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Australia lacks stem succulents but is it depauperate in plants with crassulacean acid metabolism (CAM)?

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In the flora of Australia, the driest vegetated continent, crassulacean acid metabolism (CAM), the most water-use efficient form of photosynthesis, is documented in only 0.6% of native species. Most are epiphytes and only seven terrestrial. However, much of Australia is unsurveyed, and carbon isotope signature, commonly used to assess photosynthetic pathway diversity, does not distinguish between plants with low-levels of CAM and C3 plants. We provide the first census of CAM for the Australian flora and suggest that the real frequency of CAM in the flora is double that currently known, with the number of terrestrial CAM species probably 10-fold greater. Still unresolved is the question why the large stem-succulent life — form is absent from the native Australian flora even though exotic large cacti have successfully invaded and established in Australia.

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Introduction

Australia is the driest vegetated continent and is the only warm continent with no native large stem-succulents [1,2,3]. Crassulacean acid metabolism (CAM), a water-use efficient form of photosynthesis typically associated with leaf and stem succulence, also appears poorly represented in Australia. If 6% of vascular plants worldwide exhibit CAM [4], Australia should host ~1300 CAM species [5]. At present CAM has been documented in only 120 named species (Table 1). Most are epiphytes, a mere seven are terrestrial.

Ellenberg [2] suggested that rainfall in arid Australia is too unpredictable to support the massive water-storing succulent life-form found amongst cacti, agaves and euphorbs. He identified a rainfall predictability envelope within which the majority of large succulents in the Americas and Africa are found and argued that the lack of such environments in Australia explained the lack of large succulents in Australia (Figure 1a). Nonetheless, exotic large succulents have successfully invaded native vegetation in Australia, occupying areas of rainfall predictability outside Ellenberg's envelope (Figure 1b–d). For example, in the 1920s, 1.5 billion tons of the obligate CAM stem-succulent *Opuntia stricta* infested 25 million ha of eastern Australia [6,7]. The *Opuntia* incursion has been explained as an anomaly enabled by the destruction of native woody vegetation [2,8,9]. However, 90 years after the virtual eradication of *Opuntia* by the introduced moth, *Cactoblastus cactorum*, around 27 species of opuntioid cacti have naturalized across a range of soil types and climatic zones in south eastern Australia [10] infesting 1 million ha in South Australia alone [11], again outside the Ellenberg envelope (Figure 1d). Furthermore, we now know that *Agave tequilana*, a large obligate CAM leaf-succulent native to Central America, can achieve high rates of biomass accumulation under Australian rainfall conditions [12,13].

The apparent underrepresentation of CAM and succulence in the Australian terrestrial flora is somewhat of an enigma. Worldwide, CAM has evolved over 60 times in 35 families of vascular plants and succulence has appeared in many major plant lineages [14,15], although the appearance of large stem-succulents is less common. Increasing aridity and falling CO_2 concentration during the Miocene are thought to have provided the ecological opportunity for a global surge in the diversification of succulent and CAM lineages [3,14]. But apparently in Australia, the Miocene and Pliocene expansion of arid

Table 1

The evidence for CAM in the 107 endemic Australian vascular plants for which CAM is currently documented. Unless specified otherwise, the evidence is for leaf tissue. Species are listed if they are Australian natives and they exhibit at least one of the following three characteristics: an organ has a δ13C value less negative than −20‰, a tissue exhibits nocturnal acidification, or an organ exhibits a gas-exchange pattern characteristic of CAM.

Family, genus and species	Habit	$\delta^{13}C$ ‰	ΔH^+ $\mu mol\ g^{-1}$ fwt	CAM gas-exchange
Aizoaceae				
Carpobrotus rossii (Haw) Schwantes	T	−21.8 [17]	6 [17]	
Disphyma crassifolium subsp. clavellatum (Haw) Chinnock	T	−20.7 [17]	96 [17], 10 [17]	
Anacampserotaceae				
Anacampseros australiana J.M. Black	T	−23.8 [44]	58 [44]	Yes[A]
Apocynaceae				
Dischidia major (Vahl) Merr.	E	−16.0 [45], −17.8 [27]		
Dischidia nummularia R.Br.	E	−15.7 to −17.6 [27]		
Dischidia ovata Benth.	E	−14.8 [27]		
Hoya anulata Schltr.	E	−13.3[A]		
Hoya australis R.Br. ex J.Traill	E	−15.8 to −19.2 [27]		
Hoya australis R.Br. ex J.Traill subsp. *australis*	E	−15.9 to −18.6 [27]		
Hoya macgillivrayi F.M.Bailey	E	−18.2[A]		
Hoya pottsii J.Traill	E	−13.2[A], −18.3 [27]		
Hoya revoluta Wight ex. Hook.f.	E	−11.8 [27]		
Cynanchum viminale subsp. *australe* (R.Br.) Meve & Liede	T	−12.3 [17]	155 [17]	Yes[A]
Crassulaceae				
Crassula helmsii (Kirk) Cockayne	A		70 [46]	Yes [46]
Crassula sieberiana (Schult. & Schulte.f.) Druce	T		~5 [24]	Yes [24]
Lycopodiaceae				
Isoetes australis S.Williams	A		56 [28]	
Isoetes drummondii A.Braun	A		78 [28]	
Montiaceae				
Calandrinia polyandra Benth	T	−22.2 [25], −26.1[A]	60 [25]	Yes [25]
Orchidaceae				
Bulbophyllum aurantiacum F.Muell.	E	−12.4 [27]		
Bulbophyllum baileyi F.Muell.	L	−16.8 [27]		
Bulbophyllum bowkettiae F.M. Bailey	E	−17.0[A]		
Bulbophyllum gadgarrense Rupp	E	−15.7[A]		
Bulbophyllum globuliforme Nicholls	E	−11.1[A]		
Bulbophyllum gracillimum (Rolfe) Rolfe	E	−12.6[A]		
Bulbophyllum longiflorum Thouars	E	−12.7[A]		
Bulbophyllum macphersonii Rupp	E	−12.2 [27], −15.2[A]		
Bulbophyllum minutissimum F.Muell.	E	−12.3[A], −17.0 [27]		
Bulbophyllum shepherdii (F.Muell.) Rchb.f.	E	−12.1 [27], −13.9 [27]	13 [27]	
Bulbophyllum sladeanum A.D.Hawkes	E	−13.2[A]		
Bulbophyllum wadsworthii Dockrill	E	−18.6[A]		
Bulbophyllum windsorense B.Gray & D.L. Jones	E	−18.2[A]		
Cadetia maideniana (Schltr.) Schltr.	E	−13.1 [27], −14.3[A]		
Cadetia wariana Schltr.	E	−14.9[A], −16.1 [27]		
Chiloschista phyllorhiza (F.Muell.) Schltr. (root)	E	−16.0[A], −17.5 [27]	12–40 [27]	
Cymbidium canaliculatum R.Br.	E	−17.4[A], −18.7 [27]		
Dendrobium aemulum R.Br.	E	−13.4[A]		
Dendrobium antennatum Lindl.	E	−13.5[A], −14.1 [27]		
Dendrobium aphyllum (Roxb.) C.E.C. Fisch.	E	−13.9[A]		
Dendrobium beckleri F. Muell.	E	−14.7 [27]	25 [27], 35 [27]	
Dendrobium bifalce Lindl.	E	−18.1 [27]		
Dendrobium bigibbum Lindl.	E	−11.9 [27], −14.3[A]		
Dendrobium cacatua M.A.Clem. & *D.L.Jones*	E	−16.6[A]		
Dendrobium callitrophilum B.Gray & D.L. Jones	E	−11.5[A]		
Dendrobium canaliculatum R.Br.	E	−12.0[A], −13.1 [26]		
Dendrobium comptonii Rendle	E	−19.5[A]		
Dendrobium x delicatum (F.M.Bailey) F.M. Bailey	E	−16.7[A]		
Dendrobium dicuphum F.Muell.	E	−14.1 [27]		
Dendrobium discolor Lindl.	E	−13.8 [27], −15.4[A]		
Dendrobium gracilicaule F.Muell.	E	−18.3 to −25.2 [27]		
Dendrobium x gracillimum (Rupp) Leaney	E	−17.8[A]		
Dendrobium johannis Rchb.f.	E	−13.8[A], −13.9 [26]		
Dendrobium lichenastrum (F.Muell.) Kraenzl.	E	−12.6 to −17.3[A] [27]		
Dendrobium litorale Schltr.	E	−12.5[A]		

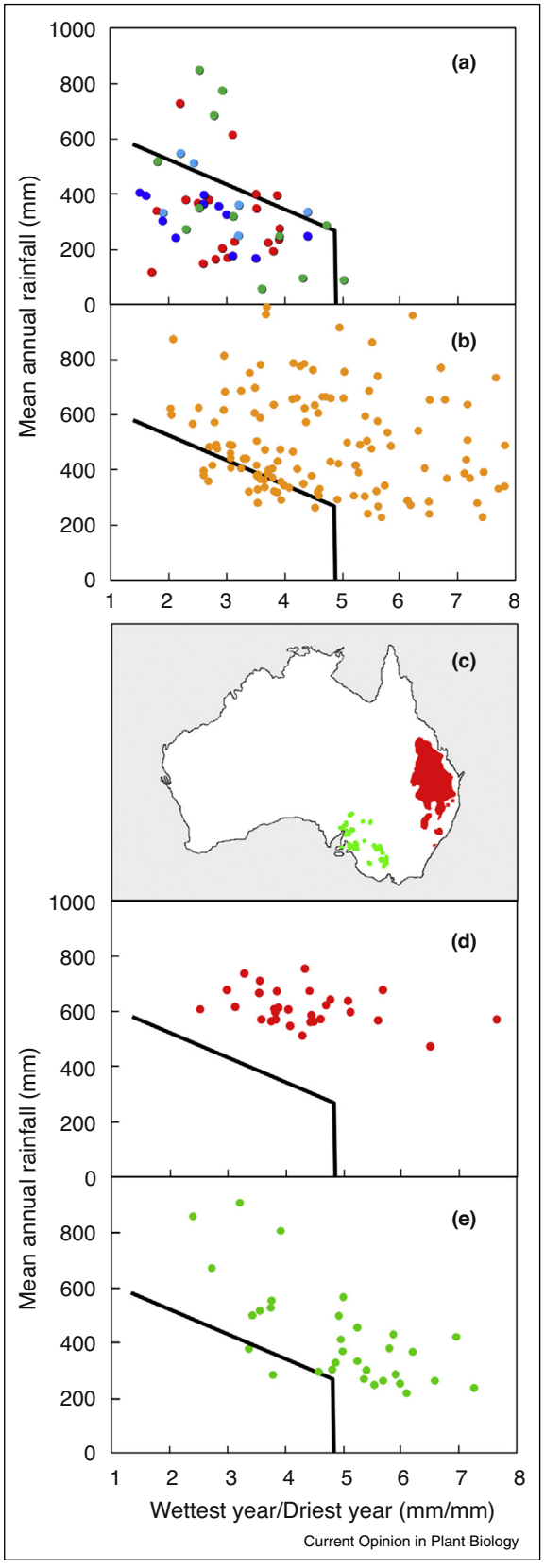
Table 1 (*Continued*)

Family, genus and species	Habit	$\delta^{13}C$ ‰	ΔH^+ μmol g^{-1} fwt	CAM gas-exchange
Dendrobium nindii W.Hill	E	−13.5 [27]		
Dendrobium prenticei (F.Muell.) Nicholls	E	−15.6[A]		
Dendrobium speciosum Sm.	E	−14.5 to −15.9 [4]	3 [26]	
Dendrobium x superbiens Rchb.f.	E	−13.8[A]		
Dendrobium tetragonum A.Cunn.	E	−15.8[A], −18.2 [27]		
Dendrobium toressae (F.M. Bailey) Dockrill	E	−16.6[A], −17.6 [27]		
Didymoplexis pallens Griff.	E	−17.2[A]		
Dockrillia bowmanii (Benth.) M.A.Clem. & D.L.Jones	E	−13.5[A]		
Dockrillia brevicauda (D.L.Jones & M.A.Clem.) M.A.Clem. & D.L.Jones	E	−10.9[A]		
Dockrillia calamiformis (Lodd.) M.A.Clem. & D.L. Jones	E	−15.5[A]		
Dockrillia cucumerina (MacLeay ex Lindl.) Brieger	E	−12.9[A], −13.5 [27]		
Dockrillia dolichophylla (D.L. Jones & M.A. Clem.) M.A. Clem. & D.L. Jones	E	−13.5[A]		
Dockrillia linguiformis (Sw.) Brieger	E	−11.9 [27], −15.5[A]	4 [27]	
Dockrillia mortii (F.Muell.) Rauschert	E	−16.6[A]		
Dockrillia nugentii (F.M. Bailey) M.A. Clem. & D.L. Jones	E	−15.8[A]		
Dockrillia pugioniformis (A.Cunn.)	E	−13.4[A], −15.4 [27]	11 [27], 18 [27]	
Dockrillia racemosa (Nicholls) Rauschert (=		−14.5 [27], −14.7[A]		
Dockrillia rigida (R.Br.) Rauschert	E	−14.9[A], −15.0 [27]		
Dockrillia schoenina (Lindl.) M.A. Clem. & D.L. Jones	E	−13.8[A], −14.7 [27]		
Dockrillia teretifolia (R.Br.) Brieger	E	−15.8 [27], −15.9 [27]	21 [27]	
Dockrillia wassellii (S.T.Blake) Brieger	E	−13.1 [27]		
Eria irukandjiana St.Cloud	E	−19.8 [27]		
Flickingeria convexa (Blume) A.D.Hawkes	E	−13.0 [27]		
Grastidium luteocilium (Rupp) Rauschert	E	−18.7 [27]		
Luisia teretifolia Gaudich.	E	−14.7 [27]		
Micropera fasciculata (Lindl.) Garay	E	−12.7 [27], −14.4 [27]		
Mobilabium hamatum Rupp	E	−16.1 [27]		
Oberonia complanata (A.Cunn.) M.A. Clem. & D.L. Jones	E	−17.8 [27], −18.2 [27]		
Phalaenopsis amabilis subsp. rosenstromii (F.M. Bailey) Christenson	E	−14.1 [26]		
Pholidota imbricata Lindl.	E	−11.8 [26], −15.5 [27]		
Plectorrhiza tridentata (Lindl.) Dockrill	E	−15.4 [27]	35 [27]	
Pomatocalpa macphersonii (F. Muell.) T.E. Hunt	E	−16.3 [27]		
Rhinerrhiza divitiflora (F. Muell. ex Benth.) Rupp	E	−14.2 [27], −15.5 [27]		
Robiquetia gracilistipes (Schltr.) J.J. Sm.	E	−13.5 [27], −15.2 [27]		
Robiquetia wassellii Dockrill	E	−13.9 [27], −14.5 [27]		
Saccolabiopsis armitii (F. Muell.) Dockrill	E	−15.2 [27]		
Sarcochilus ceciliae F.Muell.	L	−13.4 [27], −15.3 [27]		
Sarcochilus falcatus R.Br.	E	−14.9 [27], −15.0 [27]	34 [27]	
Sarcochilus hillii (F.Muell.) F. Muell.	E	−13.8 [27]		
Sarcochilus moorei (Rchb.f.) Schltr.	E	−15.3 [27]		
Schoenorchis micrantha Reinw. ex Blume	E	−14.6 [27], −14.8 [27]		
Taeniophyllum malianum Schltr. (root)	E	−15.8 [27]		
Thrixspermum congestum (F.M. Bailey) Dockrill	E	−14.9 [27], −16.7 [27]		
Trachoma stellatum M.A. Clem., D.L. Jones, B. Gray & J.J. Wood	E	−13.6 [27]		
Trachoma subluteum (Rupp) Garay	E	−15.2 [27]		
Trichoglottis australiensis Dockrill	E	−14.1[A]		
Vanda hindsii Lindl.	E	−14.8 [27]		
Polypodiaceae				
Microsorum punctatum (L.) Copel.	T, L, E	−22.6 [26], −25.2 [27]	39 [26]	Yes [26]
Platycerium veitchii (Underw.) C. Chr.	L	−22.6 [47]	4 [26]	Yes [26]
Pyrrosia longifolia (Burm.f.) C.V. Morton	E, L	−13.6, −14.2 [27]	77 [26]	Yes [26]
Pyrrosia confluens (R.Br.) Ching	E, L	−19.3 to −24.2 [27]		
Pyrrosia confluens var. dielsii (C. Chr.) Hovenkamp	E, L	−17.3 to −20.1 [27]		
Rubiaceae				
Hydnophytum moseleyanum Becc.	E	−17.7[A], −21.8 [27]		
Myrmecodia beccarii Hook.f.	E	−20.7 [27]	20 [48]	Yes [48]

A = aquatic, E = epiphyte, L = lithophyte, T = terrestrial. Plant nomenclature is according to the Australian Plant Census [16] except we recognize the recent transfer of *Sarcostemma* to *Cynanchum*, and except in Orchidaceae for which the APC treatment has not yet been completed. For Orchidaceae nomenclature follows the Queensland Plant Census [40] except for the three taxa that do not occur in Queensland: *Dendrobium comptonii*, *D. dicuphum* and *Sarcochilus moorei*. Many orchid taxa have had new or resurrected names published in the last decade [41,42,43] some of which are in common use. These names are provided in the supplementary files.

[A] This manuscript.

Figure 1



(a) The climate characteristics of sites within which tall stem-succulents dominate the vegetation in SW USA and Mexico (●), South America (●), South Africa (●) and North Africa (●) in relation to the 'Ellenberg envelope' (bold line) that delineates the annual rainfall and rainfall-variability environment within which tall stem-succulents most commonly grow (redrawn from [2]). **(b)** The 'Ellenberg envelope' in relation to rainfall climates at 143 selected Australian meteorological stations [39] with more than 30 years of recorded rainfall information. **(c)** Areas in Australia infested by *Opuntia stricta* during the late 1920s (■; redrawn from [6]) and by *Opuntia rotunda* in 2009 (●; redrawn from [11]). **(d)** The rainfall climates within which *Opuntia stricta* grew in Australia in the late 1920s (●) in relation to the 'Ellenberg envelope'. **(e)** The rainfall climates within which *Opuntia rotunda* grows in Australia at present (●) in relation to the 'Ellenberg envelope'.

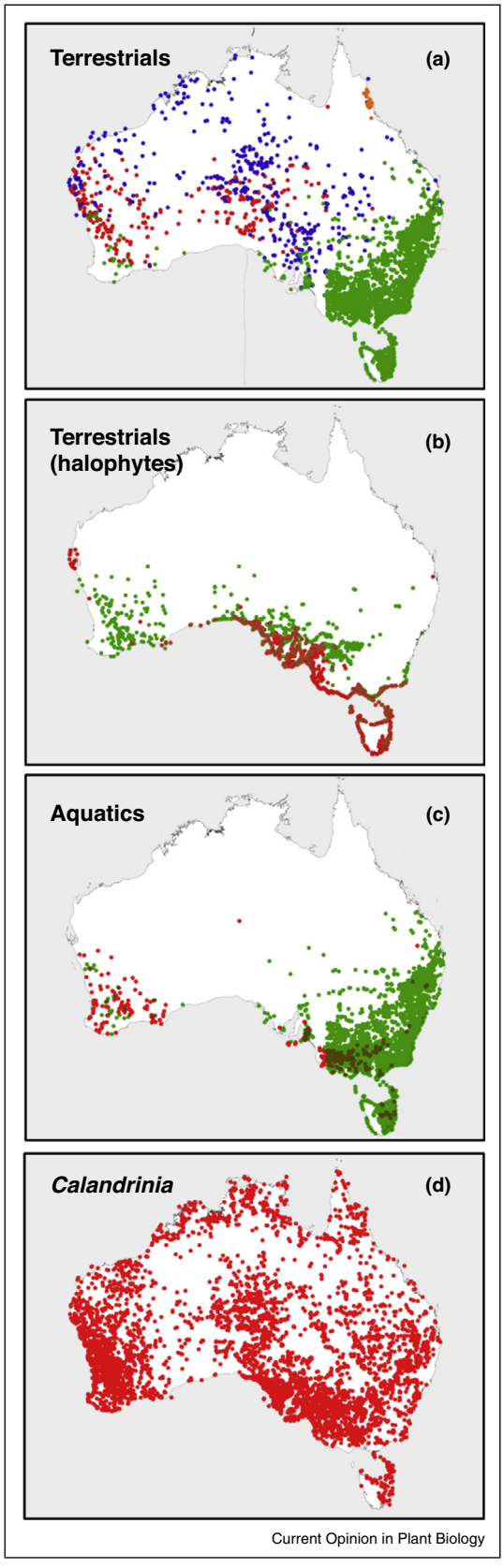
habitat to its current cover of about 70% was not a driver for diversification in lineages with stem-succulence. It may have been that lineages with a disposition to develop stem-succulence were not present in Australia or did not arrive via trans-oceanic dispersal. Perhaps the combination of increasingly stochastic rainfall, warmer temperatures and low nutrient soils may have selected for small size and leaf succulence in native or exotic lineages with succulence or a predisposition to it. It may be pertinent to note that large stem-succulents have evolved in the genus *Euphorbia* in Africa but none of the ~30 native *Euphorbia* in Australia is stem-succulent [16]. If stem-succulent lineages did arrive they did not establish.

The Australian terrestrial CAM flora

The current tally of terrestrial CAM flora, of which some species are halophytes, is undoubtedly a gross underestimate (Figure 2). There are no published surveys of terrestrial plants in the extensive arid central and seasonally dry tropical regions. The only published survey of CAM terrestrial plants in Australia was restricted to salt lake and coastal habitats of southern Western Australia [17], and was mainly based on $\delta^{13}C$ values as indicators of CAM. The isotopic method allows the identification of species in which CAM is the major contributor to carbon gain but does not resolve weakly expressed CAM well or CAM in plants with C4 photosynthesis [18,19,20•,21••,22]. Detection of low-level CAM and facultative CAM require measurements of nocturnal acid accumulation and gas-exchange.

Of the documented Australian terrestrial CAM species, only *Cynanchum viminale* ssp. *australe* (formerly *Sarcostemma* [23]), a scrambler that may attain 2 m in height by way of essentially leaf-less thin woody cladodes, exhibits a $\delta^{13}C$ value, −12.3‰, that is commensurate with CAM as the predominant source of carbon [17]. The $\delta^{13}C$ value-based conclusion is supported by gas-exchange (Figure 3). The isotopic signals of the other known native CAM terrestrials all indicate a small contribution of CAM to carbon gain. A value of −26.5‰ initially led to the categorization of the small perennial *Crassula sieberiana* as a C3 plant [17]. CAM

Figure 2



Collection location of all specimens in Australian herbaria [30] of **(a)** The CAM terrestrials *Calandrinia polyandra* (●), *Crassula sieberiana* (●), *Microsorum punctatum* (●) and *Cynanchum viminale* subsp. *australe* (●); **(b)** The CAM terrestrial halophytes *Carpobrotus rossii* (●) and *Disphyma crassifolium* ssp. *clavellatum* (●). **(c)** The CAM aquatics *Crassula helmsii* (●) and *Isoetes* spp. (●). **(d)** Collection location of all specimens in Australian herbaria of the genus *Calandrinia* (●).

was detected subsequently following measurements of nocturnal acidification and gas-exchange [24]. Variable $\delta^{13}C$ values of −26.1 to −22.2‰ and −25.2 to −22.6‰ respectively for *Calandrinia polyandra*, a small leaf-succulent of sandy semi-arid habitats, and *Microsorum punctatum*, a fern of the coastal tropics, consistently predict plants in which nocturnal CO_2 uptake is present but is substantially less than diurnal uptake by C3 photosynthesis [17,25]. The constitutive nature of CAM in *Microsorum* and facultative CAM in *Calandrinia* required demonstration by gas-exchange [25,26]. $\delta^{13}C$ values of −21.8‰ and −21.9‰ respectively for the coastal salt-tolerant leaf-succulents, *Carpobrotus rossii* and *Disphyma crassifolium* ssp. *clavellatum*, are consistent with a substantial contribution of dark CO_2 fixation to net carbon gain [17]. In both species nocturnal acidification increases following a reduction in the availability of water.

CAM in Australia's epiphytic and lithophytic flora

Around 90% of Australia's known CAM plants are epiphytes and lithophytes, mostly orchids (Table 1). Proportionally more Australian epiphytes have been surveyed for CAM than have terrestrials (Table 1; 27), mainly because there are fewer epiphyte species known, many are accessible in collections, and their distribution is overwhelmingly localized in the moist and seasonally-moist forests on the northern and eastern coastal fringes (Figure 4). The number of recognized CAM epiphytes in Australia is unlikely to more than double as nearly all *Dischidia*, *Hoya*, rubiaceous ant-plants and succulent ferns have been sampled, as have a substantial proportion of the epiphytic orchids [27].

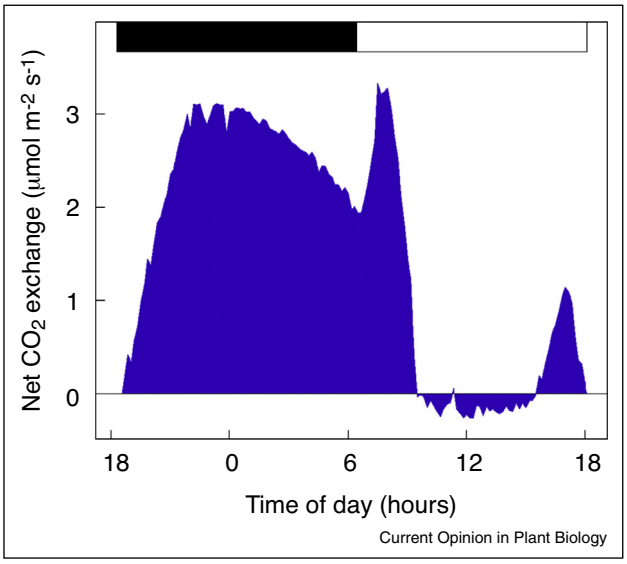
CAM in the Australian aquatic flora

Amongst Australian aquatics, CAM is documented in three species, two temperate *Isoetes* species [28] and in the pan-global *Crassula helmsii* (Figure 4). On the basis of the Australian members of lineages in which aquatic CAM has been reported elsewhere such as *Lilaeopsis* (Apiaceae; 3 spp. in Australia), *Vallisneria* (Hydrocharitaceae; 8 spp. in Australia) and *Isoetes* (Isoetaceae; 15 spp. in Australia) [16], we predict that Australia probably supports up to 20 aquatic species with CAM.

The expression of CAM in Australian plants — predictions

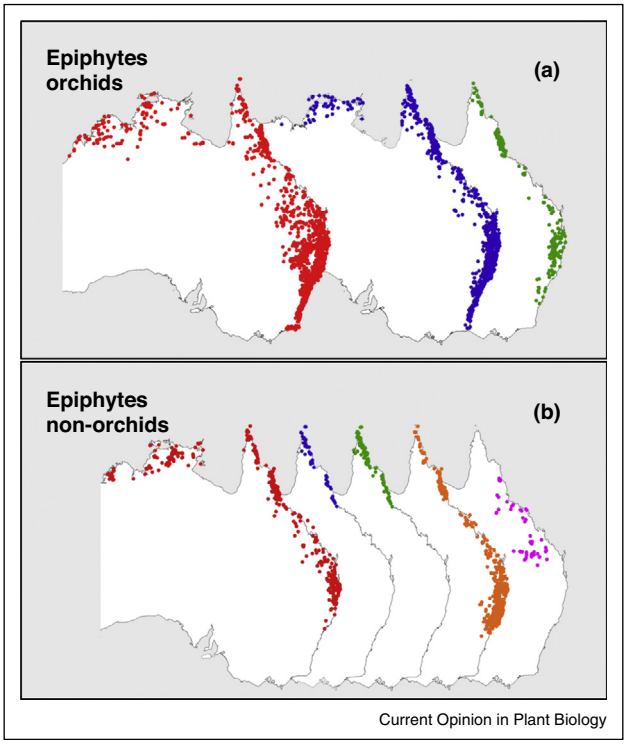
We estimate, on the basis of already documented CAM species [4] and the numbers of unsurveyed species in

Figure 3



Twenty-four hour gas-exchange by a cladode of a well-watered *Cynanchum viminale* ssp. *australe*. Gas-exchange was measured using a Licor 6400 portable gas-exchange system with a LI 6400-005 clear conifer chamber at Townsville, Australia (lat. - 19.3202994° S, 146.7623168° E) during a cloudless day in a naturally illuminated shade-house. Maximum PAR was 600 μmol m^{-2} s^{-1}.

Figure 4



Collection location of all specimens in Australian herbaria [30] of known CAM epiphytes (including lithophytes). **(a)** From left to right, the orchids *Dendrobium* and *Dockrillia* spp. (●), *Bulbophyllum* spp. (●), and other genera (●). **(b)** From left to right, *Hoya* spp. (●), the ant-plants *Myrmecodia* and *Hydnophytum* spp. (●), *Dischidia* spp. (●), *Pyrrosia* spp. (●) and the lithophytic colonial fern, *Platycerium veitchii* (●).

lineages known to include CAM taxa, that CAM is present in about 1.2% of Australian vascular plants (Table 2), roughly 255 species, of which 31% are terrestrial, 61% are epiphytes/lithophytes and 8% aquatics.

The prediction suggests there are 10× more Australian CAM terrestrial species than documented at present. We expect new CAM species to be discovered amongst the terrestrial genera in which CAM is known in Australia. There are about 30 unsurveyed *Carpobrotus*, *Crassula*, *Cynanchum* and *Microsorum* taxa. In this context, the potential incidence of CAM in *Calandrinia* (=*Parakeelya* [29]), the most species rich and geographically widespread CAM-evolving terrestrial lineage in Australia (Figure 2), has a substantial effect on our estimate. On the basis that Winter *et al.* [17] observed CAM in three of five *Calandrinia* (one identified and two unidentified species) we assumed that CAM is present in two thirds of the more than 60 *Calandrinia* species [30]. If this assumption is correct, then over 50% of the terrestrial CAM species in Australia would be *Calandrinia*. Although little is known of its origins in Australia, *Calandrinia* may be the model lineage for which ecological, geographical, and organismal trait data can be combined with phylogenetic knowledge, to explore hypotheses about how the Australian condition has selected for the sub-set of small CAM leaf-succulents present. The promise of *Calandrinia*, particularly in the context of exploring how ecological shifts may occur frequently and rapidly among closely related species [31•], is that it is widely distributed across the Australian continent, in both tropical and temperate regions and in summer and winter rainfall environments. The genus is closely related to other Montiaceae, Cactaceae and Portulaceae for which extensive phylogenetic, photosynthetic and anatomical resolution is available

Table 2

Predicted number of species with CAM in the Australian vascular flora. The Australian vascular flora was assumed to contain 21,645 species [5]. CAM plants constitute about 6% of the global vascular flora [4].

Plant habit	Predicted number of CAM species	% of Australian vascular flora
Epiphytes/lithophytes	155	0.72
Terrestrial	80	0.37
Aquatic	20	0.09
Total	255	1.18

[15,32,33,49]. A detailed study of phylogeny of Australian *Calandrinia* in the context of biogeography and historical contingency could establish how CAM and succulence are expressed in relation to where particular lineages existed in the past, the connectivity and nature/availability of different environments through time, and the relative competitive ability of new lineages and lineages that already occupy them[34,35,36••]. Did the *Calandrinia* lineage arrive by transoceanic dispersal during the Miocene when arid landscapes were expanding in Australia? Was the lineage originally temperate, tropical or arid adapted, and did it diversify rapidly? Are traits such as CAM, facultative CAM, tuber formation, or interactions with fire, soil and rainfall predictability associated with the expansion into different habitats?

We also assume CAM may exist in some members of lineages in which CAM has been reported elsewhere [see 4] but not yet in Australian taxa. These include *Bulbine* (Xanthorrhoeaceae; 5 Australian of ~80 spp. globally), *Ceropegia* (Apocynaceae; 1 of 257 spp. globally), *Cissus* (Vitaceae; 13 of 477 spp. globally), *Euphorbia* (Euphorbiaceae; ~ 30 of 2,118 spp. globally), *Senecio* (Compositae; ~110 of 3,140 spp. globally), *Peperomia* (Piperaceae; 6 of 1,929 spp. globally), *Plectranthus* (Lamiaceae; 40 of 361 spp. globally) and *Portulaca* (Portulacaceae; 19 of 150 spp. globally). Although CAM has not been reported in the asclepid *Brachystelma* (Apocynaceae; 1 of 187 spp. globally) and *Gunniopsis* (Aizoaceae; an endemic Australian genus of 14 spp.), their succulent-leaves and seasonal habit suggest CAM potential.

No Australian terrestrial CAM orchids are known and our terrestrial estimate does not assume that any exist. However, although apparently rare in orchids of the Neotropics [37], CAM occurs in terrestrial orchids of Afro-Madagascan drylands [38•]. Bearing in mind that about 80% of the roughly 1000 species of orchids in Australia are terrestrial, if CAM is prevalent in terrestrial orchids of Australian drylands, the estimated number of terrestrial CAM plants in Australia could increase markedly.

The known Australian terrestrial CAM flora, with the exception of *Cynanchum*, are small (<15 cm tall), generally ephemeral plants that inhabit clay pans, shallow depressions, seeps around rocks, dunes and saline fringes, often in sandy, gravelly or skeletal low-nutrient soils. Of the few species examined to date, again with the exception of *Cynanchum*, in none is CAM the predominant mode of photosynthesis, but all exhibit a pronounced facultative CAM component. The best documented examples are *Calandrinia polyandra* which can switch between exclusively C3 and CAM modes of photosynthesis in response to changes in water availability [25] and *Crassula sieberiana* [24].

In comparison to the terrestrial flora, pronounced CAM appears proportionally more common in the Australian epiphytes. To date the only evidence for facultative CAM in an Australian epiphyte is in the ant-plant fern *Leconopteris sinuosa* (JAM Holtum, unpublished data).

Conclusion

It is as yet unclear how the palaeohistory of landscape and climate, and the origins and composition of its flora, have resulted in the distinctive terrestrial and epiphytic succulent plant assemblages of contemporary Australia. The principal patterns emerging about CAM in the Australian flora are that the frequency of CAM is about 20% of the planetary value and CAM is about twice as common in epiphytes as in terrestrial species. Low levels of CAM with a pronounced facultative component are a predominant feature of the terrestrial CAM plants sampled in Australia to date. In epiphytes, high levels of constitutive CAM are more common, and there is evidence of facultative CAM in only one species. Confirmation of these patterns requires more extensive sampling of the Australian flora, including determinations of titratable acidity and gas-exchange.

The absence of large stem succulents in Australia also remains enigmatic. We demonstrate here that environments that support large stem-succulents may be uncommon in contemporary Australia, but they exist. There must be more to the absence of large stem-succulents than just the lack of dry environments with a predictable rainy season. Perhaps there was insufficient niche space in existing vegetation assemblages with their associated fire-regimes, or perhaps taxa with the evolutionary capacity to develop stem-succulence simply did not make it to Australia. Deeper exploration of the Australian extant succulents will surely be informative.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pbi.2016.03.018.

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