THE SOUTHWEST AUSTRALIAN FLORISTIC REGION: Evolution and Conservation of a Global Hot Spot of Biodiversity

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■ **Abstract**   Like South Africa's Greater Cape Floristic Region, the Southwest Australian Floristic Region (SWAFR) is species rich, with a Mediterranean climate and old, weathered, nutrient-deficient landscapes. This region has 7380 native vascular plants (species/subspecies): one third described since 1970, 49% endemic, and 2500 of conservation concern. Origins are complex. Molecular phylogenies suggest multiple dispersal events into, out of, and within the SWAFR throughout the Cretaceous and Cenozoic; in many phylogenetically unrelated clades; and from many directions. Either explosive speciation or steady cladogenesis occurred among some woody sclerophyll and herbaceous families from the mid-Tertiary in response to progressive aridity. Genomic coalescence was sometimes involved. Rainforest taxa went extinct by the Pleistocene. Old lineages nevertheless persist as one endemic order (Dasypogonales) and 6–11 endemic families. Such a rich flora on old landscapes that have been exposed to European land-use practices is highly threatened. Conservation programs must minimize soil removal and use local germplasm in restoration programs.

INTRODUCTION

The Southwest Australian Floristic Region (SWAFR) occupies 302,627 km^2 on a temperate margin of the world's most arid and insular populated continent. The region is island-like (Carlquist 1974, Hopper 1979), a relatively wet continental refuge, bordered on two sides by ocean, and isolated by arid lands to the north, northeast, and east.

During the past few decades, scientists have made extraordinary leaps forward in the discovery, collection, and description of new flowering plant species in this region, without parallel among the world's temperate floras (Figure 1). These
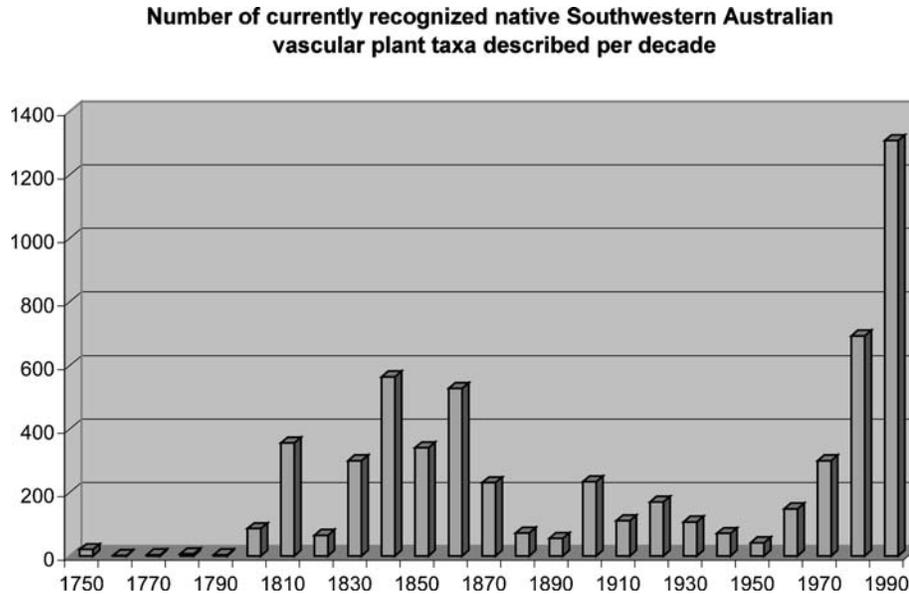
**Number of currently recognized native Southwestern Australian
vascular plant taxa described per decade**

Figure 1   The number of currently recognized native SWAFR vascular plant species de-
scribed per decade since the 1750s, derived from a total of 6759 described species listed
on the Western Australian Herbarium's FLORABASE in February 2004. Intraspecific taxa,
unpublished species with a manuscript name, and phrase-name species are not included.

advances highlight an accentuated degree of local speciation, eclipsed in temperate
regions only by that of the Greater Cape flora of South Africa (Cowling et al. 1996,
Goldblatt & Manning 2002, Linder 2003).

The SWAFR is topographically unique among the world's five regions of
Mediterranean climate (Hooker 1860; Hopper 1979, 2004; Cowling et al. 1996,
2004; Dallman 1998): It is a flat, stable, highly-weathered low plateau with granite
occasionally emergent as domed inselbergs (Anand & Paine 2002). There are a
few small quartzitic mountainous areas; the Stirling Range is the tallest, reaching
only 1109 m (Figure 2*a*, see color insert). The SWAFR has enjoyed a maritime
climate since the Jurassic, and it has been unglaciated since the Permian. This
region is dominated by old landscapes with nutrient-deficient soils (Hopper et al.
1996a,b).

Like other Mediterranean regions, the SWAFR has a fossil record rich in
closed rainforest taxa dating back to the Cretaceous (McLoughlin & Hill 1996,
McLoughlin & McNamara 2001). However, it is unique in that all such taxa
were extinct by the start of the Quaternary, following the onset and persistence
of aridity in Australia that began in the Oligocene/Miocene (Frakes 1999). In
SWAFR vegetation, only sclerophyllous shrubs, trees, and herbs have adapted to
the nutrient-deficient, highly weathered soils that now dominate as either eucalypt

forests, woodlands, mallee (lignotuberous, multistemmed eucalypts), or kwongan (shrublands and herbfields) (Figure 2*c*) (Beard 1990).

Recently the SWAFR was listed among 25 global biodiversity hot spots—those regions on Earth richest in endemic species under threat (Myers et al. 2000). Such plant richness is surprising given the subdued topography and simple rainfall and vegetation gradients evident in the region (Figure 2). This hot-spot status raises two fundamental questions that have challenged many authors since Hooker (1860) first summarized austral phytogeographic data: (a) How has such an extraordinarily rich endemic flora evolved, especially given the region's subdued, nutrient-poor terrain with few mountains? and (b) Why is the flora so threatened and how might its conservation be secured? Since Hopper (1979) addressed aspects of the first question in this series 25 years ago, many important discoveries and insights have been published (references in Pate & Beard 1984; Hobbs 1992; Pate & Hopper 1993; Cowling et al. 1996; Hopper et al. 1996b; Hopper 1997; Crisp et al. 1999; Coates et al. 2000; James 1992, 2000; Beard et al. 2000; Coates & Atkins 2001; Lambers et al. 2003; Lamont 2003). It is timely, therefore, to highlight recent advances in the understanding of the evolution of the SWAFR flora and to briefly explore applications to the challenging task of conservation. A more detailed elaboration and reference list is available elsewhere (Hopper 2004).

EVOLUTIONARY HYPOTHESES

Evidence reviewed by Hopper (1979) led to the formulation of the following hypotheses and conclusions accounting for the extraordinary species richness and high endemism of flora on southwest Australia's subdued landscapes:

1. The vascular flora comprises at least 3600 species; 68%, but possibly 75–80%, of which are endemic based on ongoing taxonomic description of local endemics.

2. The flora is richest in the coastal and inland kwongan of the Transitional Rainfall Zone (300–800 mm rainfall per annum, modified to 300–600 mm herein to embrace the Transitional Rainfall Province (TRP) and Southeast Coastal Province (SCP). The flora is relatively species-poor in the high rainfall forests (800–1500 mm, modified as the High Rainfall Province (HRP) to 600–1500 mm herein) and in arid zone communities (<300 mm) (Figures 2*b*, 5).

3. There is a subtle trend for recently evolved taxa to occur more frequently than expected in the TRP/SCP compared with the HRP, whereas the reverse trend applies with the persistence of mesothermic relictual sclerophyllous taxa in stable, high-rainfall areas or locally wet habitats elsewhere.

4. These trends are correlated in the SWAFR with patterns of landscape evolution and climatic history. Topography, soils, and climate are considerably more diverse in the TRP/SCP near the west and south coasts and inland down its western margins than in the HRP and arid zone.

5. Today's predominantly sclerophyllous SWAFR flora evolved from old lineages in isolated pockets on nutrient-deficient soils in landscapes dominated by rainforests that are now locally extinct.

6. Explosive recent speciation of sclerophyllous taxa, especially in the TRP/SCP, was caused by greater population dissection and lability than seen in the HRP or arid zone, arising from more diverse topography and the erosional dynamism and climatic stresses of the late Tertiary and Quaternary.

7. Biological, ecological, and genetic correlates and causes of explosive speciation and endemism were poorly known, but they differed from those then recorded in other Mediterranean regions; the southwest flora included few rapidly evolving annuals and few species-specific hymenopteran pollinators.

Thus, like parts of California (Stebbins & Major 1965), the SWAFR's TRP/SCP was hypothesized to be a semiarid speciation hot spot of late-Tertiary antiquity, whereas the HRP was an area more conducive to evolutionary stability and persistence over longer periods. The arid zone is a predictably harsh region favoring relatively few recently evolved taxa able to survive punishing conditions.

Hopper (1979) emphasized that much remained to be done to test these hypotheses. Furthermore, exciting work on the contribution to speciation of chromosome repatterning in small populations had only just begun. This work had led to the development of two further hypotheses (James 1981):

1. Two bursts of speciation had occurred. The first involved widespread dysploid and polyploid speciation in the Cretaceous to early Tertiary, resulting in the evolution of endemic Australian families, tribes, and genera. This was followed by a period of relative cytoevolutionary stability as genera, subgenera, and sections radiated. A more recent, late-Tertiary to Quaternary second phase of intense cytoevolution ensued, giving rise to modern dysploid and polyploid species and races.

2. According to the genomic coalescence hypothesis, such cytoevolutionary change arose under intense selection to conserve heterozygosity in the face of inbreeding imposed by small disjunct population structures (James 1992, 2000).

REVISED RICHNESS AND ENDEMISM ANALYSES

An Unexpected Rate of Recent Descriptions of New Species

For a century following the pioneering botanical work on the SWAFR flora, the estimated number of species remained at 3600 (Hooker 1860, Beard 1970). Many authors regarded the SWAFR as the species-poor cousin of the world's five Mediterranean regions. Few realized that the taxonomic impediment for understanding and conserving the SWAFR flora was as great as that applying to many tropical rainforest regions. Since then, however, the number of described SWAFR species has

increased by one third and is still rising significantly (Figure 1), primarily owing to the establishment of systematic and evolutionary research and training programs at universities and herbaria in the 1960s, and subsequently fueled by burgeoning interests in environmental conservation and, most recently, in molecular systematics. The long-term effects of a recent decline in university teaching programs in systematics have yet to impact these trends.

Although increasingly recognized by many authors (Carlquist 1974; Hopper 1979, 1992, 1997; Marchant 1991; Cowling et al. 1996; Ornduff 1996; Goldblatt & Manning 2002), this taxonomic impediment of many recently discovered but yet to be described species is not considered by others (e.g., Crisp et al. 1999, Beard et al. 2000), leading to widely divergent published estimates of the number of species in the SWAFR. However, counting described and manuscript species and infraspecific taxa listed on Western Australian Herbarium databases (Paczkowska & Chapman 2000; S.D. Hopper & P. Gioia, unpublished data) yields a total of 7380 native species/subspecies. We count both species and subspecies because most of the latter (∼8% of the 7380 taxa) have proven to be species when subjected to modern critical study (e.g., Hopper & Brown 2001; Hopper 2004). Given present trends in discovery and description (Figure 1), it seems probable that the SWAFR will have at least 8000 native species when taxonomic survey is close to completion some decades from now (Hopper 1992, Hopper et al. 1996b). More than a decade ago, Marchant (1991) independently estimated 9000 species, a figure that encompasses both native (8000) and naturalized (1000) species/subspecies.

Major Taxa

As established two centuries ago by Robert Brown and colleagues on Flinders' *Investigator* expedition (Hopper 2003, 2004), the rich diversity of the SWAFR flora is primarily among its angiosperms, especially woody families: Myrtaceae (1283 species/subspecies), Proteaceae (859), Fabaceae (540), Mimosaceae (503), Orchidaceae (374), Ericaceae (including Epacridaceae, 297), Asteraceae (280), Goodeniaceae (207), Cyperaceae (199) and Stylidiaceae (178) (Figure 3, see color insert) (Paczkowska & Chapman 2000; Beard et al. 2000; S.D. Hopper & P. Gioia, unpublished data).

The importance of woody taxa is evident also in the ten largest genera. Listed in order of number of species/subspecies, they are *Acacia* (Mimosaceae; 502 species/infraspecies), *Eucalyptus* (Myrtaceae; 362), *Grevillea* (Proteaceae; 229), *Melaleuca* (Myrtaceae; 185), *Stylidium* (Stylidiaceae; 170), *Leucopogon* (Ericaceae; 165), *Caladenia* (Orchidaceae; 162), *Verticordia* (Myrtaceae; 138), *Dryandra* (Proteaceae; 136) and *Hakea* (Proteaceae; 105). Of these, only the herbaceous Triggerplants (*Stylidium*) and the geophytic orchid genus *Caladenia* constitute nonwoody plants.

Endemics on an Old Landscape

Phylogenetically significant endemics confirmed in DNA sequence studies include one monocot order (Dasypogonales) and at least six families (the monocot

Dasypogonaceae, Ecdeiocoleaceae, and Anarthriaceae, and eudicot Cephalotaceae, Emblingiaceae, and Eremosynaceae (APG II 2003) (Figure 4, see color insert). Other high-level SWAFR endemic monocot clades regarded by some as families include Haemodoraceae subfamily Conostylidoideae, *Baxteria* and *Calectasia* of Dasypogonaceae, and *Hopkinsia* and *Lyginia* of Anarthriaceae.

Based on premolecular intuitive classifications of most families and genera, 711 genera with 13% (92) endemic to the region are known (Beard et al. 2000). As a result of molecular phylogenetics, substantial changes in delimitation for many of these genera are proposed (e.g., *Banksia/Dryandra*) (Mast & Givnish 2002).

A surprising finding is that estimates of species-level endemism as high as 80–90% (Hooker 1860, Hopper 1979, Marchant 1991) have required significant downward modification as collecting has intensified. The figure of 53% (Beard et al. 2000) is now superseded by an even lower 49% (S. Hopper and P. Gioia, manuscript in preparation). Even though recently described species/subspecies are often narrow-range endemics, the ranges of many SWAFR species/subspecies have been extended, at least marginally, beyond the region's borders.

The presence of endemic families and the endemic order Dasypogonales signal prolonged conditions for the persistence of relict taxa in the SWAFR. It is indeed one of the oldest landscapes on Earth. Its essential flatness is due to the absence of mountain building since the Carboniferous-Permian glaciation, which lasted from 320 to 290 Mya (Playford 1999). Moreover, some granite inselbergs have had their summits exposed since the mid-Cretaceous (Watchman & Twidale 2002). Combined with the absence of inundation or glaciation since the Permian, this great antiquity of landforms renders the SWAFR among the oldest unglaciated regions on Earth. Younger landscape elements, such as extensive Tertiary laterites and Quaternary coastal limestones, dunes, and wetlands, are also found in the region. However, in comparison with postglacial landscapes common in the northern hemisphere and parts of southeast Australia, most of the SWAFR is extraordinarily old (Anand & Paine 2002, Wyrwoll 1988).

Not surprisingly, with such exceptional opportunities for continuous terrestrial evolution, local endemism is prominent in components of both the flora and the less vagile fauna (Hopper et al. 1990, 1996b; Cowling et al. 1994; Brown et al. 1998; Harvey 2002). Hopper and colleagues (Hopper et al. 1996b; Hopper 1997, 2000) hypothesized that natural selection has resulted in mechanisms promoting local persistence rather than wide dispersal and colonizing. This persistence may be a result of the prolonged absence of major geomorphological agents of soil disturbance and rejuvenation, as seen during glaciation, mountain building, and vulcanism. Only along coastlines and rivers, in other wetlands, and around rock outcrops has wholesale and regular soil disturbance been prominent, with the biota consequently exhibiting better mechanisms for long-distance dispersal and colonization. Indeed, local endemism and attendant landscape continuity seen in the SWAFR may well be a model for what many other regions on Earth were like prior to Quaternary glacial cycles.

Biological Correlates of Narrow Endemism

Cowling et al. (1994) found that local and regional endemics constituted 6% and 22%, respectively, of the 1422 species from communities of the Fitzgerald District (Figure 5, see color insert). Endemics were both overrepresented in species-rich families such as Proteaceae, Myrtaceae, Fabaceae, and Ericaceae and underrepresented in Asteraceae and Orchidaceae. Endemics were also virtually absent from less nutrient-impoverished coastal calcareous sands, but as expected, they constituted up to 30% of kwongan communities on highly infertile quartzites and siliceous sands. Biologically, the narrow-range endemics were equally likely to be shrubs or graminoids. These shrubs were of medium height; with soil or canopy-stored seed dispersed either by wind, vertebrates, ants, or ballistically in roughly equal proportion; and with estimated medium (10–100 m) to short (<10 m) seed-dispersal distances. No local endemics were recorded among tall shrubs (>2 m) or among woody shrubs lacking seed storage [such as *Billardiera* (*Sollya*) *heterophylla*, Pittosporaceae].

Threatened endemic SWAFR taxa similarly are mostly woody perennials, one third of which are short-lived disturbance opportunists and obligate seeders after fire (e.g., species of *Acacia* and *Grevillea*) (Hopper et al. 1990, Bell 2001). Perennial herbs feature prominently among the remaining threatened taxa. More than half of these are orchids. Spring flowering occurs in two thirds of the threatened taxa, and 40% have flowers likely to be pollinated by birds and/or mammals. This is almost three times the proportion (15%) of the SWAFR flora at large that is vertebrate pollinated (Keighery 1982, Hopper & Burbidge 1986, Brown et al. 1997), a striking figure in itself.

TOWARD A NEW PHYTOGEOGRAPHIC UNDERSTANDING

Detailed vegetation mapping of the SWAFR (Figure 2*c*) (Diels 1906, Beard 1990) has been followed up by recent floristic analyses of all 7380 southwest species/subspecies represented in collections of the Western Australian Herbarium (standardized for collection effort; S.D. Hopper & P. Gioia, unpublished data) as well as by plant community studies at the regional and local level. It is now possible to explore phytogeographic patterns in the whole flora. Modern floristic data support the inland boundary of the SWAFR approximating the 300-mm rainfall isohyet (Figure 2*b*) as originally proposed by Diels (1906).

Although the TRP/SCP kwongan districts are richer in species than are the HRP forests (Hopper 1979, 1992), intensified collection of the flora has revealed that there are many centers of species richness throughout the whole SWAFR (Figure 5*a*) (Gioia & Pigott 2000). These centers are most evident close to the coast in both the TRP/SCP and the HRP, but they can also be found inland, tapering off toward the arid margins of the region. They largely coincide with centers of endemism (Figure 5*b*).

Classification of the richness centers according to their composite species revealed the presence of three major phytogeographical provinces and 11 floristic districts in the SWAFR (Figure 5). This new classification closely approximates the scheme proposed by Hopper (1979, 1992), except that, as mentioned above, the HRP extends out to the 600-mm isohyet rather than the 800-mm isohyet used to define the earlier High Rainfall Zone and the Transitional Rainfall Zone is split into two provinces, the TRP and the SCP (Figure 5). The latter is novel, and it bears limited resemblance to vegetation-based bioregions currently enjoying wide use (Beard 1990; cf. Figure 2). Although some support for the new floristic classification exists, especially in relation to upland refugial centers (Hopper 1979, Hopkins et al. 1983, Lamont et al. 1984, Hopper et al. 1997, Mast 2000), further exploration of the classification is warranted to test its usefulness as a predictive model of species richness and endemism.

Many SWAFR floristic studies have established moderate to high diversity within habitats and among adjacent habitats, with extraordinarily rapid turnover of species across southwest landscapes (Cowling et al. 1994, 1996; Hopper 2004). At the extreme level in kwongan heathlands at Mt. Lesueur, quadrats on the same lateritic upland landform just 1 km apart may display up to a 60% difference in species composition (Hopkins & Griffin 1984).

Richardson et al. (1995) explored correlates of coexistence of *Banksia* species in the SWAFR, finding coexistence to be complexly linked to local and regional processes that are generally unrelated to growth form or regeneration class of sympatric species, as niche theory would predict. Rather, coexistence appears to be mediated by edaphic specialization and marked spatial and temporal variation in recruitment opportunities associated with interactions of soil type, fire, drought, flooding, and disease. Lottery recruitment models are likely to apply, and simplistic explanations should be questioned (Grubb 1992). This insight is not unique to banksias among SWAFR taxa (e.g., Yates et al. 2003). Much more experimental demographic and ecophysiological research is needed to advance understanding of how species-rich communities of SWAFR flora are assembled and ecologically maintained.

NEW INSIGHTS INTO EVOLUTIONARY ORIGINS

Simple ecological hypotheses such as soil mosaics being a primary cause of speciation (Beard et al. 2000) are insufficient to account for the origins of the rich SWAFR flora. Data from ecology, biogeography, genetics, phylogenetics, paleontology, geomorphology, and paleoclimatology are all needed to unravel this challenging question.

The Fossil Record, Geomorphology, and Paleoclimates

Significant advances in paleontology, plate tectonics, and geomorphology during the past two decades have generated fresh insights regarding origins of the SWAFR's flora (Powell et al. 1988; McLoughlin & Hill 1996; Hopper et al.

1996a,b; Anderson et al. 1999; McLoughlin & McNamara 2001; McLoughlin 2001; Hopper 2003; Atahn et al. 2004). For example, the discovery of fossils of extant genera such as *Banksia/Dryandra* (Proteaceae) and *Agonis* (Myrtaceae) as old as early- to mid-Tertiary indicate great antiquity and stability of some contemporary plant lineages.

The SWAFR's high-latitude Eocene floras were conspicuously rich in families such as the Myrtaceae and Proteaceae, suggesting that a long history of speciation underpins the species richness of the flora (McLoughlin & Hill 1996). Similar to contemporary SWAFR vegetation, the proportional representation of taxa in these Eocene communities varied over relatively short distances (McLoughlin & Hill 1996, Itzstein-Davey 2003). Perhaps low dispersal capabilities of many components of the flora also have significant antiquity.

The rifting of Antarctica from southern Australia resulted in an uplift of the Stirling Range in the mid-Cretaceous (Powell et al. 1988, McLoughlin 2001). This has remained an important center of floristic richness and endemism in the SWAFR (Figure 5). Central parts of the Australian plate were also downwarped and inundated during the Cretaceous, resulting in many islands along the east, south, and west margins of the SWAFR. These islands may have played a significant part in the early evolution of endemism of the extant flora. In light of new evidence regarding the unexpected antiquity of some flowering plant lineages, subsequent periods of high sea level and island formation, especially in the Eocene, are certain to have played such a part.

The early stages of a shift toward drier conditions across Australia associated with the final rifting of the continent from Antarctica are evident in Oligocene (45–25 Mya) fossil floras. These are less diverse than their Eocene predecessors and have significant proportions of scleromorphous elements, such as *Banksia/ Dryandra*. For example, the West Dale and Tambellup floras have a "striking increase in the representation of myrtacean remains and a corresponding decline in the proportions of *Nothofagus* [Nothofagaceae] and *Gymnostoma* [Casuarinaceae]" (McLoughlin & Hill 1996, p. 76). Extensive silcretes, laterites, and calcretes also developed at this time, possibly suggesting stronger seasonality of rainfall. If so, this would imply a significant increase in fire frequency.

Regional habitat diversity and opportunities for speciation were enhanced by moderate post-Eocene uplift of the west and southern margins of the Yilgarn Craton (Anand & Paine 2002) along the Darling Range and Ravensthorpe Ramp, respectively. Coastal rivers were rejuvenated, dissecting the Cretaceous–early Tertiary plateau duricrusts into numerous insular/peninsula remnants bordered by erosional and depositional soils (see map in Hopper 1979). The plateau margins thereafter had relatively rugged and more diverse topographical features than did inland areas (Figure 2*a*), albeit at subdued elevations from a global perspective. Evidence is mounting that the flora responded spectacularly to this regional variation in habitat diversity following the mid-Tertiary onset of aridity.

Final separation of Australia from Antarctica in the Oligocene initiated climatic changes that established the Australian deserts, arching inland from the Great

Australian Bight across the Nullarbor Plain to eventually enclose the SWAFR as early as 30 Mya (Frakes 1999). This emplaced a belt of semiarid transitional rainfall on the area of greatest fragmentation of lateritic duircrusts flanking the more mesic, high-rainfall forested areas of the SWAFR, forming one of the world's major plant speciation hot spots (Hopper 1979, 1992).

The downwarping of central Australia in the Cretaceous was terminated when Miocene seas completed formation of the Nullarbor limestones commenced in the Eocene. The Nullarbor Plain formed an edaphic barrier to east-west migration for terrestrial species adapted to acidic soils derived from the granitoid bedrock of much of the SWAFR. Barriers to migration and emigration were thus enhanced for the SWAFR, conserving the flora's long-standing regional endemism.

Not all plant lineages in the SWAFR are so limited in dispersal that they were contained within these borders throughout their phylogeny. There is increasing evidence of multiple dispersal events into, out of, and within the SWAFR throughout the Cretaceous and Cenozoic, in many phylogenetically unrelated clades, and from many directions (Figure 6) (McLoughlin 2001, Crisp et al. 1999).

Essentially modern floras, with the addition of small amounts of closed forest *Nothofagus*, araucarian, and podocarp conifer species, are seen in late-Tertiary and Quaternary fossil deposits. Inland areas had increased abundance and diversity of pollen of Myrtaceae, Poaceae, *Acacia*, and Asteraceae, suggesting seasonal rainfall. A slight rise in temperatures in the early Miocene (25–20 Mya) was accompanied by renewed formation of laterite, silcrete, and calcrete as well as lake sedimentation. This period was followed by sharp declines to cold and substantially fluctuating conditions from the mid- to late Miocene onward.

It seems probable that a mildly seasonal Mediterranean climate was present in southwest Australia from this period 20 Mya to the present. Closure of the Indonesian seaway in the Pliocene, an event of global significance, led to more rapid drying out of Australia from ~3–5 Mya (J. Dodson, personal communication) and possibly signaled the onset of conditions similar to today's.

The similarity of Pliocene floras (Atahan et al. 2004, Dodson & Macphail 2004) to contemporary vegetation suggests only moderate impacts of Quaternary ice age

Figure 6   Historical biogeographic tracks along which congruent patterns of speciation have occurred within and from outside the SWAFR, as inferred from molecular phylogenetic studies (from Crisp et al. 1999, Hopper 2004). (*A*) Track names within southwest Australia are (*1*) Transitional Rainfall NW-SE, (*2*) South Coast HRP-SCP, (*3*) West Coast HRP-TRP, (*4*) SW-Inland HRP-TRP, and (*5*) High Rainfall N-S. (*B*) Track names from the SWAFR elsewhere are (*1*) SW-Arid Australia, (*2*) SW-SE Australia, (*3*) SW-Monsoon Australia, (*4*) SW-NE Australia, (*5*) SW-E Australia, (*6*) SW-Tasmania, (*7*) Trans-Indian Ocean, (*8*) Pan-Temperate, and (*9*) South Pacific. Major areas of the southwest identified (*a*, *b*, *c*, *d*) allow for more precise track descriptors. For example, the SWc-Arid Australia track is for speciation events involving SWAFR taxa from only the Southeast Coastal Province (*c*) and sister taxa in Arid Australia.
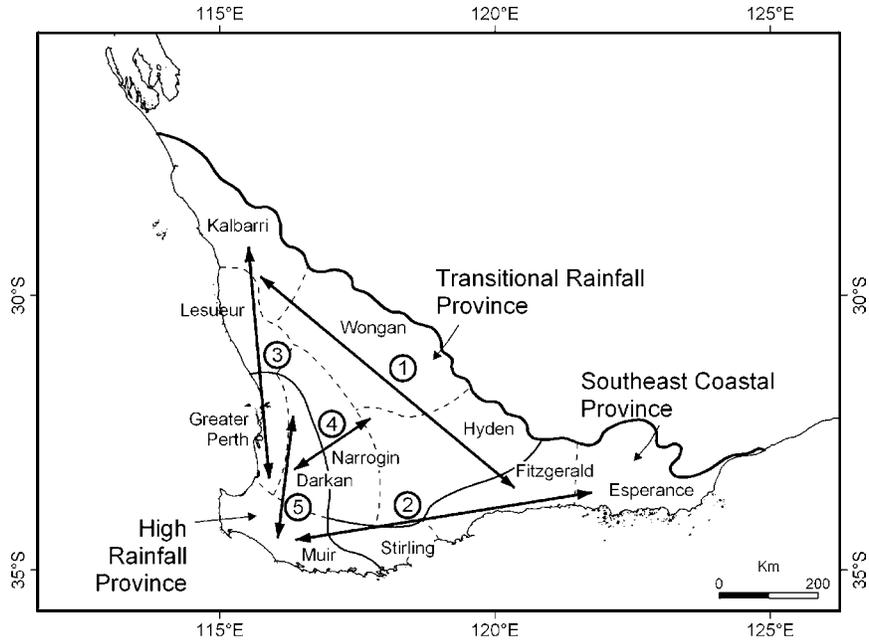
(a) Southwestern Australia
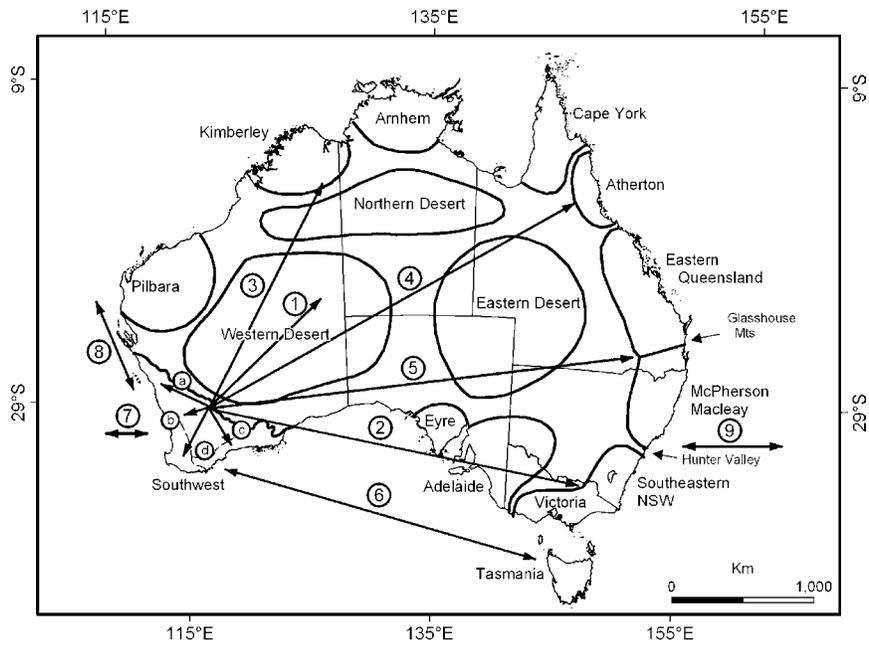
(b) Australian continent

climatic oscillations in the SWAFR, probably most pronounced in the TRP/SCP as hypothesized by several authors (Hopper 1979, 1992; Hopper et al. 1996b). Firm evidence of fire is seen in the common occurrence of charcoal in these Pliocene deposits. Also noteworthy is the persistence of rare *Nothofagus* and podocarp and araucarian rainforest conifers alongside such obvious postfire opportunists as species of Gyrostemonaceae (Pate & Hopper 1993, Bell 2001). The closed rainforest taxa were extinct by 2.6 Mya. Early concepts of a wet mid-Holocene in the SWAFR are not supported by a repeat palynological survey of key lake deposits (Newsome & Pickett 1993).

Molecular Phylogenetic Tests of Evolutionary Hypotheses

Molecular phylogenetics provides powerful tools to test the above hypotheses from independent and rigorously analyzed biological data sets. Although much remains to be done, significant recent progress allows for first glimpses of likely congruence or noncongruence of phylogenetic pattern among SWAFR lineages.

SPECIATION AND EXTINCTION RATES   If, as predicted (Hopper 1979, 1992), a period of explosive speciation in SWAFR taxa occurred in the late Tertiary and Quaternary after a slower period of radiation, unresolved polytomies arising from fewer steadily branching clades or grades and linking many crown taxa should be evident in the molecular phylogenies. Such a pattern was evident for Aizoaceae in the Greater Cape floristic region of South Africa, providing support for the hypothesis that explosive speciation occurred especially among the subfamily Ruschioideae of the succulent karoo (Klak et al. 2004).

Species-level molecular phylogenies are steadily accumulating for SWAFR genera and often contain large late-branching polytomies, e.g., in *Daviesia* (Fabaceae, Crisp & Cook 2003), *Eucalyptus* (Steane et al. 2002), *Acacia* (Miller & Bayer 2001), *Leucopogon* (Ericaceae) (Taffe et al. 2001, Quinn et al. 2003), and *Stylidium* (Coates et al. 2003). Coates et al. (2003) proposed a Pliocene origin for radiation in the *S. caricifolium* complex, and a late-Miocene to early-Pliocene date is also likely for *Conostylis* (Haemodoraceae) S. Hopper, M. Chase and M. Fay, unpublished data). This is consistent with evidence that climatic variation was significant in the Pliocene as well as the Quaternary (Dodson & Macphail 2004). Large unresolved late-branching polytomies are also seen in molecular cladograms for two major arid zone families: Myoporaceae and Chenopodiaceae (Kelchner 2003, Shepherd et al. 2004).

There are exceptions to this inferred explosive speciation pattern, however, with a more even and steady accumulation of species in late-branching nodes. Examples include *Gastrolobium* (Fabaceae) (Chandler et al. 2001) and Restionaceae (Linder et al. 2003). *Banksia* provides a transitional model with some clades steadily branching and others showing moderately sized terminal polytomies (Mast & Givnish 2002). Further work is needed for a conclusive statement on speciation rates in the SWAFR, but greater complexity than just a major Neogene explosive speciation episode is already evident.

An earlier phase of explosive speciation at tribal/generic level, hypothesized originally from chromosome number patterns (James 1981), is suggested by large polytomies at or near the spine of family or tribal cladistic trees in Rhamnaceae (Richardson et al. 2000), Myrtaceae (Wilson et al. 2001), and Fabaceae (Doyle et al. 2000). Conversely, such a pattern is not evident for Restionaceae (Linder et al. 2003) or Haemodoraceae (Hopper et al. 1999), where a steady accumulation of early branches has been documented. A more complex situation than previously envisioned seems to apply here as well.

Discriminating between patterns due to speciation and those due to extinction processes is a major challenge in interpreting molecular phylogenies. How should an early-branching clade with a few species that is sister to a much richer clade be interpreted—as an evolutionarily quiescent lineage or as the remnants of a richer clade with most members now extinct? In the absence of a fossil record, resolution of this question is problematic. New evidence and approaches are needed.

Although regional extinction of closed rainforest taxa in the Quaternary occurred, it is instructive to enquire where early-branching extant clades of SWAFR taxa persist. Is there evidence of more buffering from extinction in the HRP than in the TRP/SCP (Hopper 1979), or do old relictual clades persist throughout the SWAFR?

OLD RELICTUAL CLADES   Of the 54 species of the psilotid, lycopsid, fern, cycad, cupressid conifer, and podocarp lineages found in the SWAFR, 43 occur in the HRP, 32 in the SCP, and 28 in the TRP. Given that the TRP is three times larger than the HRP and more than twice as large as the SCP, a disproportionate number of these old vascular plant lineages occur in the HRP and SCP. Moreover, 17 of the 54 species extend from the HRP into the TRP, whereas 26 extend from the HRP into the SCP. These statistics support the hypothesis that the more mesic southern Provinces are ancestral to the drier northwest and northern TRP in the phylogenetic radiation of older components of the flora. This pattern is also evident in the distributions of *Selaginella gracillima* (Selaginaceae), *Podocarpus drouynianus* (Podocarpaceae), and some but not all *Actinostrobus* and *Callitris* (Cupressaceae).

Members of the endemic order Dasypogonales (Figure 4*a,b,c*) occur mainly in moist habitats of the HRP and SCP, with some taxa extending into well-drained soils of the TRP. A similar situation prevails for the endemic Cephalotaceae, Eremosynaceae, and oldest members of Colchicaceae (*Burchardia*) (Vinnersten & Reeves 2003) and Haemodoraceae subfamily Conostylidoideae (*Tribonanthes*) (Hopper et al. 1999). Their current distributions support the hypothesis that refugial habitats for old lineages are prevalent in the HRP and SCP.

The Albany Pitcher Plant *Cephalotus follicularis* (Figure 4*k*), the classic SWAFR endemic discovered in 1802 (Hopper 2004), belongs to Oxalidales (Bradford & Barnes 2001). Its closest relatives are either the monogeneric South American Brunelliaceae or *Brunellia* together with the family Cunoniaceae. In turn, these three families are sister to Elaeocarpaceae. *Cephalotus* is a highly divergent relict of a rainforest lineage that has persisted in the SWAFR by inhabiting swamp margins

that are moist year round. However, other endemic SWAFR families, including Anarthriaceae, Ecdeicoleaceae, and Emblingiaceae (Figure 4), are most at home in the moisture-retaining soils of the semiarid TRP, SCP, and HRP.

The divergence time of the two genera of Ecdeiocoleaceae (*Ecdeiocolea* and *Georgeantha*) (Figure 4*i*) was estimated as 75–50 Mya, whereas Ecdeiocoleaceae as a family likely diverged from Poaceae 85–60 Mya (Bremer 2002). The divergence of *Anarthria* from the common ancestor of *Lyginia* and *Hopkinsia* (Figure 4) was estimated at between 70 and 35 Mya (Bremer 2002). Anarthriaceae likely diverged from Restionaceae 100 to 80 Mya. These estimates, derived from molecular phylogenetic data, corroborate the hypothesis based on fossil studies that the TRP kwongan taxa are of considerable antiquity (Hopper et al. 1996b, McLoughlin & McNamara 2001).

It appears that waterlogged or moisture-retaining soils throughout the SWAFR provide habitat for the phylogenetically relictual taxa of the region, with a tendency for these to be concentrated in the southern HRP and SCP rather than the more northerly and drier TRP. These are likely to be the taxa with relatively low extinction rates, best suited to studies aimed at assessing speciation rates and patterns.

RECENTLY SPECIATED CLADES   The patterns emerging from molecular phylogenetic studies are more complex and individualistic than early hypotheses regarding the TRP/SCP speciation hot spot suggested (Hopper 1979, 2004). This complexity is exemplified by an analysis of the distributions of SWAFR taxa in species-level molecular phylogenies of the largely SWAFR endemic poison pea genus *Gastrolobium* (Fabaceae) (Figure 3*b*) and related genera (Chandler et al. 2001).

Within this lineage, the earliest branching clade is the *G. spinosum* group. This group mainly grows on lateritic and granite outcrops in the SCP and TRP, but it also has satellite taxa evolving from independent TRP/SCP groups into the HRP (*G. cuneatum* and *G. bilobum*) (Figure 3*b*). The group also has taxa from the SCP's Esperance District (Figure 5), giving rise to the only two species in the genus extending widely into the Australian arid zone and its margins (bird-pollinated *G. grandiflorum* and *G. brevipes*).

Essentially, these patterns within the SWAFR are repeated in subsequent clades of *Gastrolobium*. There are complex allopatric replacement series across the semiarid TRP and SCP, with multiple origins of offshoot species to the HRP, local radiations of taxa in the SCP's Stirling Range (Figure 5) (especially of taxa previously placed in *Nemcia*), and a terminal radiation of mainly bird-pollinated species previously placed in *Brachysema* and *Jansonia* that reinvaded and speciated within the HRP.

Thus the hypothesis that recent speciation is accentuated in the TRP/SCP relative to the HRP (Hopper 1979) is supported by the *Gastrolobium* study, but the degree of involvement of HRP taxa is reasonably high and present at all levels in the cladogram except the earliest branches. With the arid zone taxa *G. grandiflorum* and *G. brevipes*, the genus also exemplifies how a predominantly southwestern endemic has spawned widespread congeners out into Australia's deserts.

Cytogeography and Infraspecific Phylogeography

Historical biogeographic patterns revealed by molecular phylogenetic studies of many taxa above the species level are mirrored by patterns of genetic differentiation within species in the SWAFR. For example, a perennial herb of rock outcrops, *Isotoma petraea* (Campanulaceae–Lobeliaceae), ranges across arid southern Australia as a series of uniformly diploid outbreeding, chromosomally invariant populations until it reaches the margins of the SWAFR. There, formation of chromosomal rings in translocation heterozygotes is associated with a shift to inbreeding. The number of chromosomes in the ring increases toward the southwest until all seven pairs are bound up in one super ring in populations at the extreme southwest margin of the Wongan District of the TRP (James 1965, 1992, 2000). Recent DNA phylogeographic studies affirm this cytogeographic hypothesis (Bussell et al. 2002), thus providing an example of directional chromosomal divergence from the arid zone into the SWAFR. A similar phylogeographic pattern has been hypothesized recently for sandalwood (*Santalum spicatum*, Santalaceae) (Byrne et al. 2003).

Evidence of complex intraspecific phylogeographic divergence, some likely to date back to the Pliocene, is emerging from studies of a range of TRP/SCP taxa, including species of *Acacia*, *Eucalyptus*, *Banksia*, *Geleznowia* (Rutaceae), and *Stylidium* (Coates 2000, Byrne 2003). *Lambertia orbifolia* (Proteaceae), *Acacia anomala*, and *Laxmannia sessiflora* (Lomandraceae) provide similar HRP examples (James et al. 1999, Coates 2000). As case after case accumulates, the evidence that this is a flora with anciently and complexly fragmented population systems becomes compelling.

BIOGEOGRAPHICAL TRACKS WITHIN AND OUTSIDE THE SWAFR   The   overriding emergent hypothesis from a review of molecular phylogenetic studies (Hopper 2004) is that the SWAFR has a vascular flora of multiple origins. The flora is made up of lineages that originated within and from outside the area and at a range of times from the Carboniferous (*Selaginella*) to the late Cenozoic. As a way of summarizing and synthesizing these multiple origins, Figure 6 depicts a predictive hypothesis on general patterns for the SWAFR that is evident from the literature using track analysis (Hopper 2004). This hypothesis identifies relationships between areas of endemism through lines along which congruent speciation in independent lineages has occurred.

Formal analysis of these new tracks is possible using approaches such as cladistic biogeography (Crisp et al. 1999). An elegant start was made by Mast (2000, Mast & Givnish 2002) on Proteaceae tribe Banksieae (*Banksia/Dryandra*, *Musgravea*, and *Austromuellera*). Dispersal-vicariance analysis proposed an ancestral taxon for the tribe distributed across the Southwest-Northeast Australian Track followed by a vicariance event, possibly triggered by island formation during the late-Cretaceous downwarping and marine inundation of parts of the Australian plate.

An SWAFR origin for the subtribe Banksiinae (*Banksia/Dryandra*) was resolved, with two later expansions east followed by vicariance events along the Southwest-Southeast or Southwest-East Australia Tracks associated with Eocene or Miocene flooding of the Nullarbor Plain and the Oligocene onset of aridity in the same region. Within the SWAFR, two major centers of endemism were identified on areas down the northwest coast and southern coast. Although not elaborated in detail by Mast (2000, Mast & Givnish 2002), an examination of his phylogeny reveals congruent examples of speciation in *Banksia* within the SWAFR along all five tracks illustrated in Figure 6.

Interesting examples highlighting other tracks in Figure 6 include a biogeographic subtree analysis of the *Melaleuca* group (Brown et al. 2001), the papilionoid legume genistoid subtribe Brongniartieae with six Australian and four tropical American genera (Thompson et al. 2001), and the prostrate monotypic shrub *Emblingia calceolifolia* (Emblingiaceae) (Figure 4), which is a highly distinctive member of a widely dispersed group of brassicalean families (Chandler & Bayer 2000). An African connection to the SWAFR is evident in studies of Proteaceae (Barker et al. 2002), *Pelargonium* (Geraniaceae, Bakker et al. 1998), and Aizoaceae (Klak et al. 2003).

Adaptive Radiation

Most work on adaptive radiation in SWAFR plants has been descriptive and narrative, sometimes backed up by experimental studies of function (Carlquist 1974, Pate et al. 1984, Lamont & Enright 2000, Lambers et al. 2003, Lamont 2003). The complexity of growth form and scope for exploration of adaptive radiation in the SWAFR is substantial. Pate et al. (1984) noted the exceptional diversity of form and function within families and genera of what appeared to be a "highly random nature," indicating complex and perhaps ancient but ongoing evolutionary pathways. Only reproductive attributes such as fruit dispersal patterns in kwongan plants aligned with and displayed homogeneity within generic and family-level boundaries. Several books and reviews on the SWAFR richly illustrate this theme (e.g., Pate & McComb 1981, Pate & Beard 1984, Hobbs 1992, Pate & Hopper 1993, Hopper et al. 1996a, Abbott & Burrows 2003).

Narrative accounts of adaptation are fraught with difficulties, however. There is a fundamental difference between a functional evolutionary adaptation and an effect or correlation, and this difference requires sophisticated experimentation and phylogenetic knowledge to resolve (Williams 1966, Brandon 1990).

Additional penetrating recent work addressing adaptive radiation in a phylogenetic context has emerged for thickened roots in SWAFR *Daviesia* (Crisp & Cook 2003) and for sclerophylly and leaf xeromorphy in *Banksia/Dryandra* (Mast & Givnish 2002). However, hypotheses of adaptive radiation are difficult to test unequivocally, even within a well-resolved phylogeny. Much more experimental research at the population level within well-resolved phylogenies is needed to advance understanding of the evolution of functional traits before hypotheses of adaptive radiation can be convincingly invoked.

Genetic Systems and Speciation

Chromosome repatterning is frequently observed among related species or populations, sometimes without obvious ecological or morphological change. This correlation suggests a possible role for chromosome repatterning in speciation. Yet how chromosome changes might become fixed in populations remains a complex and controversial subject that is poorly documented (Levin 2002). The dilemma is that all structural mutations must arise at low frequencies and occur as heterozygotes, where the meiotic irregularities they cause should confer low fitness and high genetic load on their carriers, which should in turn cause natural selection to purge them.

However, under the genomic coalescence hypothesis, James (1992) proposed that chromosomal mutations that link supergenes heterozygous for recessive lethals will be elevated to high frequencies by natural selection in inbreeding populations. This process was demonstrated in a series of papers exploring the evolution of complex translocation heterozygosity in the granite outcrop herb *Isotoma petraea*, as discussed above (James 1965, 1981, 2000; Bussell et al. 2002). In this species, seed abortion reflecting high genetic load is evident in the southwest populations, yet the populations persist through intense natural selection favoring chromosome restructuring to conserve heterozygosity in the face of inbreeding.

Aspects of the genomic coalescence hypothesis have been elaborated in other groups of SWAFR plants, including *Stylidium*, *Drosera*, *Dampiera* (Goodeniaceae), *Boronia* (Rutaceae), and Myrtaceae (Coates & James 1996, James 2000, Coates et al. 2003, Shan et al. 2004). Perhaps the most penetrating recent exploration was the study of chromosome number reduction, self-pollination, and lethal polymorphisms in a population of the paper lily *Laxmannia sessiliflora* (Lomandraceae) (James et al. 1999). This line of research might be profitably applied to other species-rich floras where chromosome repatterning is evident.

Indeed, many fundamental questions regarding plant speciation have been barely addressed in the SWAFR or elsewhere, but new approaches show considerable promise in helping elucidate the processes involved (Coates et al. 2003, Lamont & Weins 2003, Hopper 2004, Rieseberg & Wendel 2004).

Natural Hybridization

In SWAFR *Banksia* and eucalypts, rates of detected natural hybridization are several times less than those found in eastern Australia (Hopper 1994a). This pattern has been attributed to the above-mentioned evolutionary patterns in the SWAFR, resulting in narrower geographical ranges, less sympatry, and long periods of time to evolve divergent genetic systems incapable of coalescing when sympatry is achieved. Nevertheless, some interesting case studies of natural hybridization have emerged in the SWAFR. These include evidence for selective pollinator behavior in *Anigozanthos* (Hopper & Burbidge 1986; Hopper 1994a), for ancient allopolyploid speciation (Krauss & Hopper 2001), and for anthropogenic disturbance that creates habitat that breaks down phenological barriers in *Banksia* species (Lamont et al. 2003).

CONSERVATION BIOLOGY

Changes wrought on the SWAFR following European colonization have profoundly altered most vegetation. The region now has more species of threatened plants (2500) than other Australian states and most countries of the world (Figure 7) (Hopper et al. 1990; Hopper 1997, 2004; Brown et al. 1998; Coates & Atkins 2001). Conservation issues include massive habitat loss and fragmentation, root-rot disease (*Phytophthora*) impacting 2500 species, displacement by 900 invasive weeds, and rising saline groundwater tables threatening 400 taxa. Moreover, a significant taxonomic impediment is patently evident in a comparison of Figures 1 and 7. Until plants are recognized as distinct and named, their specific conservation needs will not be addressed and their fate is reliant on other nontargeted strategies such as the accidental inclusion of populations into protected areas (Hopper 1994b, 1997). This is a significant issue in a flora with 14% of species/subspecies still without names (Paczkowska & Chapman 2000, Hopper 2004).

Overall, the challenge of conserving the SWAFR flora is daunting. Managers need all the help scientists can provide to deal with such biodiversity hot spots. Otherwise diversity becomes tyranny, and conservation outcomes languish as managers ignore the problems or move on to other jobs with such rapidity that there is no hope of understanding or effectively dealing with the hot spot. Such an approach
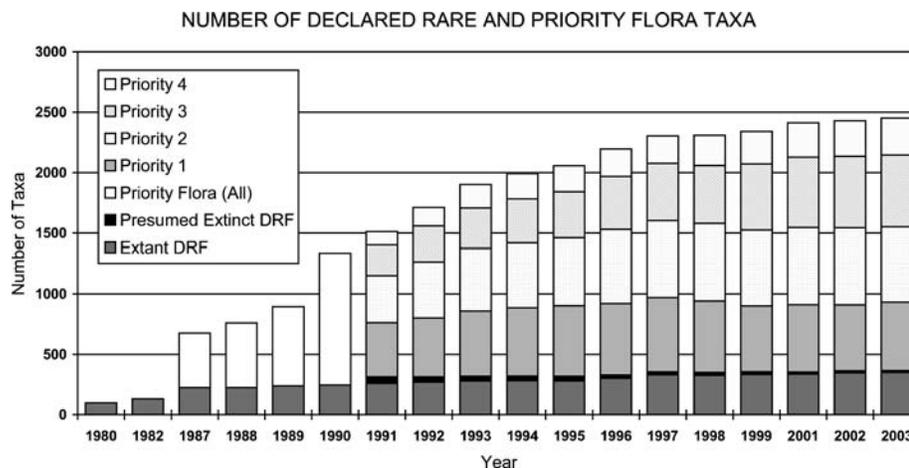

Figure 7 Number of threatened Western Australian plant species/subspecies from 1980–2003 declared as *Rare Flora* (DRF) under the Wildlife Conservation Act, including presumed extinct DRF. Also included are priority taxa in need of urgent survey to determine their conservation status (priority 1–3) and taxa adequately surveyed but in need of monitoring (priority 4). Figure courtesy of Ken Atkins, Department of Conservation and Land Management, Perth, Australia.

is in stark contrast to the world view of indigenous people, who lived sustainably with most biodiversity and passed it on to future generations.

Modern conservation of the SWAFR's flora has relied traditionally on a protected-areas approach (Figure 2*d*) that has achieved variable outcomes, from comprehensive coverage in forested districts of the HRP to almost no representation in heavily cleared parts of agricultural districts in the TRP. More recently, the emergent disciplines of conservation biology and restoration ecology have been applied as Western Australians grapple with the extraordinary conservation challenge they face (Hobbs 1992, Dixon 1994, Hopper et al. 1996a, Hopper 1997, Coates & Atkins 2001, Hobbs & Yates 2003, Cochrane 2004).

Beginning with the early listing of rare and poorly known flora in 1979 by a handful of botanists, plant conservation biology in the SWAFR has moved on to sophisticated mapping, monitoring, and process-focused research aimed at repair, recovery, and restoration by a diverse cadre of workers. It is much too early to know whether effective and sustainable conservation will be achieved.

Conservation genetics remains a strength of work in the SWAFR (Coates et al. 2000). Perhaps of greatest interest in terms of future research is James's (1992, 2000) proposal that high genetic diversity in some circumstances can be a signal for a species in trouble with impeded evolutionary capability and, conversely, that "allelically depauperate lineages of the Gondwana-like wetter regions are probably not inbred and debilitated, rather they are probably highly adapted with little genetic load and unimpeded recombination systems." (James 2000, p. 346). This hypothesis calls for a significant re-evaluation of how patterns of genetic architecture are used to define population-level conservation priorities.

From an ecological perspective, the SWAFR has a remarkably high level of turnover of plant species across the landscape, requiring caution in the application of broadscale conservation management approaches. Regeneration and recruitment work has highlighted the importance of understanding fire- and smoke-stimulated germination (Flematti et al. 2004); the ephemeral nature of some seed banks; as well as the impact of fragmentation on mating systems, pollination, and seed set. Removal of topsoil makes the landscape especially vulnerable to loss of seed and helpful symbionts of native plants, as well as massive weed invasion. The minimization of bulldozing is therefore a vital conservation strategy. Risk assessment, ex situ strategies, species recovery, and landscape restoration are crucial emergent activities for integrated conservation outcomes, but care for protected areas of remnant vegetation (Figure 2*d*), especially programs involving local communities as active stewards, remains an important and effective priority.

Barely perceived conservation consequences are arising from altered disturbance regimes such as the loss of digging by locally extinct marsupials (Garkaklis et al. 2003). Moreover, complex ecological interactions between insects and paleoendemic flora such as Ecdeiocoleaceae (Figure 4*i*) highlight the need for increasingly sophisticated conservation management (Main 1996). There is continued debate on what the appropriate scale and diversity of management regimes for

biodiversity conservation, particularly in forests, should be (Abbott & Burrows 1999, 2003; Wardell-Johnson & Horwitz 2000).

Given the geohistorical context of the SWAFR and known high levels of genetic divergence among populations of species, it is reasonable to hypothesize that many rare and threatened plants have evolved over long periods in disjunct small populations. Consequently, they would be more resilient to the effects of contemporary fragmentation than would be plants from elsewhere that have naturally large continuous population structures. Predictions of accelerated extinction rates due to habitat loss may not hold in such circumstances, or at least, these rates may be slower than elsewhere (Hopper et al. 1990, Brooks et al. 2002). Active research is under way to further test this hypothesis (Hobbs & Yates 2003). Potential global climate change also poses significant challenges to the SWAFR (Mooney et al. 2001). Although the prognosis is daunting, given the ongoing interaction of destructive processes in the SWAFR, local commitment to conserve this globally significant floral heritage remains strong.

COMPARISONS WITH SOUTH AFRICA'S GREATER CAPE FLORISTIC REGION

In many respects, the region on Earth most similar to the SWAFR is the Greater Cape Floristic Region in South Africa, including the Cape and Succulent Karoo global biodiversity hot spots (Cowling et al. 1996, Myers et al. 2000, Goldblatt & Manning 2002, Linder 2003). Both the SWAFR and Greater Cape Mediterranean regions are floristically rich; have a climate that has been oceanically moderated since the Jurassic; have been unglaciated since the Permian; and are dominated by old, weathered, nutrient-deficient landscapes. These regions also share rainfall regimes that are more reliable than those seen in California and Spain (Cowling et al. 2004).

The Greater Cape Floristic Region is much richer in species and genera than the SWAFR, but it has approximately the same number of families, including a comparable five to six endemics (Goldblatt & Manning 2002). The exceptional richness of the Greater Cape flora, unparalleled for a temperate region, may be due to the greater (Cretaceous) age of the Namib Desert compared with the Australian deserts of Oligocene age or younger. Climatic transitional areas between the Namib and mesic southwest Cape mountains have existed for a much longer period, facilitating explosive speciation in succulent karoo and adjacent areas (e.g., Klak et al. 2003, 2004). Also, the more rugged topography of the Greater Cape Floristic Region within a similar stable, oceanically moderated Mediterranean region has offered greater opportunities for genetic divergence and speciation (Goldblatt & Manning 2002, Linder 2003). Comparative phylogenetic studies, only just beginning (Bakker et al. 1998, Barker et al. 2002, Linder et al. 2003), need to be undertaken to test such hypotheses and search for general patterns across unrelated lineages.

Some illuminating ecological comparisons between climatically matched sites in kwongan and fynbos (Cowling & Witkowski 1994, Cowling et al. 1994) as well as comparative studies of species flocks in Proteaceae (Cowling et al. 1996, Cowling & Lamont 1998) have been completed. These have demonstrated, for example, that Proteaceae in the SWAFR are richer in species overall and locally, more common in transitional rather than high rainfall districts, and have higher gamma (geographical) diversity. Proteaceae from the SWAFR also more commonly resprout after fire, produce serotinous fruits, are vertebrate pollinated, and grow taller than their Cape congeners. Harsher climatic conditions in the SWAFR had been hypothesized to favor resprouters over nonsprouters (Cowling & Lamont 1998).

A study of matched sites on south coastal districts on both continents (Fitzgerald River District, SCP, in the SWAFR) showed that woody plants with leaf spines and canopy-stored seed were more common in the SWAFR on nutrient-poor soils, whereas the Cape's less impoverished calcareous and limestone sands had far more species with bird-dispersed fruits and interfire germination (Cowling & Witkowski 1994). Nevertheless, strong convergence was documented between SWAFR and Cape shrublands in a wide range of other growth form and function traits. Narrow-range endemics in the SWAFR are more likely to be graminoids, or shrubs with either canopy-stored or soil-stored seeds of various dispersal agents (wind, vertebrates, ants, and ballistic), compared with the predominant low shrubs with soil-stored, ant-dispersed seeds in the Cape (Cowling et al. 1994). Differences may be due to phylogenetic contingency and regional processes (Herrera 1992), such as the availability of less impoverished coastal habitat in the Cape for nearby rainforest elements to occupy compared with the SWAFR's complete isolation by desert from rainforest taxa. Further work along these lines, especially that addressing phylogenetics and chromosomal aspects of speciation, would be valuable.

Exciting work on the impact of smoke on seed germination in the SWAFR was stimulated by discoveries in South Africa (Dixon et al. 1995, Roche et al. 1997, Tieu et al. 2001, Flematti et al. 2004). This exemplifies the ongoing benefit of collaborative comparative studies.

CONCLUSIONS

Significant advances in understanding the SWAFR flora have occurred since 1979. The SWAFR has proven to be a botanical frontier, as poorly inventoried three decades ago as many tropical rainforest regions. The SWAFR is now recognized as one of the world's 25 global biodiversity hot spots, the only region in Australia accorded this status.

A sharper focus on landscape evolution and the fossil record have highlighted the remarkable antiquity and stability of the SWAFR, which has been free of glaciers and marine inundation since the Permian, with little orogeny since. The species richness, high endemism, and rapid turnover of species over short distances across the landscape are ancient, extending at least as far back as the Eocene. Such antiquity has resulted in remarkably sophisticated evolutionary responses to living

on a flat, stable, highly weathered, nutrient-deficient landscape with subtle soil mosaics. Examples of coping with rarity in naturally fragmented populations are common in the flora, and complex interplays between chromosomal systems and ecological adaptation have occurred, with explosive speciation as an incidental by-product in some groups.

The region thus exemplifies plant evolution in temperate environments at its most sophisticated and durable. However, such a flora, exposed to European land-use practices, is highly threatened. Fundamental changes in attitudes toward land use and the intrinsic value of plant life are needed to go hand in hand with a commitment to protect, repair, and restore native vegetation in the face of uncertainty. These changes will require the inspiration and training of new cohorts of plant conservation biologists as well as continuing strong local support, which thankfully is forthcoming.

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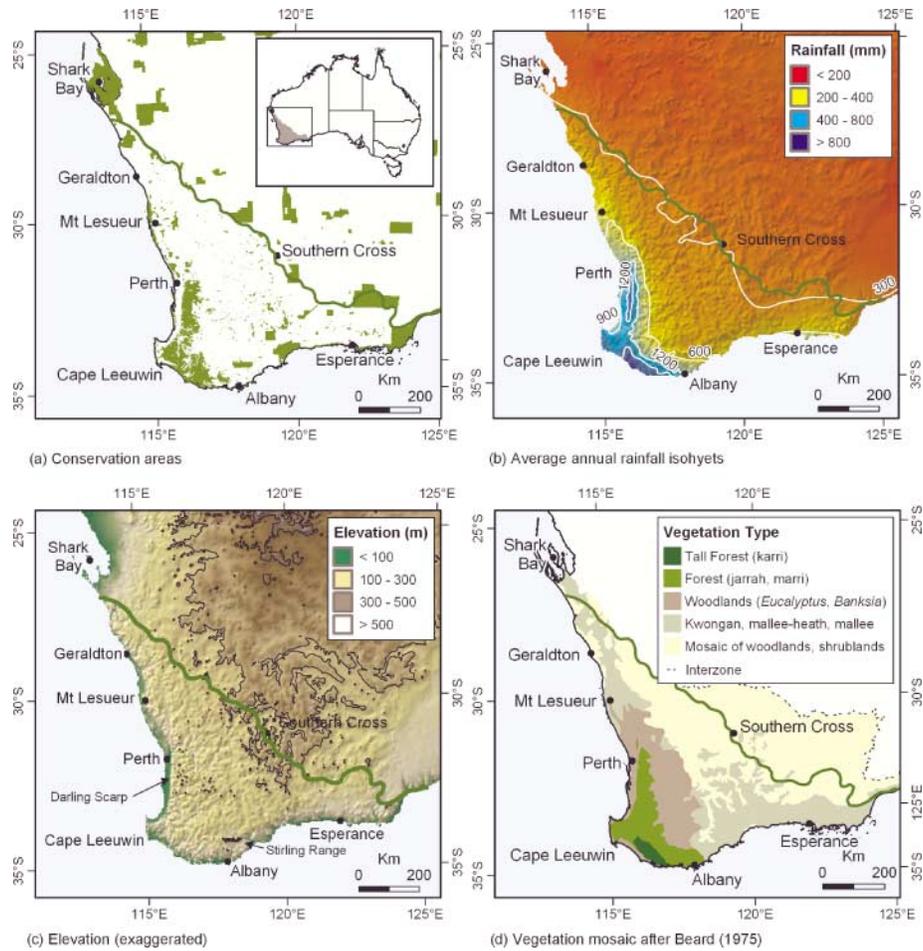
Figure 2 The SWAFR illustrating (*a*) protected conservation areas, (*b*) rainfall, (*c*) topography, and (*d*) vegetation.
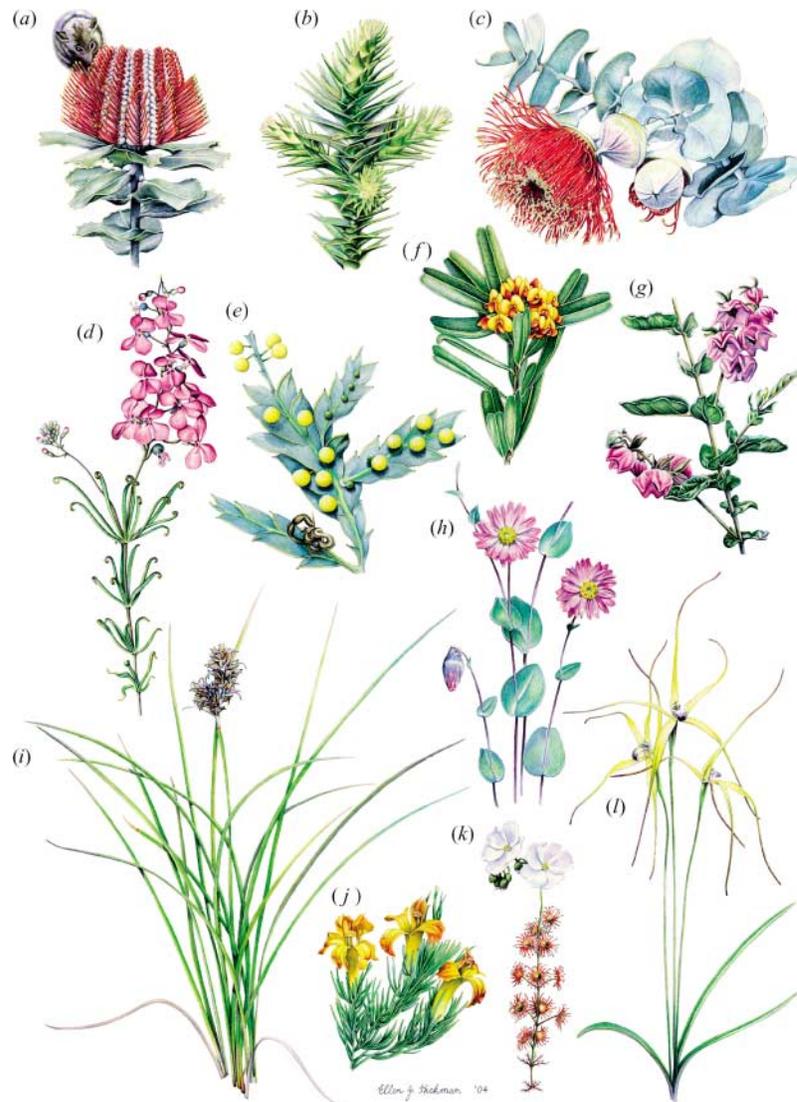
Figure 3 Representatives of the most species-rich families of flowering plants in the SWAFR. (*a*) Proteaceae (*Banksia coccinea*) on which is perched a nectar-feeding SWAFR endemic honey possum *Tarsipes rostratus*, (*b*) Ericaceae (*Andersonia axilliflora*), (*c*) Myrtaceae (*Eucalyptus rhodantha*), (*d*) Stylidiaceae (*Stylidium scandens*), (*e*) Mimosaceae (*Acacia glaucoptera*), (*f*) Fabaceae (*Gastrolobium bilobum*), (*g*) Sterculiaceae (*Thomasia montana*), (*h*) Asteraceae (*Rhodanthe manglesii*), (*i*) Cyperaceae (*Lepidosperma costale*), (*j*) Goodeniaceae (*Lechenaultia superba*), (*k*) Droseraceae (*Drosera fimbriata*), and (*l*) Orchidaceae (*Caladenia elegans*). Illustrated and printed with permission by Ellen Hickman.

Figure 4   Representatives of the order, families, and subfamilies endemic to the SWAFR. (*a*) Eremosynaceae (*Eremosyne pectinata*), (*b*) Emblingiaceae (*Emblingia calceoliflora*), (*c*) Dasypogonales (Dasypogonaceae *sens. str.*; *Kingia australis*), (*d*) Dasypogonales (Dasypogonaceae/Calectasiaceae *Calectasia grandiflora*), (*e*) Anarthriaceae/Lyginiaceae (*Lyginia barbata*), (*f*) Haemodoraceae subfamily Conostylidoideae (*Anigozanthos flavidus*), (*g*) Anarthriaceae/Hopkinsiaceae (*Hopkinsia anaectocolea*), (*h*) Ecdeiocoleaceae—sister to the grasses (*Ecdeiocolea monostachya*), (*i*) Anarthriaceae (*Anarthria scabra*), (*j*) Cephalotaceae (*Cephalotus follicularis*), and (*k*) Dasypogonales (Dasypogonaceae/Baxteriaceae *Baxteria australis*). Illustrated and printed with permission by Ellen Hickman.
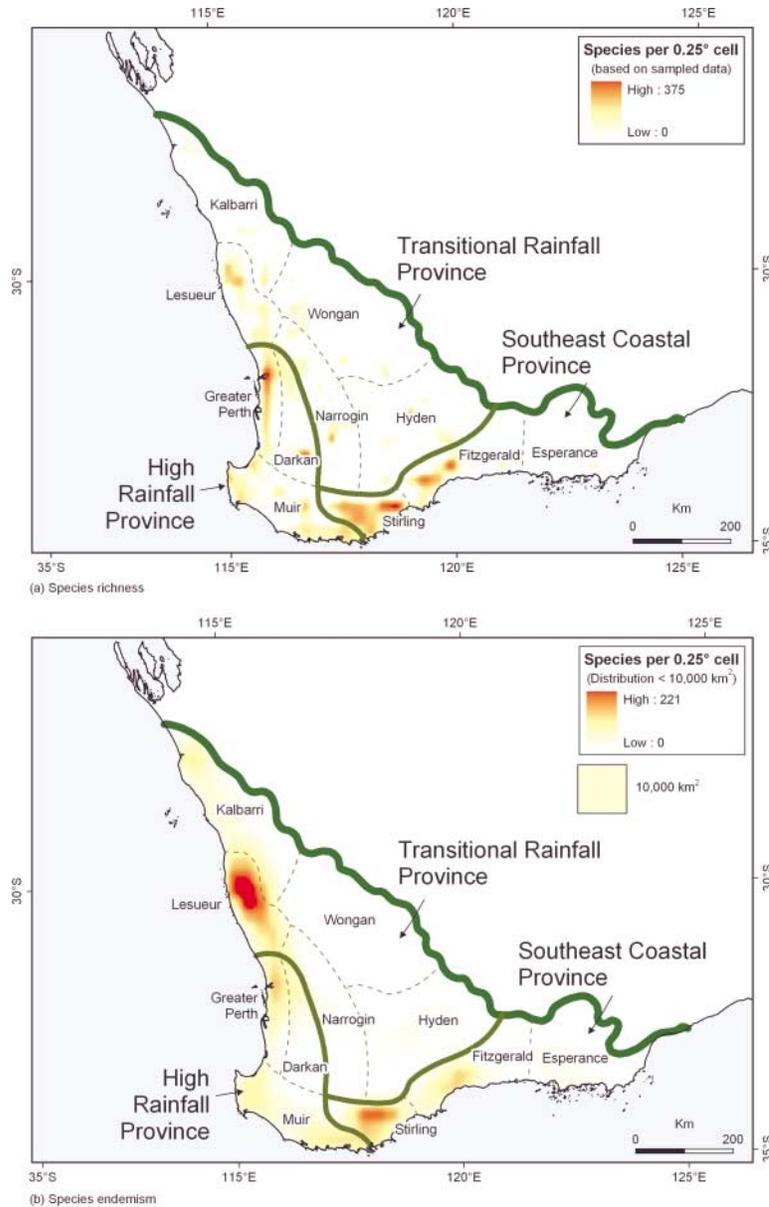
Figure 5 Phytogeographic maps of the SWAFR showing Botanical Provinces and Districts. Shown are (*a*) the species richness in 0.25° latitude by 0.25° longitude grids and (*b*) the richness in 0.25° latitude by 0.25° longitude grids of local endemics with a geographical distribution occupying <10,000 km² , as determined from specimen labels at the Western Australian Herbarium and adjusted for collection intensity (S.D. Hopper & P. Gioia, unpublished data).