factor in angiosperm evolution. Am Nat 106:311–20

Baker HG (1965) Characteristics and modes of origin of weeds. In: Baker HG, Stebbins GL (eds) The genetics of colonizing species. Academic, New York, pp 147–168

Baker HG, Stebbins GL (1965) The genetics of colonizing species. Academic, New York

Bakker FT, Helbrugge D, Culham A, Gibby M (1998) Phylogenetic relationships within *Pelargonium* sect. *Peristera* (Geraniaceae) inferred from nrDNA and cpDNA comparisons. Plant Syst Evol 211:273–287

Bakker FT, Culham A, Marais EM, Gibby M (2005) Nested radiation in Cape *Pelargonium*. In: Bakker FT, Chatrou LW, Gravendeel B, Pelser PB (eds) Plant species-level systematics. ARG Gantner Verlag, Ruggell, Liechtenstein, pp 75–100

Barthlott W, Porembski S (eds) (2000) Biodiversity on Inselbergs. Springer Verlag, Heidelberg

Beard JS, Chapman AR, Gioia P (2000) Species richness and endemism in the Western Australian flora. J Biogeog 27:1257–1268

Bellingham PJ, Sparrow AD (2000) Resprouting as a life history strategy in woody plant communities. Oikos 89:409–416

Beresford Q (2001) Developmentalism and its environmental legacy: the Western Australia Wheatbelt, 1900–1990s. Austral J Polit Hist 47:403–414

Berg RY (1975) Myrmecochorous plants in Australia and their dispersal by ants. Austral J Bot 23:475–508

Berry PE, Riina R (2005) Insights into the diversity of the Pantepui flora and the biogeographic complexity of the Guayana Shield. Biol Skr 55:145–167

Bhagwat SA, Willis KJ (2008) Species persistence in northerly glacial refugia of Europe: a matter of chance or biogeographical traits? J Biogeogr 35:464–482

Bierman PR (1994) Using in situ produced cosmogenic isotopes to estimate rates of landscape evolution: a review from the geomorphic perspective. J Geol Res 99:13885–13896

Bond WJ, Keeley JE (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends Ecol Evol 20:387–394

Bond WJ, Midgley JJ (2001) Ecology of sprouting in woody plants: the persistence niche. Trends Ecol Evol 16:45–51

Bond WJ, van Wilgen BW (1996) Fire and plants. Chapman & Hall, London

Bond WJ, Midgley JJ, Vlok J (1988) When is an island not an island? Insular effects and their causes in fynbos shrublands. Oecologia 77:515–521

Bond WJ, Yeaton R, Stock WD (1991) Myrmecochory in Cape Fynbos. In: Huxley CR, Cutler DF (eds) Ant-plant interactions. Oxford University Press, Oxford, pp 448–462

Born J, Linder HP, Desmet P (2007) The greater Cape Floristic region. J Biogeogr 34:147–162

Branagan D (2008) Australia—a Cenozoic history. Geol Soc London Spec Publ 301:189–213

Broadhurst LM, Lowe A, Coates DJ, Cunningham SA, McDonald M, Vesk PA, Yates C (2008) Seed supply for broadscale restoration: maximizing evolutionary potential. Evol Appl 1:587–597

Brooker MIH, Hopper SD (1989) A new series, Rigentes, of Eucalyptus (Myrtaceae) comprising three new species endemic to Western Australia. Nuytsia 7:5–13

Brown JM (1989) Regional variation in kwongan in the central wheatbelt of Western Australia. Austral J Ecol 14:345–355

Brown JH, Lomolino MV (2000) Concluding remarks: historical perspective and the future of island biogeography theory. Glob Ecol Biogeogr 9:87–92

Brown AP, Thomson-Dans C, Marchant N (eds) (1998) Western Australia's threatened flora. Dept. Conservation and Land Management, Perth

Brown AP, Dundas P, Dixon KW, Hopper SD (2008) Orchids of Western Australia. University of Western Australia Press, Perth

Brundrett M (2004) Diversity and classification of mycorrhizal associations. Biol Rev 79:473–495

Brundrett M (2009) Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. Pl Soil, in press

Brundu G, Lupi R, Zapelli I, Fossati T, Patrigani G, Camarda I, Sala F, Castiglione S (2008) The origin of clonal diversity and structure of Populus alba in Sardinia: evidence from nuclear and plastid microsatellite markers. Ann Bot 102:997–1006

Bussell JD, Waycott M, Chappill JA, James SH (2002) Molecular phylogenetic analysis of the evolution of complex hybridity in Isotoma petraea. Evolution 56:1296–1302

Bussell JD, Hood P, Alacs EA et al (2006) Rapid genetic delineation of local provenance seed-collection zones for effective rehabilitation of an urban bushland remnant. Austral Ecol 31:164–175

Byrne M (2007) Phylogeography provides an evolutionary context for a diverse and ancient flora. Austral J Bot 55:316–325

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

Byrne M, Macdonald B, Coates DJ (1999) Divergence in the chloroplast genome and nuclear rDNA of the rare Western Australian plant Lambertia orbifolia Gardner (Proteaceae). Mol Ecol 8:1789–1796

Byrne M, Elliott CP, Yates C, Coates DJ (2007) Extensive pollen dispersal in a bird-pollinated shrub, *Calothamnus quadrifidus*, in a fragmented landscape. Mol Ecol 16:1303–1314

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

Cain ML, Milligan BG, Strand AE (2000) Long-distance seed dispersal in plant populations. Am J Bot 87:1217–1227

Calviño-Cancela M, Dunn RR, van Etten EJB, Lamont BB (2006) Emus as non-standard seed dispersers and their potential for long-distance dispersal. Ecography 29:632–640

Campbell NA, Hopper SD, Caccetta PA (2000) Mapping granite outcrops in the Western Australian Wheatbelt using Landsat TM data. J Roy Soc West Austral 83:109–113

Cape Special Feature (2006) Divers Distrib 12:1–123

Carlgren K, Mattsson L (2001) Swedish soil fertility experiments. Acta Agric Scand, Sect B — Plant Soil Sci 51:49–76

Carlquist S (1974) Island Biology. Columbia University Press, New York

Carstens P (2007) Always here even tomorrow. The enduring spirit of the South African Nama in the modern world. Xlibris, Bloomington

Carter B (2006) Nyungah land records of invasion and theft of aboriginal land on the Swan River 1829–1850. Swan Valley Nyungah Community, Guildford Western Australia

Chen XY, Barton CE (1991) Onset of aridity and dune building in central Australia: sedimentological and magnetostratigraphic evidence from Lake Amadeus. Palaeogeograph Palaeoclimatol Palaeoecol 84:55–73

Chen L, James SH, Stace HM (1997) Self-incompatibility, seed abortion and clonality in the breeding systems of several Western Australian *Drosera* species (Droseraceae). Austral J Bot 45:191–201

Clark CM, Tilman D (2008) Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. Nature 451:712–715

Coates DJ (2000) Defining conservation units in a rich and fragmented flora: implications for the management of genetic resources and evolutionary processes in south-west Australian plants. Austral J Bot 48:329–339

Coates DJ, Carstairs S, Hamley VL (2003) Evolutionary patterns and genetic structure in localized and widespread species in the Stylidium caricifolium complex (Stylidiaceae). Am J Bot 90:997–1008

Cordell D, Drangert J-O, White S (2009) The story of phosphorus: global food security and food for thought. Glob Environ Change 19:292–305

Cowling RM (1987) Fire and its role in coexistence and speciation in the Gondwanan shrublands. S Af J Sci 83:106–112

Cowling RM (ed) (1992) The ecology of fynbos. Nutrients, fire and diversity. Oxford Univ Press, Cape Town

Cowling RM, Bond WJ (1991) How small reserves can be? An empirical approach in the Cape fynbos. Biol Cons 58:243–256

Cowling RM, Lamont BB (1998) On the nature of Gondwanan species flocks: diversity of Proteaceae in Mediterranean south-western Australia and South Africa. Austral J Bot 46:335–355

Cowling RM, Pierce SM (1999) Namaqualand: a succulent desert. Fernwood, Vlaeberg, South Africa

Cowling RM, Richardson DM (1995) Fynbos: South Africa's unique floral kingdom. Fernwood, Vlaeberg, South Africa

Cowling RM, Pierce SM, Stock WD, Cocks M (1994) Why are there so many myrmecochorous species in the Cape fynbos? In: Arianoutsou M, Groves RH (eds) Plant animal interactions in Mediterranean type ecosystems. Kluwer, Dordrecht, pp 159–168

Cowling RM, Rundel PW, Lamont BB, Arroyo MK, Arianoutsou M (1996) Plant diversity in mediterranean-climate regions. Trends Ecol Evol 11:362–366

Cowling RM, Pressey RL, Rouget M, Lombard AT (2003) A conservation plan for a global biodiversity hotspot—the Cape Floristic Region, South Africa. Biol Cons 112:191–216

Cowling RM, Ojeda F, Lamont BB, Rundel PW, Lechmere-Oertel R (2005a) Rainfall reliability, a neglected factor in explaining convergence and divergence of plant traits in fire-prone mediterranean-climate ecosystems. Global Ecol Biogeogr 14:509–519

Cowling RM, Proches S, Vlok JHJ (2005b) On the origin of southern African subtropical thicket vegetation. S Af J Bot 71:1–23

Cowling RM, Proches S, Partridge TC (2009) Explaining the uniqueness of the Cape flora: Incorporating geomorphic evolution as a factor for explaining its diversification. Mol Phyl Evol 51:64–74

Cramer VA, Hobbs RJ (2007) Old fields dynamics and restoration of abandoned farmland, science and practice of ecological restoration series. Island, Washington DC

Cramer VA, Hobbs RJ, Standish RJ (2008) What's new about old fields? Land abandonment and ecosystem assembly. Trends Ecol Evol 23:104–112

Crisp MD, Arroyo MTK, Cook LG, Gandolfo MA, Jordan GJ, McGlone MS, Weston PH, Westoby M, Wilf P, Linder HP (2009) Phylogenetic biome conservatism on a global scale. Nature 458:754–756

Dallman P (1998) Plant life in the World's Mediterranean climates. Califonia Native Plant Society, University of California Press, Berkeley

Damgaard J, Klass K-D, Picker MD, Buder G (2008) Phylogeny of the Heelwalkers (Insecta: Mantophasmatodea) based on mtDNA sequences, with evidence for additional taxa in South Africa. Mol Phylogenet Evol 47:443–462

Darwin CR (1859) On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life, 1st edn. John Murray, London

Darwin CR (1862) On the various contrivances by which British and foreign orchids are fertilised by insects. John Murray, London

Darwin C (1875a) Insectivorous plants. John Murray, London

Darwin C (1875b) The movements and habits of climbing plants, 2nd edn. John Murray, London

Darwin CR (1876) The effects of cross and self fertilisation in the vegetable kingdom. John Murray, London

Deacon HJ, Jury MR, Ellis F (1992) Selective regime and time. In: Cowling RM (ed) The ecology of fynbos. Nutrients, fire and diversity. Oxford Univ Press, Cape Town, pp 6–22

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

Dirnböck T, Hobbs RJ, Lambeck RJ, Caccetta PA (2002) Vegetation distribution in relation to topographically driven processes in southwestern Australia. Appl Veg Sci 5:147–158

Dodson JR, Westoby M (eds) (1985) Are Australian ecosystems different? Proc Ecol Soc Aust 14:1–250

Donoghue MJ (2008) A phylogenetic perspective on the distribution of plant diversity. PNAS 105:1149–1155

Donoghue MJ, Bell CD, Li J (2001) Phylogenetic patterns in Northern Hemisphere plant geography. Int J Plt Sci 162(6 Suppl):S41–S52

Douglas AE (2009) The microbial dimension in insect nutritional ecology. Funct Ecol 23:38–47

Duller GAT (2000) Dating methods: geochronology and landscape evolution. Prog Phys Geogr 24:111–116

Dynesius M, Jansson R (2000) Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. Proc Natl Acad Sci USA 97:9115–9120

Ellis AG, Johnson SD (2009) The evolution of floral variation without pollinator shifts in Gorteria diffusa (Asteraceae). Am J Bot 96:793–801

Ellis A, Weis A, Gaut B (2006) Evolutionary radiation of "stone plants" in the genus Argyroderma (Aizoaceae): unravelling the effects of landscape, habitat, and flowering time. Evolution 60:39–55

Ellison AM, Gotelli NJ (2009) Energetics and the evolution of carnivorous plants—Darwin's 'most wonderful plants in the world'. J Exp Bot 60:19–42

Erfmeier A, Bruelheide H (2004) Comparison of native and invasive Rhododendron ponticum populations: growth, reproduction and morphology under field conditions. Flora—Morphol Distrib Funct Ecol Plants 199:120–133

Fiedler PL (1986) Concepts of rarity in vascular plant species, with special reference to the genus Calochortus Pursh (Liliaceae). Taxon 35:502–518

Fisher JL, Veneklaas EJ, Lambers H, Loneragan WA (2006) Enhanced soil and leaf nutrient status of a Western Australian Banksia woodland community invaded by Ehrharta calycina and Pelargonium capitatum. Plt Soil 284:253–264

Forest F, Grenyer R, Rouget M, Davies TJ, Cowling RM, Faith DP, Balmford A, Manning JC, Proches S, van der Bank M, Reeves G, Hedderson TAJ, Savolainen V (2007) Preserving the evolutionary potential of floras in biodiversity hotspots. Nature 445:757–760

Gadgil M, Solbrig OT (1972) The concept of r- and K-selection: evidence from wild flowers and some theoretical considerations. Am Nat 106:14–31

Gale S (1992) Long-term landscape evolution in Australia. Earth Surface Processes Landforms 17:323–343

García MB (2008) Life history and population size variability in a relict plant. Different routes towards long-term persistence. Divers Distrib 14:106–113

George R, Clarke J, English P (2006) Modern and palaeogeographic trends in the salinisation of the Western Australian Wheatbelt. Proc Aust Earth Sci Conv 1–21

Ghiselin MT (1969) The triumph of the Darwinian method, 1st edn. University of California Press, Berkeley

Gibson N (ed) (2007) Translation of Diels 1906 The Plant Life of Western Australia, Leipzig. Conserv Sci West Austral 6:1–373

Gilbert FS (1980) The equilibrium theory of island biogeography: fact or fiction? J Biogeogr 7:209–235

Gill AM (1977) Plant traits adaptive to fires in Mediterranean land ecosystems. In: Mooney HA, Conrad CE (eds) Proceedings of the Symposium on the Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems .USDA For. Serv. Gen. Tech. Rep. WO-3:17–26

Gitzendanner MA, Soltis PS (2000) Patterns of genetic variation in rare and widespread plant congeners. Am J Bot 87:783–792

Givnish TJ, McDiarmid RW, Buck WR (1986) Fire adaptation in Neblinaria celiae (Theaceae), a high-elevation rosette shrub endemic to a wet equatorial tepui. Oecologia 70:481–485

Givnish TJ, Sytsma KJ, Smith JF, Hahn WJ, Benzing DH, Burkhardt EM (2000) Molecular evolution and adaptive radiation in Brocchinia (Bromeliaceae: Pitcairnioideae) atop tepuis of the Guyana Shield. In: Givnish TJ, Sytsma KJ (eds) Molecular evolution and adaptive radiation. Cambridge University Press, Cambridge, pp 259–311

Goldblatt P (1986) Cytology and systematics of the Morea fugax complex (Iridaceae). Ann Missouri Bot Gard 73:140–157

Goldblatt P, Manning JC (2000) Cape Plants. A Conspectus of the Cape Flora of South Africa. Strelitzia 9:1–743

Goldblatt P, Manning JC (2002) Plant diversity of the Cape Region of Southern Africa. Ann Missouri Bot Gard 89:281–302

Goldblatt P, Savolainen V, Porteous O, Sostaric I, Powell M, Reeves G, Manning JC, Barraclough TG, Chase MW (2002) Radiation in the Cape flora and the phylogeny of peacock irises Moraea (Iridaceae) based on four plastid DNA regions. Mol Phylogenet Evol 25:341–360

Gomez C, Espadaler X (1998) Myrmecochorus dispersal distances: a world survey. J Biogeogr 25:573–580

Goudie AS, Eckardt F (1999) The evolution of the morphological framework of the central Namib Desert, Namibia, since the early Cretaceous. Geogr Ann 81A:443–458

Gould SJ (1988) Wonderful life. The burgess shale and the nature of history. Penguin Books, London

Gould SJ, Vrba ES (1982) Exaptation—a missing term in the science of form. Paleobiol 8:4–15

Grant PR, Grant BR (2008) How and why species multiply. The radiation of Darwin's Finches. Princeton University Press, Princeton

Grime J (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am Nat 111:1169–1194

Groves RH (1991) The biogeography of mediterranean plant invasions. In: Groves RH, di Castri F (eds) Biogeography of mediterranean invasions. Cambridge University Press, Cambridge, UK, pp 427–438

Groves RH, Kilby MJ (1993) Introduced flora of mediterranean-climate regions—convergence or divergence? In: Tharnoss CA (ed) Proceedings of the Sixth International Conference on Mediterranean Climate Ecosystems. Maleme, Crete, pp 351–356

Gurnis M, Muller RD, Moresi L (1998) Cretaceous vertical motion of Australia and the Australian-Antarctic discordance. Science 279:1499–1504

Hallam SJ (1975) Fire and Hearth, a study of Aboriginal usage and European usurpation in South-western Australia. Australian Institute of Aboriginal Studies, Canberra

Hampe A (2004) Bioclimate envelope models: what they detect and what they hide. Global Ecol Biogeogr 13:469–476

Hardy CR, Linder HP (2005) Intraspecific variability and timing in ancestral ecology reconstruction: a test case from the Cape flora. Syst Biol 54:299–316

Harrison S, Viers JH, Thorne JH, Grace JB (2008) Favorable environments and the persistence of naturally rare species. Cons Lett 1:65–74

Harvey PH, Pagel M (1991) The Comparative Method in Evolutionary Biology. OxfordUniv Press, Oxford

He T, Krauss SL, Lamont BB, Miller BP, Enright NJ (2004) Long-distance seed dispersal in a metapopulation of *Banksia hookeriana* inferred from a population allocation analysis of amplified fragment length polymorphism data. Mol Ecol 13:1099–1109

He T, Lamont BB, Krauss SL, Enright NJ, Miller BP (2008) Covariation between intraspecific genetic diversity and species diversity within a plant functional group. J Ecol 96:956–961

He T, Lamont BB, Krauss SL, Enright NJ, Miller BP, Gove AD (2009) Ants cannot account for interpopulation dispersal of the arillate pea *Daviesia triflora*. New Phytol 181:725–733

Herrera CM (1992) Historical effects and sorting processes as explanations for contemporary ecological patterns: character syndromes in Mediterranean woody plants. Amer Nat 140:421–446

Hesse PP, McTainsh GH (2003) Australian dust deposits: modern processes and the Quaternary record. Quat Sci Rev 22:2007–35

Heubl G, Bringmann G, Meimberg H (2006) Molecular phylogeny and character evolution of carnivorous plant families in Caryophyllales—revisited. Pl Biol 8:821–830

Hill RS (1998) Fossil evidence for the onset of xeromorphy and scleromorphy in Australian Proteaceae. Austral Syst Bot 11:391–400

Hill RS, Brodribb TJ (2001) Macrofossil evidence for the onset of xeromorphy in Australian Casuarrinaceae and tribe Banksieae (Proteaceae). J Medit Ecol 2:127–136

Hill MO, Roy DB, Thompson K (2002) Hemeroby, urbanity and ruderality: bioindicators of disturbance and human impact. J Appl Ecol 39:708–720

Hilton-Taylor C (1996) Patterns and characteristics of the flora of the Succulent Karoo Biome, southern Africa. In: van der Maesen LJE, van der Bergt XM, van Medenbach de Rooy JM (eds) The biodiversity of African plants. Kluwer, Dordrecht, pp 58-72

Hobbs RJ, Atkins L (1991) Interactions between annuals and woody perennials in a Western Australian nature reserve. J Veg Sci 2:643–654

Hobbs PR, Sayre K, Gupta R (2008) The role of conservation agriculture in sustainable agriculture. Phil Trans R Soc B 363:543–555

Holmes PM, Richardson DM (1999) Protocols for restoration based on recruitment dynamics, community structure, and ecosystem function: perspectives from South African fynbos. Rest Ecol 7:215–230

Holmes PM, Richardson DM, van Wilgen BW, Gelderblom C (2000) Recovery of South African fynbos vegetation following alien woody plant clearing and fire: implications for restoration. Austral Ecol 25:631–639

Hopper SD (1977) The structure and dynamics of a hybrid population of Anigozanthos manglesii D. Don and A. humilis Lindl. Austral J Bot 25:413–422

Hopper SD (1978) An experimental study of competitive interference between Anigozanthos manglesii D. Don, A. humilis Lindl. and their hybrids (Haemodoraceae). Austral J Bot 26:807–817

Hopper SD (1979) Biogeographical aspects of speciation in the south west Australian flora. Annu Rev Ecol Syst 10:399–422

Hopper SD (1997) An Australian perspective on plant conservation biology in practice. In: Fiedler PL, Kareiva PM (eds) Conservation biology for the coming decade. Chapman and Hall, New York, pp 255–278

Hopper SD (2002) Weeds on granite outcrops in temperate Australia, South Africa and the USA. In: Jacob HP, Dodd J, Moore J (eds) Weeds threats now and forever 13th Australian Weeds Conference Papers & Proceedings. Plant Protection Society of WA, Perth, pp 96–99

Hopper SD (2003) An evolutionary perspective on south-west Western Australian landscapes, biodiversity and fire: a review and management implications. In: Abbott I, Burrows N (eds) Fire in ecosystems of South-west Western Australia: impacts and management. Backhuys, Leiden, pp 9–35

Hopper SD (2005) Deserts through time. In: Nikulinsky P, Hopper SD (eds) Soul of the desert. Fremantle Arts Centre, Fremantle, pp 10–23

Hopper SD (2007) New life for systematics. Science 316:1097

Hopper SD, Barlow BA (2000) Sidney Herbert James 1933–1998. Austral J Bot 48:287–295

Hopper SD, Brown AP (2007) A revision of Australia's hammer orchids (Drakaea: Orchidaceae), with some field data on species-specific sexually deceived wasp pollinators. Austral Syst Bot 20:252–285

Hopper SD, Campbell NA (1977) A multivariate morphometric study of species relationships in kangaroo paws (Anigozanthos Labill. and Macropidia Drumm. ex Harv. : Haemodoraceae). Austral J Bot 25:523–544

Hopper SD, Gioia P (2004) The Southwest Australian Floristic Region: evolution and conservation of a global hot spot of biodiversity. Annu Rev Ecol Syst 35:623–650

Hopper SD, Lambers H (2009) Darwin as a plant scientist: a Southern Hemisphere perspective. Trends Plt Sci, in press

Hopper SD, van Leeuwen S, Brown AP, Patrick SJ (1990) Western Australia's endangered flora. Dept Conservation Land Management, Perth, p 140

Hopper SD, Harvey MS, Chappill JA, Main AR, Main BY (1996) The Western Australian biota as Gondwanan Heritage—a review. In: Hopper SD, Chappill JA, Harvey MS, George AS (eds) Gondwanan Heritage: past, present and future of the Western Australian Biota. Surrey Beatty & Sons, Chipping Norton, NSW, pp 1–46

Hopper SD, Brown AP, Marchant NG (1997) Plants of Western Australian granite outcrops. J Roy Soc West Austral 80:141–158

Hopper SD, Smith RJ, Fay MF, Manning JC, Chase MW (2009) Molecular phylogenetics of Haemodoraceae in the Greater Cape and Southwest Australian Floristic Regions. Mol Phylogenet Evol 51:19–30

Hörandl E (2006) The complex causality of geographical parthenogenesis. New Phytol 171:525–538

Horton DR (2000) The pure state of nature: sacred cows, destructive myths and the environment. Allen & Unwin, Sydney

Horwitz P, Bradshaw D, Hopper SD, Davies P, Froend R, Bradshaw F (2008) Hydrological change escalates risk of ecosystem stress in Australia's threatened biodiversity hotspot. J R Soc West Austral 91:1–11

Houghton J (2004) Global warming the complete briefing, 3rd edn. Cambridge University Press, Cambridge

Huber O (1995a) Vegetation. Fl Ven Guy 1:97–160

Huber O (1995b) Conservation of the Venezuelan Guyana. Fl Ven Guy 1:193–218

Huber O (2006) Herbaceous ecosystems on the Guayana Shield, a regional overview. J Biogeogr 33:464–475

Hussey BMJ, Keighery GJ, Dodd J, Lloyd SG, Cousens RD (2007) Western weeds a guide to the weeds of Western Australia, 2nd edn. Weeds Society of Western Australia, Perth

Jahn B, Donner B, Muller PJ, Rohl U, Schneider RR, Wefer G (2003) Pleistocene variations in dust input and marine productivity in the northern Benguela current: evidence of evolution of global glacial-interglacial cycles. Palaeogeograph Palaeoclimatol Palaeoecol 193:515–533

James SH (1992) Inbreeding, self-fertilisation, lethal genes and genomic coalescence. Heredity 68:449–456

James SH (2000) Genetic systems in the south-west flora: implications for conservation strategies for Australian plant species. Austral J Bot 48:341–347

James SH, Keighery GJ, Moorrees A, Waycott M (1999) Genomic coalescence in a population of Laxmannia sessiliflora (Angiospermae, Anthericaceae): an association of lethal polymorphism, self-pollination and chromosome number reduction. Heredity 82:364–372

Janssen T, Bremer K (2004) The age of major monocot groups inferred from 800+ rbcL sequences. Bot J Linn Soc 146:385–398

Jansson R (2003) Global patterns in endemism explained by past climate change. Proc R Soc Lond [Biol] 270:583–590

Jansson R, Davies TJ (2008) Global variation in diversification rates of flowering plants: energy vs. climate change. Ecol Lett 11:173–183

Jansson R, Dynesius M (2002) The fate of clades in a world of recurrent climatic change: Milankovitch oscillations and evolution. Annu Rev Ecol Syst 33:741–777

Jarvis C (2007) Order out of chaos: linnaean plant names and their types. The Linnean Society of London, London

Johansen D, Latta RG (2003) Mitochondrial haplotype distribution, seed dispersal and patterns of postglacial expansion of ponderosa pine. Mol Ecol 12:293–298

Johnson SD (2006) Pollinator-driven speciation in plants. In: Harder LD, Barrett SCH (eds) The ecology and evolution of flowers. Oxford University Press, Oxford, UK, pp 296–306

Johnson SD, Steiner KE (2003) Specialized pollination systems in southern Africa. S Afr J Sci 99:345–348

Keighery GJ, Halse SA, Harvey MS, McKenzie NL (eds) (2004) A biodiversity survey of the Western Australian agricultural zone. Records of the WA Museum, Supplement No. 67, Welshpool

Keller LF, Waller DM (2002) Inbreeding effects in wild populations. Trends Ecol Evol 17:230–241

Kemper J, Cowling RM, Richardson DM (1999) Fragmentation of South African renosterveld shrublands: effects on plant community structure and conservation implications. Biol Cons 90:103–111

Kennington WJ, James SH (1997) Contrasting patterns of clonality in two closely related mallee species from Western Australia, Eucalyptus argutifolia and E. obtusiflora (Myrtaceae). Austral J Bot 45:679–689

Keynes RD (ed) (1988) Charles Darwin's beagle diary. Cambridge University Press, Cambridge

Keynes RD (2002) Fossils, finches and Fuegians. Oxford University Press, Oxford

King LC (1962) Morphology of the earth. Oliver & Boyd, Edinburgh

Kinnear JE, Onus ML, Sumner NR (1998) Fox control and rock-wallaby population dynamics—II. An update. Wildl Res 25:81–88

Kinnear JE, Main AR (1979) Niche theory and macropodid nutrition. J Roy Soc WestAustral 62:65–74

Kinnear JE, Cockson A, Christensen PES, Main AR (1979) The nutritional biology of the ruminants and ruminant-like animals—a new approach. Comp Biochem Physiol 64A:357–365

Klak C, Reeves G, Hedderson T (2004) Unmatched tempo of evolution in Southern African semi-desert ice plants. Nature 427:63–65

Knapp S, Wheeler Q (eds) (2009) Letters to Linnaeus. The Linnean Society of London, London

Knight CA, Molinari NA, Petrov DA (2005) The large genome constraint hypothesis: evolution, ecology and phenotype. Ann Bot 95:177–190

Knowles LL (2001) Did the Pleistocene glaciations promote divergence? Tests of explicit refugial models in montane grasshoppers. Mol Ecol 10:691–701

Koch JM, Hobbs RJ (2007) Synthesis: Is Alcoa successfully restoring a Jarrah forest ecosystem after bauxite mining in Western Australia? Rest Ecol 15:S137–S144

Koerner L (1999) Linnaeus nature and nation. Harvard University Press, Cambridge, MA

Krauss SL, He T (2006) Rapid genetic identification of local provenance seed collection zones for ecological restoration and biodiversity conservation. J Nat Cons 14:190–199

Krauss SL, Hermanutz L, Hopper SD, Coates DJ (2007) Population-size effects on seeds and seedlings from fragmented eucalypt populations: implications for seed sourcing for ecological restoration. Austral J Bot 55:390–399

Krauss SL, He T, Barrett LG, Lamont BB, Enright NJ, Miller BP, Hanley ME (2009) Contrasting impacts of pollen and seed dispersal on spatial genetic structure in the bird-pollinated Banksia hookeriana. Heredity 102:274–285

Lambers H, Shane MW (2007) Phosphorus nutrition of Australian Proteaceae and Cyperaceae: a strategy on old landscapes with prolonged oceanically buffered climates. S Afr J Bot 73:274–275

Lambers H, Chapin FS, Pons TL (1998) Plant physiological ecology. Springer-Verlag, New York

Lambers H, Raven JA, Shaver GR, Smith SE (2008) Plant nutrient-acquisition strategies change with soil age. Trends Ecol Evol 23:95–103

Lamont B (1982) Mechanisms for enhancing nutrient uptake in plants, with particular reference to mediterranean South Africa and Western Australia. Bot Rev 48:597–689

Lavergne S, Thompson JD, Garnier E, Debussche M (2004) The biology and ecology of narrow endemic and widespread plants: a comparative study of trait variation in 20 congeneric pairs. Oikos 107:505–518

Lavers C, Field R (2006) A resource-based conceptual model of plant diversity that reassesses causality in the productivity—diversity relationship. Global Ecol Biogeogr 15:213–224

Leitch AR, Leitch IJ (2008) Genomic plasticity and the diversity of polyploid plants. Science 320:481–483

Levy DJ, Bolker BM, Tewksbury JJ, Sargent S, Haddad NM (2005) Response. Science 310:779–780

Linder HP (2005) Evolution of diversity: the Cape flora. Trends Plant Sci 10:536–541

Lindsay AM (1985) Are Australian soils different? In Dodson JR, Westoby M, eds, Are Australian Ecosystems Different? Proc Ecol Soc Austral 14:83–97

Lusk C, Bellingham P (2004) Austral challenges to northern hemisphere orthodoxy IV Southern Connections Conference: towards a southern perspective, Cape Town, South Africa, January 2004. New Phytol 162:248–251

Lynch M (1984) Destabilizing hybridization, general-purpose genotypes and geographic parthenogenesis. Quart Rev Biol 59:257–290

Magallón S, Castillo A (2009) Angiosperm diversification through time. Am J Bot 96:349–365

Main AR (1996) Ghosts of the past: Where does environmental history begin? Envir Hist 2:297–114

Malcolm JR, Liu C, Neilson RP, Hansen L, Hannah L (2006) Global warming and extinctions of endemic species from Biodiversity Hotspots. Conserv Biol 20:538–548

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

McComb JA (1966) The sex forms of species in the flora of the south-west of Western Australia. Austral J Bot 14:303–316

Midgley GF, Thuiller W (2005) Global environmental change and the uncertain fate of biodiversity. New Phytol 167:638–641

Migoń P, Lidmar-Bergström K (2002) Deep weathering through time in central and northwestern Europe: problems of dating and interpretation of geological record. Catena 49:25–40

Millar CI, Stephenson NL, Stephens SL (2007) Climate change and forests of the future: managing in the face of uncertainty. Ecol Appl 17:2145–2151

Miller JR (2006) Restoration, reconciliation, and reconnecting with nature nearby. Biol Conserv 127:356–361

Miller G, Kominz MA, Browning JV, Wright JD, Mountain GS, Katz ME, Sugarman PJ, Cramer BS, Christie-Blick N, Pekar SF (2005) The Phanerozoic record of global sea-level change. Science 310:1293–1298

Minnich RA (2008) California's fading wildflowers lost legacy and biological invasions. Univ Calif Press, Berkeley

Mishler BD (2000) The need for integrated studies of the California flora. Madroño 47:803–858

Mountain A (2003) The first people of the cape. A look at their history and the impact of colonization on the Cape's indigenous people. David Philip, Claremont South Africa

Mulcahy MJ (1967) Landscapes, laterites and soils in southwestern Australia. In: Jennings JN, Mabbutt JA (eds) Landform studies from Australia and New Guinea. Aust Natl Univ Press, Canberra, pp 211–230

Murphy DD (1989) Conservation and confusion: wrong species, wrong scale, wrong conclusions. Conserv Biol 3:82–84

Murphy MT, Garkaklis MJ, Hardy GESJ (2005) Seed caching by woylies *Bettongia penicillata* can increase sandalwood *Santalum spicatum* regeneration in Western Australia. Austral Ecol 30:747–755

Nickrent DL, Duff RJ, Colwell AE, Wolfe AD, Young ND, Steiner KE, dePamphilis CW (1998) Molecular phylogenetic and evolutionary studies of parasitic plants. In: Soltis DE, Soltis PS, Doyle JJ (eds) Molecular systematics of plants II: DNA sequencing. Kluwer, Boston, pp 211–241

Nikulinsky P, Hopper SD (2008) Life on the rocks. The art of survival, 2nd edn. Fremantle Arts Centre, Fremantle

Nilsson MA, Arnason U, Spencer PBS, Janke A (2004) Marsupial relationships and a timeline for marsupial radiation in South Gondwana. Gene 340:189–196

Ohlemüller R, Gritti ES, Sykes MT, Thomas CD (2006) Towards European climate risk surfaces: the extent and distribution of analogous and non-analogous climates 1931–2100. Global Ecol Biogeogr 15:395–405

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

Ottewell KM, Donnellan SC, Lowe AJ, Paton DC (2009) Predicting reproductive success of insect- versus bird-pollinated scattered trees in agricultural landscapes. Biol Cons 142:888–898

Ouborg NJ, Vergeer P, Mix C (2006) The rough edges of the conservation genetics paradigm for plants. J Ecol 94:1233–1248

Parkington J (2006) Shorelines, strandlopers and shell middens archaeology of the Cape coast. Krakadouw Trust, Cape Town

Parsons RF, Hopper SD (2003) Monocotyledonous geophytes: comparison of south-western Australia with other areas of mediterranean climate. Austral J Bot 51:129–133

Pate JS (1989) Australian micro stilt plants. Trends Ecol Evol 4:45–49

Pate JS, Verboom WH (2009) Contemporary biogenic formation of clay pavements by eucalypts: further support for the phytotarium concept. Ann Bot 103:673–685

Pate JS, Weber G, Dixon KW (1984) Growth and life form of kwongan species. In: Pate JS, Beard JS (eds) Kwongan—plant life of the sandplain. University of Western Australia Press, Nedlands, Perth, pp 84–100

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

Pauw A (2007) Collapse of a pollination web in small conservation areas. Ecol 88:1759–1769

Peakall R, Ebert D, Scott LJ, Meagher PF, Offord CA (2003) Comparative genetic study confirms exceptionally low genetic variation in the ancient and endangered relictual conifer, *Wollemia nobilis* (Araucariaceae). Mol Ecol 12:2331–2343

Petit RJ, Aguinagalde I, de Beaulieu J-L, Bittkau C, Brewer S, Cheddadi R, Ennos R, Fineschi S, Grivet D, Lascoux M, Mohanty A, Muller-Starck G, Demesure-Musch B, Palme A, Martın JP, Rendell S, Vendramin GG (2003) Glacial refugia: hotspots but not melting pots of genetic diversity. Science 300:1563–1565

Phillips RD, Hopper SD, Dixon KW (2009) Pollination ecology, floral evolution and the possible impact of climate change in the Southwest Australian Biodiversity Hotspot. J Roy Soc, in press

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

Polhill R, Wiens D (1998) Mistletoes of Africa. Royal Botanic Gardens, Kew

Poot P, Lambers H (2003) Are trade-offs in allocation pattern and root morphology related to species abundance? A congeneric comparison between rare and common species in the south-western Australian flora. J Ecol 91:58–67

Poot P, Lambers H (2008) Shallow-soil endemics: adaptive advantages and constraints of a specialized root-system morphology. New Phytol 178:371–381

Press MC, Graves J (eds) (1995) Parasitic plants. Chapman and Hall, London, UK

Pressey RL, Cowling RM, Rouget M (2003) Formulating conservation targets for biodiversity pattern and process in the Cape Floristic Region, South Africa. Biol Cons 112:99–127

Proches S, Cowling RM, du Preez DR (2005a) Patterns of geophyte diversity and storage organ size in the winter-rainfall region of southern Africa. Divers Distrib 11:101–109

Proches S, Wilson JR, Veldtman R, Kalwij JM, Richardson DM, Chown SL (2005b) Landscape corridors: possible dangers? Science 310:778–779

Qian H, Ricklefs RE (2000) Large-scale processes and the Asian bias in species diversity of temperate plants. Nature 407:180–182

Ramirez N (1993) Reproductive biology in a tropical shrubland of Venezuelan Guayana. J Veg Sci 4:5–12

Raven PR, Axlerod DI (1978) Origin and relationships of the California flora. Univ Cal Publ Bot 72:1–134

Read J, Sanson GD, Caldwell E, Clissold FJ, Chatain A, Peeters P, Lamont BB, De Garine-Wichatitsky M, Jaffré T, Kerr S (2009) Correlations between leaf toughness and phenolics among species in contrasting environments of Australia and New Caledonia. Ann Bot 103:757–767

Rebelo AG (1987) Bird pollination in the Cape Flora. In: Rebelo AG (ed) A preliminary synthesis of pollination biology in the Cape Flora,. South African National Scientific Programmes Report No 141. Foundation for Research Development, CSIR, Pretoria, pp 83–108

Reiners PW, Brandon MT (2006) Using thermochronology to understand orogenic erosion. Annu Rev Earth Planet Sci 34:419–466

Renner SS (1989) Floral biological observations on Heliamphora tatei (Sarraceniaceae) and other plants from Cerro de la Neblina in Venezuela. P1ant Syst Evol 163:21–29

Renner SS, Ricklefs RE (1995) Dioecy and its correlates in the flowering plants. Am J Bot 82:596–606

Ricklefs RE (2004) A comprehensive framework for global patterns in biodiversity. Ecol Lett 7:1–15

Rivadavia F, Kondo K, Kato M, Hasebe M (2003) Phylogeny of the sundews, Drosera (Droseraceae), based on chloroplast rbcL and nuclear 18S ribosomal DNA sequences. Am J Bot 90:123–130

Rokich DP, Dixon KW, Sivasithsamparam K, Meney KA (2000) Topsoil handling and storage effects on woodland restoration in Western Australia. Restor Ecol 8:196–208

Ronce O, Perret F, Oliveri I (2000) Landscape dynamics and evolution of colonizer syndromes: interactions between reproductive effort and dispersal in a metapopulation. Evol Ecol 14:233–260

Rossetto M, Lucarotti SF, Hopper SD, Dixon KW (1997) DNA fingerprinting of Eucalyptus graniticola: a critically endangered relict species or a rare hybrid. Heredity 79:310–318

Rowe KC, Heske EJ, Brown PW, Paige KN (2004) Surviving the ice: Northern refugia and postglacial colonization. Proc Nat Acad Sci USA 101:10355–10359

Rull V (1999) A palynological record of a secondary succession after fire in the Gran Sabana, Venezuela. J Quat Sci 14:37–152

Rull V, Vegas-Vilarrubia T (2006) Unexpected biodiversity loss under global warming in the neotropical Guayana Highlands: a preliminary appraisal. Glob Chang Biol 12:1–9

Sauberer N, Zulka KP, Abensperg-Traun M, Berg H-M, Bieringer G, Milasowszky N, Moser D, Plutzar C, Pollheimer M, Storch C, Tröst R, Zechmeister H, Grabherr G (2004) Surrogate taxa for biodiversity in agricultural landscapes of eastern Austria. Biol Conserv 117:181–190

Saunders DA, Hobbs RJ, Margules CR (1990) Biological consequences of ecosystem fragmentation: a review. Conserv Biol 5:18–32

Schonswetter P, Stehlik I, Holderegger R, Tribisch A (2005) Molecular evidence for glacial refugia of mountain plants in the European Alps. Mol Ecol 14:3547–3555

Seddon G (1974) Xerophytes, xeromorphs and sclerophylls: the history of some concepts in ecology. Biol J Linn Soc 6:65–87

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

Shane MW, Dixon KW, Lambers H (2005) The occurrence of dauciform roots amongst Western Australian reeds, rushes and sedges, and the impact of phosphorus supply on dauciform-root development in Schoenus unispiculatus (Cyperaceae). New Phytol 165:887–898

Shearer BL, Crane CE, Cochrane A (2004) Quantification of the susceptibility of the native flora of the South-West Botanical Province, Western Australia, to Phytophthora cinnamomi. Austral J Bot 52:43–443

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

Smith PJ (ed) (1989) The evolving earth. Equinox, Oxford

Soderberg K, Compton JS (2007) Dust as a nutrient source for fynbos ecosystems, South Africa. Ecosystems 10:550–561

Soltis DE, Morris AB, Lachlan JSM, Manos PS, Soltis PM (2006) Comparative phylogeography of unglaciated eastern North America. Mol Ecol 15:4261–4293

Stebbins GL (1952) Aridity as a stimulus to evolution. Am Nat 86:33–44

Stebbins GL, Major J (1965) Endemism and speciation in California flora. Ecol Monogr 35:1–35

Steiner KE (1987) Breeding systems in the Cape flora. In: Rebelo AG (ed) A Preliminary Synthesis of Pollination Biology in the Cape Flora,. South African National Scientific Programmes Report No 141. Foundation for Research Development, CSIR, Pretoria, pp 22–51

Swarts ND, Sinclair EA, Krauss SL, Dixon KW (2009) Genetic diversity in fragmented populations of the critically endangered spider orchid *Caladenia huegelii*: implications for conservation. Conserv Genet, in press. doi:10.1007/s10592-008-9651-9

Swart BL, Tolley KA, Matthee CA (2009) Climate change drives speciation in the southern rock agama (Agama atra) in the Cape Floristic Region, South Africa. J Biogeogr 36:78–87

Sweedman L, Merrit D (eds) (2006) Australian seeds a guide to their collection, identification and biology. CSIRO Publishing, Melbourne, Botanic Gardens and Parks Authority, Perth, and Millennium Seed Bank, Royal Botanic Gardens, Kew

Swenson NG, Howard DJ (2005) Clustering of contact zones, hybrid zones and phylogeographic breaks in North America. Am Nat 166:581–591

Thomson K (2009) The young Charles Darwin. Yale University Press, New Haven

Tiffney BH (2008) Phylogeography, fossils, and Northern Hemisphere biogeography: The role of physiological uniformitarianism. Ann Miss Bot Gard 95:135–143

Turkington A, Phillips J, Campbell S (2005) Weathering and landscape evolution. Proceedings of the 35th Binghamton Symposium in Geomorphology, held 1–3 October, 2004. Elsevier, Amsterdam.

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

Twidale CR (1982) Granite landforms. Elsevier Scientific Publishing Company, Amsterdam

Twidale CR (1997) The great age of some Australian landforms: examples of, and possible explanations for, landscape longevity. Geol Soc Lond Spec Publ 120:13–23

Twidale CR (2007) Ancient Australian landscapes. Rosenberg, Dural

Underwood EC, Klausmeyer KR, Cox RL, Busby SM, Morrison SA, Shaw MR (2009a) Expanding the global network of protected areas to save the imperiled mediterranean biome. Cons Biol 23:43–52

Underwood EC, Viers JH, Klausmeyer KR, Cox RL, Shaw MR (2009b) Threats and biodiversity in the mediterranean biome. Diversity Distrib 15:188–197

Valiente-Banuet A, Rumebe AV, Verdú M, Callaway RM (2006) Modern quaternary plant lineages promote diversity through facilitation of ancient tertiary lineages. Proc Nat Acad Sci USA 103:16812–16817

Vallance TG, Moore DT, Groves EW (compilers) (2001) Nature's Investigator: The Diary of Robert Brown in Australia, 1801–1805. Australian Biological Resources Study, Canberra

van der Niet T, Johnson SD (2009) Patterns of plant speciation in the Cape floristic region. Mol Phylog Evol 51:85–93

van Wilgen BW, Le Maitre DC, Cowling RM (1998) Ecosystem services, efficiency, sustainability and equity: South Africa's working for water programme. Trends Ecol Evol 13:378

Verboom WH, Pate JS (2003) Relationships between cluster root-bearing taxa and laterite across landscapes in southwest Western Australia: an approach using airborne radiometric and digital elevation models. Plt Soil 248:321–333

Verboom WH, Pate JS (2006a) Bioengineering of soil profiles in semiarid ecosystems: the 'phytotarium' concept. A review. Plt Soil 289:71–102

Verboom WH, Pate JS (2006b) Evidence of active biotic influences in pedogenetic processes. Case studies from semiarid ecosystems of south-west Western Australia. Plt Soil 289:103–121

Verboom GA, Linder HP, Stock WD (2003) Phylogenetics of the grass genus Ehrharta: evidence for radiation in the summer-arid zone of the South African Cape. Evolution 57:1008–1021

Verboom GA, Archibald JK, Bakker FT, Bellstedt DU, Conrad F, Dreyer LL, Forest F, Galley C, Goldblatt P, Henning JF, Mummenhoff K, Linder HP, Muasya AM, Oberlander KC, Savolainen V, Snijman DA, van der Niet T, Nowell TL (2009) Origin and diversification of the Greater Cape flora: Ancient species repository, hot-bed of recent radiation, or both? Mol Phyl Evol 51:44–53

Vidal Romani JR, Twidale CR (2005) Landforms and geology of granite terrains. Taylor & Francis, Oxford

Viles HA, Naylor LA, Carter NEA, Chaput D (2008) Biogeomorphological disturbance regimes: progress in linking ecological and geomorphological systems. Earth Surf Process Landforms 33:1419–1435

Vinogradov AE (2003) Selfish DNA is maladaptive: evidence from the plant Red list. Trends Genet 19:609–614

Visser J (1981) South African parasitic flowering plants. Juta, Cape Town

Vitousek P, Chadwick O, Matson P, Allison S, Derry L, Kettley L, Luers A, Mecking E, Monastra V, Porder S (2003) Erosion and the rejuvenation of weathering-derived nutrient supply in an old tropical landscape. Ecosystems 6:762–772

Wackernagel M, Schulz NB, Deumling D, Linares AC, Jenkins M, Kapos V, Monfreda C, Lohi J, Myers N, Norgaard R, Randers J (2002) Tracking the ecological overshoot of the human economy. Proc Natl Acad Sci USA 99:9266–9271

Walker J, Reddell P (2007) Retrogressive succession and restoration on old landscapes. In: Walker LR, Walker J, Hobbs RJ (eds) Linking restoration and ecological succession. Springer-Verlag, New York, pp 69–89

Walker J, Thomson CH, Reddell P, Rapport DJ (2001) The importance of landscape age in influencing landscape health. Ecosyst Health 7:7–14

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

Watson JR (1991) The identification of river foreshore corridors for nature conservation in the South Coast Region of Western Australia. In: Saunders DA, Hobbs RJ (eds) Nature conservation 2: the role of corridors. Surrey Beatty & Sons, Chipping Norton NSW

Waycott M, Walker DI, James SH (1996) Genetic uniformity in Amphibolis antarctica, a dioecious seagrass. Hered 76:578–585

Whelan RJ (1995) The Ecology of Fire. Cambridge University Press, Cambridge, Cambridge Studies in Ecology

Whittaker RJ, Araújo MB, Jepson P, Ladle RJ, Watson JEM, Willis KJ (2005) Conservation Biogeography: assessment and prospect. Diversity Distrib 11:3–23

Widdowson M (1997) The geomorphological and geological importance of palaeosurfaces. Geol Soc Lond Spec Publ 120:1–12

Wiens JJ, Donoghue MJ (2004) Historical biogeography, ecology and species richness. Trends Ecol Evol 19:639–644

Wiens JJ, Graham CH (2005) Niche conservatism: Integrating evolution, ecology, and conservation biology. Annu Rev Ecol Evol Syst 36:519–539

Williams GC (1966) Adaptation and Natural Selection. Princeton University Press, Princeton, New Jersey, A critique of some current evolutionary thought

Willis KJ, Niklas KJ (2004) The role of Quaternary environmental change in plant macroevolution: the exception or the rule? Phil Trans R Soc Lond B 359:159–172

Willson MF, Rice BL, Westoby M (1990) Seed dispersal spectra: a comparison of temperate plant communities. J Veg Sci 1:547–562

Wilson CA, Calvin CL (2007) An origin of aerial branch parasitisim in the mistletoe family, Loranthaceae. Am J Bot 93:787–796

Wisheu C, Rosenzweig ML, Olsvig-Whittaker L, Shmida A (2000) What makes nutrient-poor mediterranean heathlands so rich in plant diversity? Evol Ecol Res 2:935–955

Yates CJ, Hopper SD, Brown A, van Leeuwen S (2003) Impact of two wildfires on endemic granite outcrop vegetation in Western Australia. J Veg Sci 14:85–194

Yates CJ, Ladd PG, Coates DJ, McArthur S (2007a) Hierarchies of cause: understanding rarity in an endemic shrub *Verticordia staminosa* (Myrtaceae) with a highly restricted distribution. Austral J Bot 55:194–205

Yates CJ, Elliott C, Byrne M, Coates DJ, Fairman R (2007b) Seed production, germinability and seedling growth for a bird-pollinated shrub in fragments of kwongan in south-west Australia. Biol Conserv 136:306–314

Yates CJ, Coates DJ, Elliott C, Byrne M (2007c) Composition of the pollinator community, pollination and the mating system for a shrub in fragments of species rich kwongan in south-west Western Australia. Biodivers Cons 16:1379–1395

Zachos J, Pagani M, Sloan L, Thomas E, Billups K (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292:686–93