Fossil evidence for a hyperdiverse sclerophyll flora under a non–Mediterranean-type climate

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The spectacular diversity of sclerophyll plants in the Cape Floristic Region in South Africa and Australia's Southwest Floristic Region has been attributed to either explosive radiation on infertile soils under fire-prone, summer-dry climates or sustained accretion of species under inferred stable climate regimes. However, the very poor fossil record of these regions has made these ideas difficult to test. Here, we reconstruct ecological-scale plant species richness from an exceptionally well-preserved fossil flora. We show that a hyperdiverse sclerophyll flora existed under high-rainfall, summer-wet climates in the Early Pleistocene in southeastern Australia. The sclerophyll flora of this region must, therefore, have suffered subsequent extinctions to result in its current relatively low diversity. This regional loss of sclerophyll diversity occurred at the same time as a loss of rainforest diversity and cannot be explained by ecological substitution of species of one ecological type by another type. We show that sclerophyll hyperdiversity has developed in distinctly non-Mediterranean climates, and this diversity is, therefore, more likely a response to long-term climate stability. Climate stability may have both reduced the intensity of extinctions associated with the Pleistocene climate cycles and promoted the accumulation of species richness by encouraging genetic divergence between populations and discouraging plant dispersal.

macrofossil flora | species diversity | species-area curve | glacial-interglacial cycles

Mediterranean climate regions support ~20% of vascular plant species on 5% of Earth's surface (1) and show positive anomalies in the latitudinal plant species diversity gradient. Researchers have used two approaches to explain this gradient. The first approach emphasizes the importance of contemporary environmental processes. For example, some models use energy and water availability to explain global patterns of diversity (2, 3). Alternatively, historical models focus on geological-scale processes and often invoke the contrasting antiquity of tropical vs. temperate climates. For example, the tropical conservatism hypothesis (4) argues that the high diversity of tropical floras accumulated over tens of millions of years during warm, ever-wet, early-middle Cenozoic climates. This model infers that temperate floras are depauperate because they were derived relatively recently from a small number of thermophilic lineages that were able to colonize novel temperate climates during the late Cenozoic. However, these contemporary and historical models must neglect or misrepresent important processes, because they fail to predict the richness of the Mediterranean climate biome (2, 5, 6). Hyperdiverse Mediterranean climate regions, therefore, provide a test of current theories about the evolution of global patterns of species richness.

The Mediterranean climate regions are renowned for having sclerophyll floras—floras dominated by tough-leaved, slow-growing, short-statured, often woody taxa at the slow end of the leaf economics spectrum (7). Sclerophylly is particularly important in the most species-rich (on a per-area basis) of these regions, the Cape Floristic Region (CFR) in South Africa and the Southwest Floristic Region (SWFR) in Australia (1) (Fig. 1). The high species richness of SWFR cannot be explained by high topographic heterogeneity, because this region has a very flat, low-elevation landscape (1). Furthermore, CFR, although more mountainous than SWFR, is more elevationally uniform than the remaining three Mediterranean climate regions (1). Instead, authors have invoked soil infertility (5, 8), unusual climate stability at a range of temporal scales (9–11), contemporary landscape and edaphic diversity (8), Cenozoic landscape dynamics (6), or fire (10). However, many of the contemporary features used to explain the hyperdiverse southwestern regions fail to explain patterns of diversity within these continents. The phylogenetically related sclerophyll floras in the southeast Cape and southeast Australia are also exposed to widespread soil infertility, seasonal moisture stress, fire, and high landscape and edaphic diversity, but they are significantly less species-rich (5, 11, 12). Explanations for the sclerophyll hyperdiversity of CFR and SWFR must account for these parallel east–west diversity gradients.

Much of the controversy surrounding the origins of sclerophyll diversity relates to when these biomes became hyperdiverse. Several authors (1, 13, 14) have hypothesized that explosive speciation after the development of Mediterranean climates during the late Cenozoic explains most of the sclerophyll richness in CFR and SWFR. Phylogenetic and fossil evidence indicates much greater ages and progressive subsequent diversification of some of the major sclerophyll clades (5, 9, 15–19), but the timing of the development of species richness in these clades remains unclear. In particular, lower extinction rates than in other extratropical regions could contribute significantly to the greater diversity of CFR and SWFR. However, this idea contradicts the established paradigm that fire-dependent, drought-tolerant sclerophyll floras replaced moisture-dependent, fire-sensitive rainforest during the late Cenozoic (20–22).

If hyperdiverse sclerophyll floras developed in response to environmental features or processes associated with Mediterranean-type climates, we would expect that sclerophyll floras existed only as low-diversity biomes until their diversification was accelerated by the appearance of Mediterranean-type climates. Alternatively, if hyperdiverse sclerophyll floras are primarily a product of geologically long periods of relative environmental stability (9), then currently hyperdiverse regions may be those regions that have experienced the least climate variability over timescales meaningful for speciation. One potential way to resolve this question is to address the fossil record. Almost all of the relevant fossil evidence is based on pollen (5, 10), which shows decreased diversity of rainforest floras and increased abundance of sclerophyll taxa

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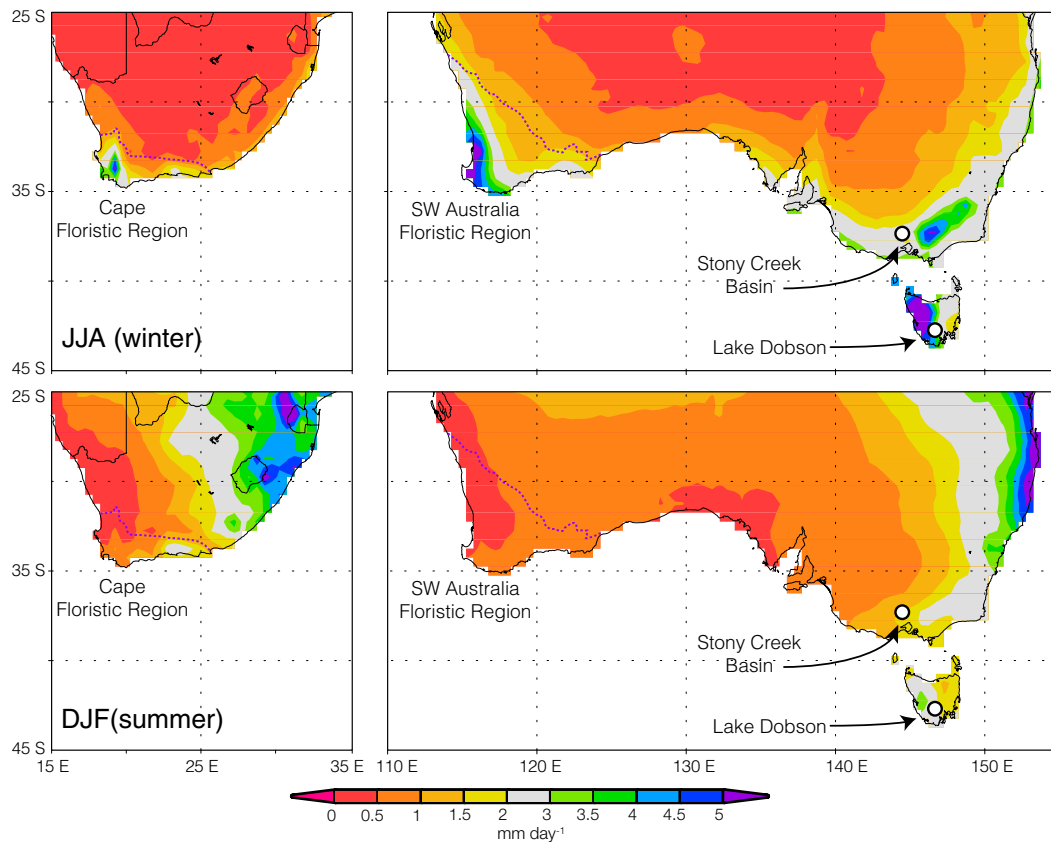
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Fig. 1. Southern Africa and southern Australia winter and summer precipitation (millimetres per day), from Climatic Research Unit TS3.10.1 data set.: *Upper*, June to August [1950–2000]; *Lower*, December to February [1950–1999]). Location of the Cape Floristic Region in South Africa and the Southwest Floristic Region in Australia and location of the fossil locality SCB and LD. Precipitation plotted with Climate Explorer (http://climexp.knmi.nl).

during the late Neogene (20, 23). Unfortunately, the fossil pollen record has low taxonomic resolution (typically to the level of genus) and therefore, is poor at detecting species extinctions and radiations, particularly for sclerophyll floras, which exhibit high species richness within genera. As a result, the fossil pollen record provides little basis for characterizing the history of species richness in this biome. However, macrofossils (leaves, flowers, fruits, etc.) have the potential to better address questions of diversity because of their higher taxonomic resolution (24).

Here, we use exceptionally preserved macrofossils recovered from a small paleolake, Stony Creek Basin (SCB), in southeast Australia (Fig. 1) to estimate standing ecological-scale species richness of Early Pleistocene sclerophyll vegetation. We used a model based on the diversity of fossil leaves at SCB and the diversity of leaves deposited in a modern analog system (Lake Dobson, Tasmania). We then compared this inferred species richness with species area curves constructed for SWFR, CFR, and eastern Australia. Our analyses show that a sclerophyll flora with species richness comparable with CFR and SWFR existed during the Early Pleistocene in a relatively mesic region that now has low-diversity sclerophyll floras. Furthermore, the fossils predate the development of current winter-dominated rainfall regimes in southeast Australia: paleoclimatic reconstructions from SCB show annual rainfall ≥ 1.5 times and summer rainfall ~ 2–2.4 times higher than today (25). The SCB fossil flora, therefore, contradicts hypotheses attempting to explain the origins of the hyperdiverse CFR and SWFR floras solely in terms of contemporary Mediterranean climates.

Results

In addition to conifers, ferns, bryophytes, and monocots, we found leaf and stem fossils of 69 sclerophyllous species of dicots in our

sample ($n = 1,118$) of the SCB sediments (Fig. 2 and *SI Appendix*, Figs. S1–S35). Of these species, 43 species were woody sclerophyll taxa typical of Australian sclerophyll floras (*Eucalyptus*, other Myrtaceae, *Acacia*, *Allocasuarina*, *Banksia*, *Hakea*, *Boronia*, Bossieae, and *Bauera*) (Fig. 2), including 19 previously described species of Ericaceae (26). The identification of several of these groups was verified by the presence of reproductive structures [*Acacia* (*SI Appendix*, Fig. S2), *Boronia* (*SI Appendix*, Fig. S3), Ericaceae (*SI Appendix*, Figs. S8–S26), *Eucalyptus*, *Leptospermum*, and *Baeckea* (*SI Appendix*, Figs. S27–S30)]. The remainder could not be placed into groups, because the Australian sclerophyll flora shows high levels of morphological convergence and apart from Proteaceae and Ericaceae (26–29), has poorly known anatomy. For example, superficially similar small, linear entire leaves with tightly revolute margins occur within Proteaceae, Fabaceae, Asteraceae, Lamiaceae, Euphorbiaceae, Ericaceae, Dilleniaceae, Tremandraceae, Frankeniaceae, Rhamnaceae, and Polygalaceae. However, the unidentified leaves were small and thick (*SI Appendix*, Figs. S1–S35), consistent with attributes of woody species. The dominance of the flora by woody species is consistent with strong taphonomic biases against preservation of herbs (30, 31).

The relationship between the species richness in a plant fossil assemblage and the species richness of the source flora is complex and involves three major potential biases. First, fossil assemblages are typically derived from sediment samples laid down over a time period (in our example, ~2,500 y). During this period, the species composition of the source vegetation may have changed (32). Second, collections of species-rich plant macrofossil assemblages typically undersample the diversity present in the sediments from which they are recovered (33–35). Third, the poor preservation potential of most macroscopic plant organs means that fossil leaf
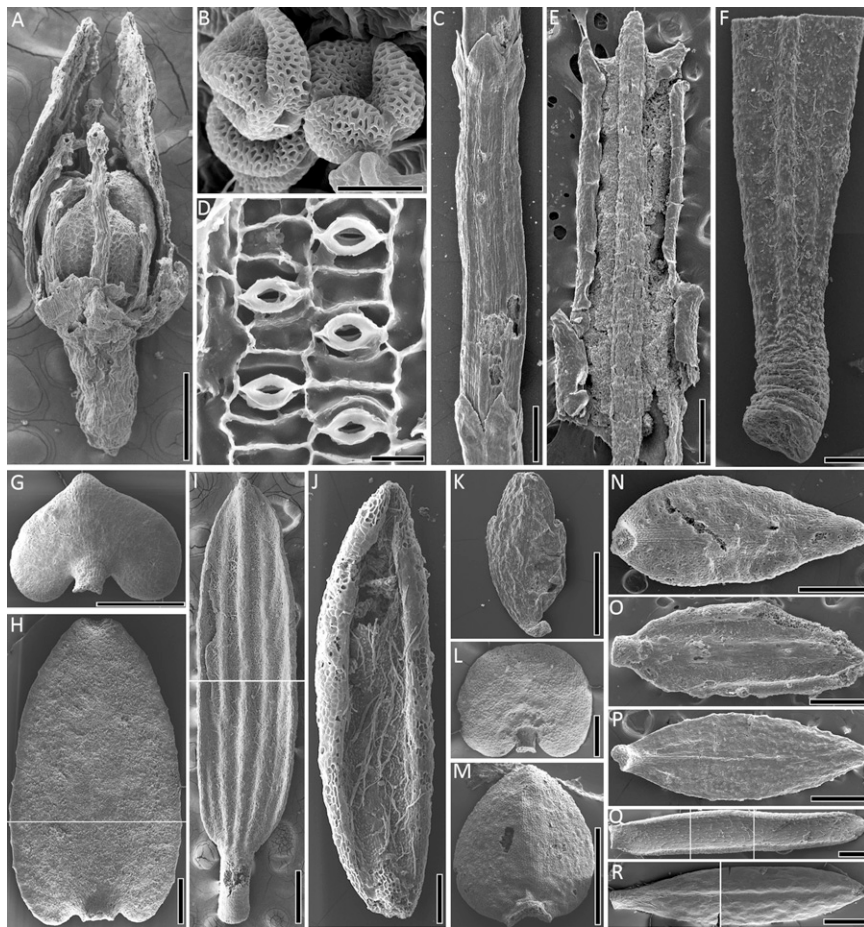
Sniderman et al.

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Fig. 2. Scanning electron micrographs illustrating the diversity and excellent preservation typical of fossils from SCB. (*A*) Flower of *Boronia cf parviflora*. (*B*) In situ pollen grains from *A*. (*C*) Foliage fragment of *Allocasuarina cf torulosa*. (*D*) Inner surface of the cuticle of *C* showing stomata and epidermal cells. (*E*) Leaf fragment of *Banksia ericifolia*. (*F*) Phyllode of an *Acacia* species. (*G*–*I*) Leaves of Ericaceae subfamily Styphelioideae; 20 anatomically distinct morphospecies of this group were present. (*J*) Leaf of Fabaceae *cf* Bossieae. (*K*) *Bauera* sp. (Cunoniaceae). (*L*–*R*) Unidentified species. *H*, *I*, *Q*, and *R* are composite images as indicated by white lines. (Scale bars: *A*, *C*, *E*–*R*, 0.5 mm; *B*, 10 μm; *D*, 20 μm.)

assemblages include only a subset of the species present in their source communities, leading to underestimates of the richness of source floras, regardless of investigator effort (31).

We established that the first bias (time averaging) was small as follows. The numbers equivalent β-diversity of the flora, $D(H_\beta)$ (36), estimated from the Shannon diversities of the individual and pooled sediment samples (37) for the SCB fossil samples was 1.03 (*SI Text*), implying that the samples effectively represent only 1.03 distinct communities (36). Resampling of the pooled flora indicated that this estimate was not significantly greater than one ($P = 0.312$). We conclude that species turnover between the four fossil samples is negligible and leads to no significant bias.

To compensate for undersampling of the sediments, we estimated the asymptotic or true richness of the fossil flora using the abundance-based coverage estimator (ACE) (38), which estimates true assemblage richness based on the relative abundances of rare taxa, those taxa with frequencies of one (singletons) up to a user-determined cutoff frequency k (10 in this case). The ACE richness estimate of the fossil flora is 90.5 species [95% confidence interval (CI) = 78.2–119.4] (Table S1), suggesting that the fossil flora, with observed species richness $S = 69$ (including 23 singletons), is strongly undersampled.

To allow for taphonomic undersampling of the source vegetation, we modeled the species richness of the Early Pleistocene SCB source vegetation by reanalyzing the only comprehensive taphonomic study of a species-rich sclerophyll flora (30). We compared assemblages of leaves recovered from surficial sediments of Lake Dobson (LD) with the species composition of LD's potential catchment area (Tables S1 and S2). LD provides a plausible analog for the SCB fossil flora, because the floras are broadly similar in sclerophylly, leaf size, and floristic composition. Also, we can assume similar source areas for leaves for both lakes. Leaves are rarely transported far, except by rivers (31), and high fall velocities strongly restrict the aerial dispersal of sclerophyllous leaves (31). We, therefore, consider that the hydrological catchment areas of ∼50 ha at both SCB and LD (*SI Text*) represent the catchments for leaves at these sites.

We then estimated that the 50 ha source vegetation at SCB contained 288 woody dicot species (95% CI = 179–380) by assuming identical ratios between the ACE estimates and species richness of the source vegetation for LD and SCB. Estimates based on rarefaction techniques and estimates using other published southern hemisphere leaf taphonomic studies yielded similar results (240–340 species) (Tables S1 and S2).

Our estimate of SCB 50 ha source vegetation woody species richness (288 species) is significantly greater than the corresponding estimates for southeast Australia (78 species; F = 72.41, $P < 0.0001$), SWFR (133 species; F = 10.18, $P = 0.002$), and CFR (148 species; F = 5.68, $P = 0.022$) (Fig. 3). Our estimate's 95% lower confidence limit (179 species) is significantly higher than the corresponding predicted richness for a similar area in southeast Australia (at $P < 0.001$) but indistinguishable from richness
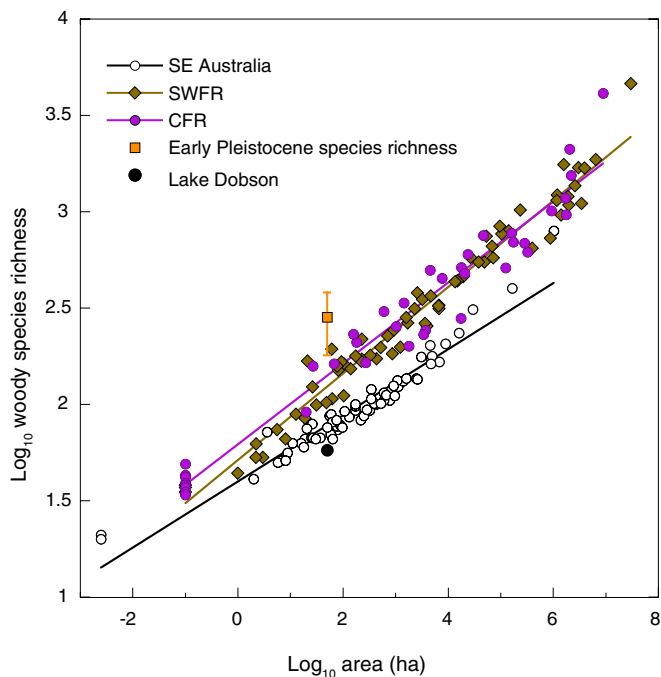
Fig. 3. Estimated woody sclerophyll species richness (288 species with 95% CI) in 50 ha vegetation during the Early Pleistocene in southeast Australia based on the SCB fossil flora. For comparison, woody species richness as a function of sampling area is shown for southeast Australia, the SWFR, and the CFR. Trend lines represent ordinary least squares regressions for the three regions (southeast Australia: $y = 1.5981 + 0.1716x$; SWFR: $y = 1.7101 + 0.2243x$; CFR: $y = 1.7915 + 0.2099x$). Also shown is woody sclerophyll species richness in the 50 ha catchment of LD, Tasmania.

predicted for SWFR ($P = 0.220$) and CFR ($P = 0.493$) (Table S3). The species/area relationships also confirmed that both CFR and SWFR have much higher woody plant diversities than southeast Australia at all spatial scales sampled ($P < 0.01$) (11) (Fig. 3 and *SI Text*). Although CFR [≥9,030 species (39)] has higher total plant species richness than SWFR [>7,380 species (5)], reflecting its much richer succulent and herbaceous component, their patterns of woody species richness are similar.

We evaluated the sensitivity of our species richness estimate to violations of our major assumptions. First, we considered the assumption that SCB and LD showed the same ratio of leaf assemblage to source vegetation species richness. The ratio observed at LD (0.314) is similar to comparable ratios observed in a New Zealand lake (mean = 0.377) (Table S2), despite large differences in leaf sclerophylly between the local floras. Even with an implausibly high ratio of one, the richness estimate for SCB source vegetation is considerably greater than the richest extant sclerophyll floras in southeast Australia, whereas any ratio ≤ 0.68 is consistent with Early Pleistocene SCB richness equaling the species richness of SWFR today. Second, the influence of underestimating catchment size at SCB should have been minor. The area of extant SWFR vegetation predicted to contain 288 woody species is 1,947 ha, ~39 times larger than our estimate of the source catchment size. More than a threefold error in estimating the catchment would require long-distance transport of plant fossils from outside of the hydrological catchment of SCB (40, 41).

Discussion

Our data are consistent with SCB having source vegetation at least as rich in woody species as SWFR or CFR on an equal area basis (Fig. 3). This inference holds even allowing for potential violations of our assumptions, such as exceptionally high representation of

the surrounding vegetation in the fossil flora. Hence, the Early Pleistocene source vegetation was much richer in sclerophyll species than any vegetation in eastern Australia today. The regional mass extinction implicit in these results has passed largely unobserved, because many species in extant diverse sclerophyll floras share the same pollen types. Macrofossil records from Tasmania and southeast Australia have hinted at the scale of late Cenozoic plant species extinctions and imply that extinctions were largely complete by the middle Pleistocene (26, 42). However, the exceptional preservation of the SCB fossil flora uniquely allows discrimination between the morphologically convergent forms that characterize sclerophyll floras.

Our results show that, during the Early Pleistocene, southern Australia supported a hyperdiverse sclerophyll flora in a high-rainfall, summer-wet climate. These results undermine the notion that summer-dry Mediterranean-type climates are necessary for the evolution of hyperdiverse sclerophyll floras and demand a new model for the origins of sclerophyll diversity. A robust model must explain why diversity in the pyrophilic sclerophyll biome decreased in southeast Australia at the same time that mesic, pyrophobic rainforests across Australia declined in area and diversity (20, 21), although that decline has generally been attributed to cooler, drier, and more fire-prone conditions that may have favored sclerophyll vegetation. In addition, such a model should explain the existence of sclerophyll-dominated vegetation in non-Mediterranean climate regions with high rainfall, such as western Tasmania (43), parts of eastern Australia (44), and New Caledonia (45). We propose that the glacial–interglacial climate cycles in the Pleistocene depleted the diversity of both sclerophyll and rainforest communities in southeastern Australia. This explanation is consistent with the model of Jansson and Dynesius (46) that, in regions where Pleistocene glacial–interglacial cycles imposed high-amplitude changes in multiple aspects of the environment, specialist species were systematically and repeatedly extirpated, leaving less speciose floras dominated by generalists.

Why would these changes result in low diversity in eastern Australia but not in SWFR? The glacial–interglacial climate cycles of the Pleistocene may have had less impact on plants in southwest Australia than southeast Australia. Thus, pollen evidence suggests that shrublands persisted through the last glacial maximum (*ca.* 21 ka) in SWFR (47), whereas most of the forested southeast became steppe or grassland (21). These zonally contrasting responses are consistent with climate reconstructions for the last glacial maximum. Coupled ocean–atmosphere climate simulations indicate that winter precipitation increased in southwest Australia but decreased in the southeast (48), and offshore sea surface temperature reconstructions indicate smaller temperature depressions in southwest Australia than southeast Australia (49). Similarly, the modern west–east species richness gradient within CFR has been interpreted as resulting from lower-amplitude Pleistocene climate cycles in the west than the east (11).

Our results support the notion that sclerophyll plant hyperdiversity can, given enough time and environmental stability, develop outside Mediterranean-type climatic regimes. The current species richness of CFR and SWFR is, thus, primarily a product of their relatively stable Pleistocene climates and not a consequence of their shared summer-dry climates. Equivalently rich sclerophyll floras in southeast Australia under late Neogene summer-wet climate regimes were depleted, because fewer species were capable of tolerating the intensified climate cycles that developed later in the Pleistocene. Hence, the SWFR and CFR floras seem anomalously species-rich today, because few extratropical regions have experienced histories of low glacial–interglacial climate variability.

The previously cryptic extinction event shown here may not be restricted to the eastern Australian sclerophyll biome, because the methodological problems that lead to the delayed detection of this extinction event apply widely. Thus, fossil pollen has low taxonomic resolution everywhere, meaning that extinctions will be

invisible in this record if even one member of each pollen group survives. Although the current work shows that macrofossils can sometimes detect extinctions that are cryptic in the fossil pollen record, suitable Early Pleistocene macrofossil records are very rare worldwide. Most importantly, the proposed mechanism for these extinctions is not specific to the eastern Australian sclerophyll biome—although different regions experienced specific patterns of Pleistocene climate change, many extratropical regions were exposed to relatively high-amplitude Pleistocene climate changes. Thus, current biogeographic patterns may be more pervasively shaped by Pleistocene extinction than previously suspected, and similar patterns of extinction may extend to biomes—such as open, sclerophyllous, partly drought-adapted biomes—widely regarded as fully adapted to Late Quaternary climate regimes.

Materials and Methods

Study Site. SCB [37.35°S, 144.13°E, 550 m above sea level (asl)] (Fig. 1) is a small (<10 ha) paleolake within a small closed catchment in upland southeast Australia deposited over *ca.* 280 kya during the Early Pleistocene between 1.83 and 1.55 Ma (40). The paleolake infill consists of *ca.* 40 m organic-rich, silty clay sediments that contain exceptionally well-preserved fossil pollen, plant macrofossils (leaves, stems, flowers, and fruits) (Fig. 2), and insects. Previous analyses indicate that the vegetation was a mosaic of diverse sclerophyll forest and temperate rainforest (26, 41), with dynamics mediated, in part, by fire (50). Modern precipitation at SCB is dominated by cool-season frontal rain associated with seasonal migration of the subtropical anticyclone (51). However, fossil beetle-based climate reconstructions indicate much higher annual and summer precipitation during the Early Pleistocene (25), consistent with the presence in the record of a diverse conifer/angiosperm rainforest, including the highly drought-sensitive genera of Podocarpaceae (41, 52).

To provide a modern analog to SCB, we examined leaf assemblages from LD (42.67°S, 146.83°E, 1,030 m asl) (Fig. 1), a small (*ca.* 3 ha) cirque lake in Mount Field National Park, Tasmania, Australia, with a hydrological catchment of *ca.* 60 ha. Intensive field sampling identified 58 woody angiosperm species in the catchment.

Fossil Sampling and Identification. We analyzed plant macrofossils from four stratigraphically sequential 3,000-mL sediment samples of 10 cm stratigraphic thickness taken between 470 and 500 cm deep in an excavation near the center of SCB. These samples were chosen, because they contained numerous macrofossils—other samples appeared to show comparable diversity to those samples analyzed but contained too few macrofossils for analysis. Pollen analyses indicate that the four samples are equivalent to the *Eucalyptus*-dominated Zone A of the pollen record of Sniderman and Haberle (50). We estimate that each sample represents *ca.* 635 y of deposition based on the age model of Sniderman and Haberle (50).

Estimation of Early Pleistocene Standing Diversity. We estimated the species richness of the Early Pleistocene source vegetation around SCB by (*i*) estimating the asymptotic richness of the SCB fossil flora, (*ii*) quantitatively examining the relationship between the richness of extant sclerophyll vegetation and its representation in lacustrine leaf assemblages on the basis of equal sampling effort, and (*iii*) evaluating the extent to which the observed richness of the SCB fossil flora may have been positively biased by time averaging. Finally, to evaluate the evolutionary and ecological significance of the Early Pleistocene sclerophyll vegetation represented at SCB, we compared the estimated richness of the SCB source vegetation with the richest extant sclerophyll vegetation in Australia and the CFR on an equal area basis (*SI Text*). We compiled separate species/area curves for southeast and southwest Australia and CFR, and we used linear models to compare their slopes and intercepts of regressions of $\log_{10}$ of species richness with $\log_{10}$ of area (*SI Text*, Figs. S1–S2, Tables S1–S5).

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Sniderman et al.

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