

Progress and prospects for understanding evolution and diversity in the southwest Australian flora

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The flora of southwest Australia has often been described as remarkable and special, both in an Australian and a global context, particularly because of its high species richness and endemism. Many explanations for the special characteristics of the region's flora have been proposed, most invoking a special evolutionary history. Relatively few studies, however, have explicitly compared either the floras or histories of southwest Australia and southeast Australia, a useful comparison as both may be assumed to have started with a similar flora and to have related histories. Such comparisons may be useful in discriminating the many factors, both historical and ahistorical, that may explain differences in richness and endemism. We analyse here flowering plant checklists from geographically comparable areas in southeastern and southwestern Australia to describe and quantify floristic differences, confirming that southwestern Australia has higher species richness but lower generic and family richness than southeastern Australia, and review previous explanations for these differences. We conclude that, while much has been achieved since Joseph Hooker first formally described these differences in 1859, much remains to be understood and knowledge gaps and paradoxes remain. Current explanations, while plausible, remain unproven, and differences in histories may or may not be the best explanations. Framing investigations of the special characteristics of southwestern Australia around null hypotheses may help provide a necessary rigour to such analyses.

KEYWORDS: biogeography, diversity, endemism, floristics, southeastern Australia, southwestern Australia.

INTRODUCTION

The flora of southwest Australia (SWA) is widely regarded as interesting and important at local, continental and global scales. Locally, many areas are rich and diverse, many species are naturally or anthropogenically rare or otherwise of conservation significance, and the flora provides an important and recognised character to SWA for the community and visitors alike. At a continental scale, SWA is one of 12 recognised centres of diversity and endemism in Australia (Crisp *et al.* 2002), while globally it is one of 25 designated global biodiversity hotspots (Myers *et al.* 2000) and one of 35 global floristic regions (Takhtajan 1986). Further, along with a small number of other temperate regions such as the Cape Floristic Region of South Africa (Manning & Goldblatt 2012) and California (Stebbins & Major 1965), the flora of SWA is unusually diverse for its latitudinal position, an outlier on a general global trend from high species richness in the tropics to lower richness polewards (Hillebrand 2004; Sniderman *et al.* 2013).

Joseph Hooker's seminal essay *On the flora of Australia, its origin, affinities and distribution* (Hooker 1859) provided an overview of the Australian flora as known at that time. Hooker was the first to formally describe special characteristics of the flora of SWA, particularly a 'remarkable' difference between the floras of southwestern and southeastern Australia (SEA) (although this had been prefigured in a letter from Robert

Brown to Joseph Banks in 1803, see Vallance *et al.* 2001). Noting first that SEA, with its greater area and productivity and more diverse topography, might be assumed to have a richer flora than SWA, Hooker concluded, following a careful enumeration and tabulation of all available data, that: (i) SWA was richer in species than SEA (3600 vs 3000 species); (ii) SWA had fewer genera and families than SEA (600/90 vs 700/125); (iii) there were more large genera (>10 species) in SWA than in SEA, and the largest genera in SWA had on average more species than the largest in SEA; (iv) most of the largest SWA genera were either small in SEA or did not occur there; (v) many of the extra genera in SEA had alliances outside Australia, while few SWA genera had such alliances (later restated as that the SWA flora was more characteristically 'Australian' than the SEA flora); (vi) SWA had a higher level of endemism than SEA; and (vii) SWA species tended to have narrower distributions than those in SEA.

In correspondence to Darwin in the late 1850s, Hooker asserted that the SWA flora was 'the most extraordinary thing in the world' (Hopper & Lambers 2009). He regarded that the special character of SWA and the differences between the floras of SWA and SEA were globally remarkable and provided an important testing ground for 'whatever theory of creation and distribution may be established' (Hooker 1859 p. liii). He regretted that current theories of geology, biogeography and evolutionary history could not adequately explain it.

Diels (1906), following his own comparison between SWA and SEA and between these and the intervening eremaeian zone, disagreed with Hooker. He focused

instead on the similarities between the two floras, noting that '[h]itherto there has always been the tendency to emphasize the differences and Hooker in particular stresses this' (Diels 1906 p. 322). He considered that the high degree of endemism in SWA, was 'over-rated', and disputed Hooker's emphasis on the global distinctiveness of the SWA–SEA comparison (Diels 1906 p. 39).

Subsequent to Diels, many authors retained a focus on the special characteristics of SWA, particularly with respect to species richness and endemism; these two special characteristics, and explanations for them, have dominated the literature. Many of the proposed explanations have been biogeographically narrative (*sensu* Ball 1976), and none have yet been adequately tested. Further, few attempts have been made since Hooker and Diels to rigorously compare the floras of SWA and SEA, to analyse the differences, and to reassess the conclusions they reached (Fox 1996). Most analyses of SWA's flora in recent years have either discussed features of the SWA flora without comparison with other areas, or have compared SWA with mediterranean-climate regions elsewhere in the world (Cowling *et al.* 1996; Cowling & Lamont 1998; Sauquet *et al.* 2009), or with other areas regarded as having a similar history (South Africa, the Venezuelan Pantepui Highlands: Hopper 2009). Fox (1996) noted that adequate modern comparisons between the floras of the SWA and SEA mediterranean-climate regions had not been made, while Sniderman *et al.* (2013) commented that comparisons between SWA and SEA may be more instructive than comparisons between SWA and mediterranean-climate regions elsewhere.

A number of recent authors have drawn attention to or described further special characteristics of the flora of SWA. Hopper *et al.* (1996 p. 8) considered that the environmental history of SWA has provided 'unparalleled opportunities for the persistence of relict terrestrial taxa'. Hopper & Gioia (2004) further noted the existence in SWA of a number of monotypic or small and phylogenetically isolated lineages, regarding this as special. Burbidge (1960) observed anecdotally that species in SWA tend on the whole to be distinct and comparatively uniform while many species in SEA are variable and less clear-cut, and attributed this to a possible greater incidence of hybridisation in SEA than SWA. Hopper (1994) concluded that hybridisation is less common in SWA than in SEA. However, Hopper & Gioia (2004) reviewed several genera where hybridisation is important and widespread in SWA; the situation is thus equivocal, and flora-wide comparisons have yet to be made.

Hooker based his conclusions regarding the unique and important characteristics of the SWA flora on an imperfect knowledge of the flora. Eight thousand Australian plant species were known at the time of his analysis and he was confident that the total Australian flora would not exceed a modest 9000–10,000 species; >24,000 species are known today (CHAH 2014). His knowledge of the flora of SWA and SEA was largely derived from a small number of collectors (Brown, Cunningham, Mitchell, Drummond, Preiss) and a handful of reports and descriptions of the flora (Brown 1810, 1814; Lehmann 1844–1848; Lindley 1838). As discussed by Diels (1906), his analyses were particularly hampered by substantial knowledge gaps regarding the eremaeen flora that interposes between the two areas but

was included to some extent in both. Finally, the classification system for plants used by Hooker is now substantially out of date, having been improved in recent years by many rigorous phylogenetic and phytogeographic analyses.

Given that much more is now known about the floras of SWA and SEA and of Australia as a whole, and that web-based biodiversity aggregators such as Australia's Virtual Herbarium (<http://avh.chah.org.au>) and the Atlas of Living Australia (<http://www.ala.org.au>) greatly simplify analyses such as those performed (by hand) by Hooker and Diels, it is timely to repeat floristic comparisons between SWA with SEA and to revisit the special characteristics Hooker enumerated. This paper provides a modern reappraisal of Hooker's conclusions, assesses anew the characteristics (if any) of the flora of SWA that are special by comparison with elsewhere in Australia, and reviews current thinking around explanations of these special characteristics. It ends with a discussion of questions that remain at least partially unanswered, and an exploration of prospects for future progress in our understanding of the flora of the region.

IS SWA STILL SPECIAL, AND IF SO, IN WHAT WAYS?

While comparisons between geographic and taxonomic patterns of floristic richness and composition in Australia is easier today than in Hooker's time, definitional aspects of exactly what is meant by SWA and SEA have become more important; the paucity of knowledge available to Hooker made definitional questions almost irrelevant. SWA is, to a large extent, an ecological island (Carlquist 1974), readily definable as the Southwest Botanical Province of Diels (1906) and Beard (1990) or the largely equivalent South West Australian Floristic Region of Hopper & Gioia (2004). However, no such clearly defined region has been demarcated for SEA, where the environment of the temperate southeast is broadly contiguous with and grades into that of the east coast subtropics and tropics (Figure 1).

In order to compare regions with approximately equal areas, we define here SWA and SEA as follows. SWA (the South West Australian Floristic Region of Hopper & Gioia 2004) comprises the Geraldton Sandplains, Avon Wheatbelt, Swan Coastal Plain, Jarrah Forest, Warren, Mallee and Esperance Sandplain IBRA (Interim Biogeographic Regionalisation for Australia) bioregions (DEWHA 2008). SEA comprises the Victorian Midlands, Southern Volcanic Plain, South East Coastal Plain, South East Corner, South Eastern Highlands, Australian Alps, Sydney Basin and New South Wales South Western Slopes IBRA bioregions. This contiguous set of bioregions constitutes a relatively well-defined area of principally erosional land surfaces centred on the Great Dividing Range and bounded to the west and northwest by the alluvial-depositional plains of the Murray Darling Depression, Riverina and Cobar Peneplain, on the south by Bass Strait and to the north by subtropical coastal areas of northern New South Wales and the MacPherson–Macleay Overlap.

While the two regions as defined clearly differ in a number of respects, we regard that they nevertheless

Table 1 Geographic and floristic statistics for Southwest Australia (SWA) and Southeast Australia (SEA).

	SWA	SEA
Land area (km ²)	302 627	321 110
Native species (endemic; % endemic)	6929 (3599; 51.9%)	4810 (659; 13.7%)
Native genera (endemic; % endemic)	698 (72; 10.3%)	916 (8; 0.9%)
Native families (endemic; % endemic)	122 (2; 1.6%)	162 (0; 0%)
Average species/genus	9.9	5.3
Average species/family	56.8	29.7
Average genera/family	5.7	5.7
Genera with >50 species	24	10
Families with >50 species	23	15

provide a useful comparison. SWA occupies generally lower latitudes than SEA (SWA 27°–35°S; SEA 33°–39°S). Hooker (1859) included Tasmania in his SEA; however, while Tasmania has clear affinities with mainland southeastern Australia and is connected to it during periods of low mean sea level, we exclude it here because it extends substantially further south (to 43°S), greatly increasing the environmental differences between the two regions. The areas of the two regions as defined are approximately equal (Table 1).

Species checklists for each bioregion based on vouchered specimen records held in Australian herbaria were obtained from <<http://avh.chah.org.au>> (download 2/1/2014). No attempt was made to correct for cases of probable incorrect determinations on some specimens. Only species names matching accepted names in the Australian Plant Census (APC) (CHAH 2004), and only species annotated in the APC as native for the region in question, were included. Higher-level taxonomy follows the APC. Table 1 provides core statistics for the two areas.

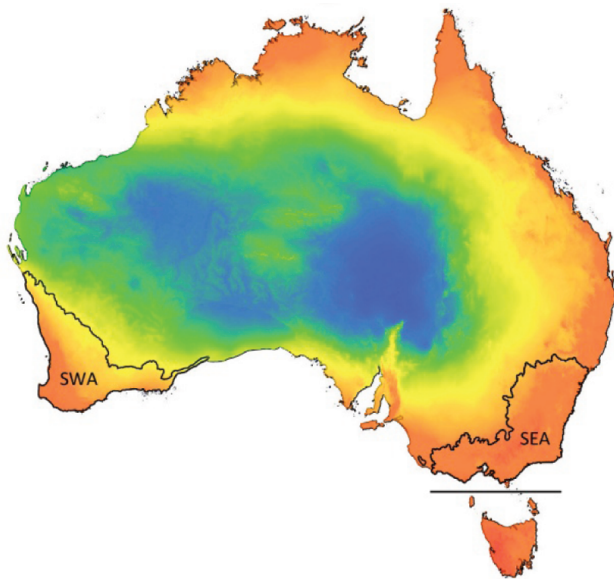


Figure 1 Mean aridity index for Australia (source: Atlas of Living Australia, red to blue indicates increasing aridity). Southwest Australia (SWA) and southeast Australia (SEA) as defined in this paper (see text) are outlined. SWA is well bounded by arid lands to the north and east; SEA is not.

Hooker's observations still stand that SWA is richer in species and poorer in genera and families than SEA; hence, its genera and families are on average more species-rich. SWA has 1.4 times more species than SEA; conversely, SEA has 1.3 times more genera and families than SWA. SWA genera on average have 10 species compared with 5 in SEA, and SWA families have on average 57 species compared with 30 in SEA.

His conclusion that most of the larger SWA genera are small or absent in SEA can no longer be supported (Table 2), although it is still the case that for most (75%) of the

Table 2 Genera with >50 species occurring in Southwest Australia (SWA) and Southeast Australia (SEA)

Genus	SWA species	SEA species	SWA/SEA species
<i>Acacia</i>	440	226	2.0
<i>Eucalyptus</i>	294	230	1.3
<i>Leucopogon</i>	204	32	6.4
<i>Stylidium</i>	200	13	15.4
<i>Grevillea</i>	195	94	2.1
<i>Melaleuca</i>	174	29	6.0
<i>Banksia</i>	156	14	11.1
<i>Caladenia</i>	110	82	1.3
<i>Gastrolobium</i>	106	0	–
<i>Hakea</i>	100	28	3.6
<i>Hibbertia</i>	97	46	2.1
<i>Verticordia</i>	94	0	–
<i>Daviesia</i>	91	15	6.1
<i>Drosera</i>	91	11	8.3
<i>Baeckea</i> ^a	85	10	8.5
<i>Eremophila</i>	81	17	4.8
<i>Goodenia</i>	62	34	1.8
<i>Synaphea</i>	60	0	–
<i>Darwinia</i>	58	12	4.8
<i>Schoenus</i>	58	23	2.5
<i>Petrophile</i>	56	4	14.0
<i>Boronia</i>	52	38	1.4
<i>Calytrix</i>	52	3	17.3
<i>Hemigenia</i>	51	2	25.5

^a *Baeckea* is a phylogenetically diverse genus and is poorly resolved taxonomically; most of the taxa currently included in it, in both SWA and SEA, will be moved to other genera in future taxonomic revisions (M E Trudgen & B Rye pers. comm. 2014)

Table 3 Families occurring in Southeast Australia (SEA) and not in Southwest Australia (SWA), and vice versa.

Families found in SEA and not in SWA	Families found in SWA and not in SEA
Endemic to Australia	
Atherospermataceae, Blandfordiaceae, Doryanthaceae, Eupomatiaceae, Petermanniaceae	Anarthriaceae, Byblidaceae, Cephalotaceae, Ecdeiocoleaceae, Emblingiaceae
Non-endemic	
Alseuosmiaceae, Amaryllidaceae, Anacardiaceae, Arecaceae, Argophyllaceae, Asteliaceae, Burmanniaceae, Cabombaceae, Caprifoliaceae, Ceratophyllaceae, Cornaceae, Corynocarpaceae, Cunoniaceae, Ebenaceae, Eriocaulaceae, Flagellariaceae, Gesneriaceae, Icacinaceae, Luzuriagaceae, Lythraceae, Melastomataceae, Meliaceae, Menispermaceae, Monimiaceae, Nothofagaceae, Orobanchaceae, Paracryphiaceae, Passifloraceae, Pennantiaceae, Phytolaccaceae, Piperaceae, Pontederiaceae, Putranjivaceae, Ripogonaceae, Salicaceae, Sapotaceae, Smilacaceae, Sparganiaceae, Symplocaceae, Thismiaceae, Trimeniaceae, Verbenaceae, Winteraceae, Zingiberaceae	Apodanthaceae, Combretaceae, Pedaliaceae, Surianaceae

shared, large genera, SWA is proportionately richer than the 1.4x overall average for the two areas.

Hooker's conclusion that many taxa that occur in SEA but not in SWA have significant alliances outside Australia is still valid (Table 3). 90% of families (44/49) found in SEA but not SWA have significant representation outside Australia, while only 44% of the small number of families (4/9) found in SWA but not SEA have representation outside Australia.

Within the overall trend towards higher species richness in SWA, a wide range in relative richness is shown by different families (Table 4). Of families that occur in both regions, Stylidiaceae, Droseraceae, Restionaceae, Proteaceae, Goodeniaceae, Ericaceae and Myrtaceae are highly to moderately SWA-skewed (SWA:SEA species ratio 13.9:2.8), while Rubiaceae, Juncaceae, Plantaginaceae, Poaceae, Polygonaceae and Campanulaceae are moderately to slightly SEA-skewed (SEA:SWA species ratio 4.1:1.6). Other families (e.g. Santalaceae, Casuarinaceae, Solanaceae, Sapindaceae, Celastraceae) show no strong skew, being equally rich in both areas.

The observation by Hooker and others that SWA has a higher overall endemism, at both species and genus level, remains valid, although Hopper & Gioia (2004) noted

Table 4 Families shared between Southwest Australia (SWA) and Southeast Australia (SEA) and with at least 10 species in each.

Family	SWA species	SEA species	SWA:SEA	SEA:SWA
Stylidiaceae	208	15	13.9	0.1
Droseraceae	92	12	7.7	0.1
Restionaceae	108	26	4.2	0.2
Proteaceae	732	215	3.4	0.3
Goodeniaceae	208	64	3.3	0.3
Ericaceae	339	114	3.0	0.3
Myrtaceae	1177	428	2.8	0.4
Malvaceae	136	50	2.7	0.4
Scrophulariaceae	95	38	2.5	0.4
Asparagaceae	104	44	2.4	0.4
Portulacaceae	32	15	2.1	0.5
Dilleniaceae	97	46	2.1	0.5
Loganiaceae	27	14	1.9	0.5
Fabaceae	1010	525	1.9	0.5
Boraginaceae	25	13	1.9	0.5
Aizoaceae	21	11	1.9	0.5
Amaranthaceae	42	22	1.9	0.5
Lamiaceae	179	94	1.9	0.5
Elaeocarpaceae	36	23	1.6	0.6
Polygalaceae	17	11	1.5	0.7
Pittosporaceae	36	24	1.5	0.7
Thymelaeaceae	46	33	1.4	0.7
Juncaginaceae	16	12	1.3	0.8
Hemerocallidaceae	34	26	1.3	0.8
Apiaceae	56	44	1.3	0.8
Rhamnaceae	96	76	1.3	0.8
Euphorbiaceae	59	47	1.3	0.8
Haloragaceae	52	43	1.2	0.8
Lentibulariaceae	14	12	1.2	0.9
Santalaceae	28	25	1.1	0.9
Casuarinaceae	28	26	1.1	0.9
Solanaceae	43	42	1.0	1.0
Sapindaceae	30	33	0.9	1.1
Celastraceae	15	17	0.9	1.1
Araliaceae	36	42	0.9	1.2
Rutaceae	127	151	0.8	1.2
Cyperaceae	176	212	0.8	1.2
Brassicaceae	40	53	0.8	1.3
Phyllanthaceae	14	19	0.7	1.4
Asteraceae	303	438	0.7	1.5
Loranthaceae	13	19	0.7	1.5
Convolvulaceae	15	23	0.7	1.5
Orchidaceae	296	472	0.6	1.6
Campanulaceae	23	37	0.6	1.6
Polygonaceae	11	25	0.4	2.3
Poaceae	147	380	0.4	2.6
Plantaginaceae	14	41	0.3	2.9
Juncaceae	14	52	0.3	3.7
Rubiaceae	15	61	0.2	4.1

The columns SWA:SEA and SEA:SWA give the proportional representation in the two regions. Families in bold have high numbers of oligotrophic-soil specialists

that estimates of endemism of the SWA flora have been steadily revised downwards in recent years. Analyses of these data show that 52% of SWA species and 10% of genera are endemic; by comparison, 14% of SEA species and 1% of SEA genera are endemic to the region as defined.

The average size of species ranges (area of occupancy, distributional area) of species in SWA and SEA was not tested for this analysis. However, Hooker's observation that SWA is characterised by species with restricted distributions compared with SEA still stands. González-Orozco *et al.* (2011), in a gridded, continent-wide analysis of distributional data for *Acacia*, showed that many grid cells in SWA included narrowly endemic species (i.e. species found in one grid cell but not its neighbours), but that few in SEA showed the same pattern.

The contention of Hopper *et al.* (1996) and Hopper & Gioia (2004) that SWA is unusually rich in small, monotypic and phylogenetically isolated lineages is not supported by this analysis. While these papers do not rigorously define the concept of an isolated lineage, their examples principally equate to small SWA families as candidates for phylogenetically isolated lineages. This analysis shows that five Australian-endemic families found in SWA and not SEA (Table 3) are all small and/or monotypic; however, the same can be said for the five Australian-endemic families found in SEA and not SWA.

In addition to the features noted by Hooker (1859), two further special characteristics of the SWA flora have been noted in the literature: its high morphological richness, and the high proportion of species that are oligotrophic specialists. Carlquist (1974) described a high morphological variance in SWA species of genera and families shared with SEA. In genera such as *Eucalyptus*, *Melaleuca*, *Banksia*, *Hakea*, *Acacia*, *Daviesia*, *Leucopogon* and *Goodenia* and families such as Rutaceae, Rhamnaceae and Styliaceae there is a consistent pattern in which 'unusual' morphologies are found in SWA representatives and not in SEA ones. Examples include extremes in cladode morphology in *Daviesia*, flower and fruit size in *Eucalyptus*, leaf morphology in *Hakea* and flower colour in *Goodenia*. While not yet formally tested, the observational evidence is strong that in many groups the SWA flora has a wider morphological amplitude than the SEA flora.

The large number of SWA plants that have specialised adaptations for oligotrophic (particularly P- and micronutrient-limited) soils has often been noted (Pate & Dell 1984; Lambers *et al.* 2010). In general, these are plants that are characteristic of kwongan on sandplains; while many habitats in SWA (and indeed in SEA) are highly oligotrophic on a global scale (Lambers *et al.* 2010), sandplains are among the most nutrient-limited in the region. Adaptations include cluster roots, parasitism and carnivory (see Lamont 1982 for review). Plants that lack these features but are nevertheless well represented in kwongan (e.g. many Myrtaceae) are assumed to have physiological mechanisms that allow them to cope with low nutrient levels. Oligotrophy-specialists are significantly over-represented among SWA-skewed families (Table 4: four of the five most-skewed families are oligotrophy-specialists), and are almost absent from SEA-skewed families.

EXPLANATIONS OF SPECIAL CHARACTERISTICS OF THE SWA FLORA

While Hooker regretted his inability to adequately explain the special characteristics of the SWA flora, subsequent authors have provided multiple explanations, favouring either single causes or multiple interacting factors that may have been important, particularly in generating its high species richness and endemism.

Diels (1906) considered that the most important difference between the floras of SWA and SEA was an almost complete lack of two significant elements—the Malaysian and Antarctic—in the SWA flora, regarding it as almost entirely autochthonous (reprising Hooker's comment that the SWA flora is 'characteristically Australian': see also Nelson 1981). He proposed competition between these two non-autochthonous and the autochthonous element in SEA as an explanation for its lesser species richness. He provided no mechanism for this competitive limitation of overall species richness, and the concept of distinct elements in the Australian biota is now largely abandoned.

Modern authors have framed hypotheses around four key factors. Two of these, environmental instability and environmental stability, focus on historical factors affecting current richness while two, habitat diversity and oligotrophy, while acknowledging that speciation occurs over time and hence history is important, are essentially ahistorical and focus on current ecological processes as explanatory.

Environmental instability

A frequent explanation for the high species diversity in SWA (Burbidge 1960; Hopper 1979; Hopper & Maslin 1978; Cowling *et al.* 1996) is that fluctuating environments during glacial cycles of the Quaternary led to a recent burst of genetic divergence (Byrne *et al.* 2011) and speciation, especially along the margins of SWA where rainfall is transitional between the mesic and eremaeian zones. A proposed mechanism is recurrent restriction of species to small, fragmented populations as arid conditions swept across the SWA's edaphically complex landscape (Nelson 1981), resulting in rapid genetic drift and/or adaptation and hence rapid speciation.

Environmental instability may or may not provide a plausible explanation for high species richness and high genetic structuring in many SWA species. Environmental stresses associated with rapidly fluctuating climate cycles in the Quaternary might be expected to result in both high extinction and high speciation rates. Higher species richness can only result if speciation exceeded extinction during these phases of environmental stress, but an emerging consensus in the literature is the opposite (Jansson & Dynesius 2002; Jansson & Davies 2008). Indeed, Dynesius & Jansson (2000) argued that rapidly fluctuating climate both increases extinction and decreases speciation (by accelerating local extinction or blending of diverging gene pools). Even if environmental instability can increase species richness, it can only explain the differences between SWA and SEA if glacial cycles were either more pronounced or more effective in SWA than SEA. While SWA is edaphically complex, SEA is topographically complex, so the same mechanism

could apply there. Byrne *et al.* (2011) provided examples of phylogeographic structuring throughout the whole mesic biome in Australia, without singling out SWA as distinctive.

Environmental stability

Sniderman *et al.* (2013) suggested that Pleistocene stability rather than instability can explain SWA's richness. They described a hyperdiverse early Pleistocene, non-Mediterranean sclerophyllous fossil flora from Victoria (SEA), and proposed that a major Pleistocene sclerophyllous extinction occurred in SEA but not SWA, perhaps because the latter was climatically more stable during this time. Other authors have invoked stable environmental conditions over longer time frames to explain the special characteristics of the SWA flora. Marchant (1973 p. 28) considered that SWA's endemism and richness became progressively established from the late Eocene and Miocene due to the 'long-standing stability of the western plateau'. Hopper (2009) elaborated this idea, proposing that much of SWA has been climatically buffered for the past 100 Ma and that a combination of a low average rate of extinction and moderate, recurrent episodes of speciation over long periods resulted in a slow build-up of richness and endemism. This is similar to the 'tropical conservatism hypothesis' (Wiens & Donoghue 2004) for high species richness in the tropics.

As an explanation for high species richness in SWA, environmental stability has the advantage that it is concordant with some broad-scale explanations of global species richness (see Mittelbach *et al.* 2007 for review); SWA and similar areas are anomalously rich because they have been anomalously climatically stable for long periods of time. As an explanation of SWA's higher species richness than SEA, it relies on a contrasting lack of historical climatic stability (and hence higher extinction rates or lower speciation rates) in SEA. This, however, would render the lower generic and family richness in SWA paradoxical; more stable climates should favour the persistence of families and genera as well as species. The reverse appears to have been the case in SWA, hence for environmental stability to explain SWA's high species richness, there would need to be an alternative explanation for its lower generic and family richness.

Habitat diversity and patchiness

Environmental diversity, especially when combined with habitat patchiness, is the primary driver of beta diversity, and higher beta diversity in a given region would be expected to lead to higher total species richness. Burgman (1988) observed very high levels of beta diversity in sandplain and halophyte habitats in SWA, regarded that this could not be adequately explained by soil or climate parameters, and suggested that the relative isolation of habitat patches may explain the high turnover rates. While SWA landscapes are topographically subdued, the edaphic complexity of much of SWA may provide high levels of habitat variation at local to regional scales. Allopatric speciation caused by reduced gene flow between patches may then drive species richness higher over time, associated with short-range endemism of the resulting species.

To explain higher species richness in SWA than SEA, a comparison would need to show that SWA is patchier than SEA. Parts of SWA are clearly edaphically complex, leading to patchier vegetation (see Hopper 1979 figure 4). An interesting question is whether the greater topographic complexity of SEA is as effective in driving allopatric speciation as the greater edaphic complexity of SWA.

Oligotrophy

SWA appears to have substantially more extensive areas of oligotrophic soils (sandplains, laterites) than SEA (although a rigorous comparison of soils in SWA and SEA has not been attempted). Oligotrophic soils in SWA, for reasons still unclear, support high species diversity including both high alpha (Hopkins *et al.* 1983) and beta (Burgman 1988) diversity. Oligotrophy specialists are dominant in kwongan, and kwongan is most extensive in parts of SWA that have the highest species richness. Similarly, a long-standing observation in SEA (Diels 1906; González-Orozco *et al.* 2011; Rice & Westoby 1983) is that the oligotrophic Hawkesbury Sandstone (New South Wales) is unusually species-rich and on a par with SWA; Blue Mountains National Park on Hawkesbury Sandstone has a higher species richness in a somewhat smaller area than Fitzgerald River National Park, a noted diversity hotspot, in SWA (Table 5). Rice & Westoby (1983) hypothesised that richness in the Hawkesbury system is principally determined by oligotrophy rather than climate or history.

The 'niche-dimension' hypothesis (Hutchinson 1957) provides a context for understanding high species richness on oligotrophic soils. While acknowledging the importance of time and evolutionary processes, this focuses instead on ecological conditions. It suggests that some areas or habitats are richer in species than others due to intrinsic ecological factors, such as greater niche dimensionality associated with trade-offs among species in their capacity to compete for multiple limiting resources (Harpole & Tilman 2007; Harpole and Suding 2011), including partitioning among different forms of soil P (Laliberté *et al.* 2013). Perhaps if SEA had areas of oligotrophic soils as extensive as those in SWA it would be as species rich.

A FRAMEWORK FOR UNDERSTANDING SPECIES RICHNESS IN SWA AND SEA

The explanations and hypotheses for differing species richness in SWA and SEA can be reduced to two key

Table 5 Species richness in Blue Mountains and Fitzgerald River National Parks.

	Area (km ²)	Native angiosperm species
Blue Mountains National Park	2482	1456 ^a
Fitzgerald River National Park	3299	1402 ^b

^a Source <http://www.bionet.nsw.gov.au>, download 1/1/14

^b Source <http://naturemap.dec.wa.gov.au>, download 1/1/14

framing questions: how many species can 'fit' in each region (determined by niche richness and habitat diversity), and of the species that can potentially fit, how many are actually present (determined by extinction, speciation and immigration operating over historical time frames). In any given area after a suitable length of time without perturbation, a dynamic equilibrium should be reached where as many species are present as can fit, species addition (through speciation and immigration) balances species subtraction (by extinction) and richness has reached its potential and will neither increase nor decrease over time. If SWA and SEA can potentially fit the same number of species, then SEA must be further below equilibrium than SWA and historical factors are needed to explain this. If, however, SWA can fit more species than SEA, then both may be at the same distance from equilibrium and historical factors may be unimportant.

Nine scenarios can be envisaged depending on the answers to these two questions (Table 6). For the SWA–SEA comparison at species level, four scenarios (5, 6, 8, 9) can be discounted as they fail to predict the observed SWA's higher richness. Three scenarios (1, 2, 4) predict greater richness in SWA, while two scenarios (3, 7) are ambiguous and may result in either more, the same, or less richness depending on the balance between factors.

The five plausible scenarios are: (i) Scenario 1, more species can fit in SWA, and SWA is closer to equilibrium than SEA (e.g. if SWA has more niches than SEA and a more stable climate history); (ii) Scenario 2, as many species can fit in SWA as SEA, and SWA is closer to equilibrium than SEA (e.g. if both areas have equivalent niche richness and SWA had a more stable climate history); (iii) Scenario 3, fewer species can fit in SWA, but SWA is closer to equilibrium than SEA (e.g. if SWA has fewer niches but a more stable climate history); this scenario may result in more, equal or fewer species in SWA depending on how much the positive effect of a more stable climate history offsets the negative effect of reduced niche richness); (iv) Scenario 4, more species can fit in SWA, and SWA and SEA are equally close to equilibrium (e.g. if SWA has more niches, and both areas have experienced equivalent climate histories); and (v) Scenario 7, more species can fit in SWA, but SWA is further from equilibrium than SEA (e.g. if SWA has more niches, and a less stable climate history); this scenario may result in more, equal or greater species richness in SWA depending on how much the positive effect of extra niche richness offsets the negative effect of more recent extinction or reduced speciation).

A central problem remains the need to understand exactly what differences (if any) in the environmental histories and ecological conditions of SWA and SEA are relevant to the development of its higher species richness. Both history-dependent and history-independent scenarios may be equally plausible. Thought experiments are useful here: would SEA and SWA differ in richness if: (i) both had similar current ecological conditions (e.g. equally large areas of oligotrophic soils) but retained their differences in evolutionary history; or conversely (ii) both had similar evolutionary histories but retained their differences in ecological conditions. Such thought experiments may help tease out the relative importance of these factors.

QUESTIONS, APPARENT PARADOXES, AND GAPS IN OUR UNDERSTANDING OF THE FLORA OF SWA AND ITS HISTORY

While much has been achieved since Hooker's time in documenting and understanding floristic patterns both within and between SWA and SEA, much remains to be understood; paradoxes and knowledge gaps remain. Five issues surrounding the flora of SWA that require further explanation and analysis are discussed briefly below. New tools that have become available since Hooker's time, particularly well-resolved and dateable molecular phylogenies and spatial analysis tools, may make some of these questions more tractable.

Is the higher endemism of SWA than SEA noteworthy?

Along with high species richness, the high endemism (although with steadily declining values, see above) in SWA is usually considered one of its most noteworthy aspects, particularly when compared with much lower values in other parts of Australia (Crisp *et al.* 1999). However, SWA is an ecological island with a relatively natural boundary, while SEA is not. Islands are noted for their high endemism, generated by reduced opportunities for recent immigration (and hence shared taxa) and increased opportunities for within-island radiations (MacArthur & Wilson 1967). SEA, by contrast, is contiguous with regions to the north, east and south that share its mesic environment. Hence, many plant species extend beyond the region as defined, and its endemism value is predictably low. However, the higher species richness of SWA compared with SEA is not predictable from these differences, and in many ways is more remarkable than its higher endemism.

Table 6 A simplified framework for comparing species richness in two different areas. Values in cells give expected comparative richness in Southwest Australia (SWA) compared with Southeast Australia (SEA) under nine different scenarios (numbered in parenthesis).

		How many species can fit in SWA compared with SEA?		
		More	The same number	Fewer
How close is SWA to equilibrium compared with SEA?	Closer	(1) Richer	(2) Richer	(3) ?
	The same	(4) Richer	(5) Equal	(6) Fewer
	Further	(7) ?	(8) Fewer	(9) Fewer

Why is SWA depauperate at genus and family level?

While the relatively depauperate nature of the flora of SWA at genus and family level has been known since Hooker's time (and confirmed in this analysis), it has received much less attention than the area's higher species richness and endemism. As with species richness, few comparative studies have been attempted to explain why SEA would be richer in genera and families but poorer in species than SWA. Extinction has been invoked to explain the absence from SWA of plants from the Tertiary rainforests (Hopper 1979) and of a suite of mesic-forest vertebrates (gliding possums, lyrebirds, logrunners) that presumably lived in them (Archer 1996). Similarly, extinctions have played a major role in shaping the flora of SEA (Crisp & Cook 2011). However, extinction alone cannot adequately explain the opposing trend in species *cf.* family and genus richness, without a further explanation as to why it would affect these different taxonomic levels differently.

Again, as with the difference in species richness, both historical and ahistorical explanations are plausible. An early phase in SWA where extinction exceeded speciation may have led to reduced richness at all taxonomic levels, followed by a phase where speciation exceeded extinction in the remaining genera and families (leading to a near-equilibrium state at species level but retaining a below-equilibrium state at higher taxonomic levels). Alternatively, recent extinctions in SWA of taxonomic groups that are rich in genera and families but relatively poor in species (or persistence or recolonisation into SEA of such groups) could explain the skew. Rainforest taxa, which are relatively well-represented in SEA but virtually absent from SWA, may be one such group. The scenarios may also be inverted: major extinctions in SEA (Sniderman *et al.* 2013) may have preferentially involved species-rich families and genera. Such scenarios, of course, merely shift the explanatory burden for the observed skew from areas (SWA *cf.* SEA) to taxonomic or ecological groups (rainforest *cf.* non-rainforest taxa). An ahistorical explanation for such skews can also be envisaged, for example if relatively few genera and families are capable of extensive radiations in SWA's oligotrophic soils.

Are observed patterns of species richness within SWA historically meaningful?

Many authors have mapped species richness within SWA and attempted to identify nodes of higher-than-average or lower-than-average richness within the area, both for individual families or genera (Speck 1958; Hopper & Maslin 1978; Lamont *et al.* 1982) and for the vascular flora as a whole (Hopkins *et al.* 1983; Hopper & Gioia 2004). Repeated patterns are found, with nodes of species richness in the northern and/or south-coastal sandplains, and the wet forests of the far southwest generally having low diversity. Across the entire flora, however, other patterns also exist: *Acacia* is richest in the wheatbelt (Hopper & Maslin 1978; Hnatiuk & Maslin 1980), *Eucalyptus* has a node of species richness in the Great Western Woodlands, while Hopper & Gioia (2004) identified a third node of richness on the Swan Coastal Plain.

As with overall richness, either or both historical and ahistorical factors may be explanatory for these patterns.

Hopper (1979) used these patterns in support of a Quaternary speciation burst in the area of intermediate rainfall designated the Transitional Rainfall Zone, while Hopper & Gioia (2004) used them to infer historical climatic stability (hence low extinction rates) in the near-coastal parts of the Transitional Rainfall Zone. However, these nodes of high species richness are also co-extensive with the largest and most contiguous areas of oligotrophic sandplains, and hence kwongan vegetation, in SWA, and the oligotrophy itself might drive the species richness.

While the patterns are undeniably real, random speciation occurring across an area would be expected to generate some pattern, including nodes of higher-than-average richness, through chance alone. No analysis has yet attempted to reject a null hypothesis of random chance for these patterns. Further, some aspects of the observed pattern (such as the low species richness in the far southwest) may be significantly different from a null model, while other parts of the pattern (such as the high-richness nodes in the Mt Lesueur, Stirlings–Fitzgerald River areas or Swan Coastal Plain) may not.

Few equivalent analyses identifying nodes of species richness are available for SEA. Hnatiuk & Maslin (1980) and González-Orozco *et al.* (2011) produced richness maps for *Acacia* for the whole of Australia, which clearly demonstrate the relatively richer flora of SWA compared with SEA, and showed a number of SEA richness nodes including the Blue Mountains. It is likely that similarly congruent patterns will be found there, perhaps allowing more powerful tests and more general inferences than those based on SWA alone.

Why have some taxonomic groups been insensitive to SWA's special circumstances?

Different plant groups appear to have responded differently to the different conditions, historical or ecological or both, in SWA and SEA (Table 4). Some of these differences may be due to the greater connectivity of SEA with other non-arid regions (northern New South Wales, Tasmania during sea-level minima), which would be expected to have provided abundant opportunities for recolonisation after unfavourable conditions and extinctions; such opportunities were largely unavailable or restricted for SWA. However, this is unlikely to be the sole cause of current differences. In particular, the question remains open as to why some species-rich families, such as Poaceae and Asteraceae, have not been influenced by whatever drivers of richness have operated in SWA.

Why are there very few species restricted to single (or a few adjacent) granite inselbergs in SWA?

Much of SWA is underlain by a single, geologically stable, highly eroded, Archaean, predominantly granitic crustal block, the Yilgarn Craton. The craton granites are exposed in a scatter of isolated, exposed inselbergs over much of SWA, the individual inselbergs often separated by extensive areas of alluvium, sandplain or laterite. If SWA is an ecological island, the inselbergs form an archipelago of even smaller ecological islands within the region; they and their skirts of light-textured, relatively rich and runoff-watered soils are usually well-separated by flatter, drier, heavier-textured and/or more oligotrophic soils. Many granite-specialist plants (e.g.

Eucalyptus caesia, *Kunzea baxteri*, various species in vernal pools on their summits) and animals occur on or around them, and are often restricted to them.

If speciation in SWA has been driven by either recent or older phases of allopatric speciation caused by climate change, or through genetic isolation in patchy habitats, then the inselbergs, especially the more isolated ones, should be ideal candidates for allopatric species radiations. It may be expected that a suite of species would be found that are very narrowly endemic, restricted to single inselbergs or closely adjacent complexes of inselbergs. On current evidence, this is not the case. Hopper *et al.* (1997) analysed records of orchids from an exhaustive survey of granite rocks throughout the Yilgarn Craton, and identified only two potential taxa restricted to single rocks out of 141 taxa recorded on inselbergs; this can be regarded as a background level of very narrow-range endemism in the SWA context. In some cases, inselberg specialists show genetic signals of isolation and drift [e.g. *Eucalyptus caesia* (Byrne & Hopper 2008); *Kunzea baxteri* (Tapper *et al.* 2014)], however, this is not usually at a level that allows taxonomic recognition. Tapper *et al.* (2014) estimated the deepest observed genetic divergence between populations of *K. baxteri* to the Pliocene, but most populations appear to show Pleistocene-age divergences; in all cases, divergences are at infra-species, population levels and have not (yet?) led to speciation.

In contrast to the situation on the granite inselbergs, Gibson *et al.* (2010) listed 10 taxa that are believed to be restricted to single banded iron formation (BIF) ranges on the edge of the Yilgarn Craton (immediately adjacent to SWA as defined here); further species are known from other BIF ranges, with more to be described in the near future. Greenstone ranges (e.g. Ravensthorpe Range) are even richer in single-range species (Markey *et al.* 2012). In this context, the apparent low prevalence of single-inselberg taxa in SWA appears to be paradoxical under current models for extensive allopatry driving speciation.

PROSPECTS FOR FURTHER WORK, AND CONCLUSIONS

Since Hooker first formalised the observation that SWA has special characteristics, regretted his inability to explain them, and proposed that understanding SWA may provide insights into general problems of evolution, many authors have sought explanations, mostly historical, for the two most striking characteristics of the SWA flora: its high species richness and endemism. Other characteristics, including its relative paucity of genera and families, have received less attention. Furthermore, most studies that have addressed these questions by comparison with other areas have used comparisons outside Australia, ignoring the area with which SWA has its closest physical, historical and floristic connections, SEA. Other studies have sought to explain SWA's special characteristics without explicit reference to outside comparisons at all, drawing conclusions based only on inferred historical processes within SWA that may or may not themselves be special.

Hooker (1859 p. xxvii) faced a similar situation at the time he was writing, pertaining to the flora of the whole

of Australia, and his comments are important in this context: 'So numerous indeed are the peculiarities of this Flora, that it has been considered as differing fundamentally, or in almost all its attributes, from those of other lands; and speculations have been entertained that its origin is either referable to another period of the world's history from that in which the existing plants of other continents have been produced, or to a separate creative effort from that which contemporaneously peopled the rest of the globe with its existing vegetation; whilst others again have supposed that the climate or some other attribute of Australia has exerted an influence on its vegetation, differing both in kind and degree from that of other climates.'

Diels (1906 p. 39) likewise felt the need to balance analyses of the differences between the regions with considerations of similarity: 'The high degree of endemism which characterizes south-western Australia has been known since Robert Brown's time, but it has always been over-rated. When, for example, Hooker (loc. cit. p. 28) states that the difference between south-eastern and south-western Australia is greater than that between Australia and the rest of the earth, he is going too far. His conclusions are based on incorrect deductions from inadequate data. A close investigation of the difference between the two sides of the continent shows that the families characteristic of the west show little difference from those of the east.'

Hopper (2009) pointed out that biogeographic and evolutionary hypotheses are only useful if they are testable, and hence able to move from narrative to analytical frameworks (Ball 1976). We add to this a further requirement, that tests should include a formal null hypothesis. In the case of SWA, one null hypothesis is 'that SWA is not special compared with other comparable regions'. The analyses with which we commenced this paper shows that this hypothesis can be rejected: some of the special characteristics raised by Hooker (1859) and discussed vigorously ever since, remain. A second null hypothesis 'that the differences in species richness between SWA and SEA are not due to differences in history', however, cannot yet be rejected and remains possible. Falsification of this null hypothesis is important, since determining exactly what needs to be explained is a necessary precursor to any explanation.

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