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Life-history characteristics and climate correlates of dioecious plant species in central southern Australia

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ABSTRACT

Context. The proportion of dioecious species can vary considerably among climates and habitats. However, studies often involve isolated communities or large diverse areas and fail to capture how proportions vary across diverse landscapes. **Aims.** To identify (1) life-history associations of terrestrial dioecious plant species in central southern Australia, (2) whether proportion of dioecy varies spatially across central southern Australia, and (3) whether proportion of dioecy is correlated with life-history and/or climate factors. **Methods.** Species growth form, pollination mechanisms and seed-dispersal features were extracted from herbarium databases to determine potential dioecy-linked traits. Distribution data for native terrestrial species in 66 Interim Biogeographical Regionalisation of Australia subregions were extracted from the Australasian Virtual Herbarium to calculate the proportion of total native species richness that are dioecious. Climate data for each subregion were also obtained from Terrestrial Ecology Research Network databases to investigate relationships among climate, life-history traits and dioecy. **Key results.** Woodiness, abiotic pollination and endozoochory were more prevalent in dioecious than non-dioecious taxa. Proportion of dioecy ranged from 1.7% to 8.5% among subregions and correlated negatively with annual temperature range, January to March rainfall and precipitation seasonality and with average annual daily mean, minimum, maximum and average annual minimum temperature. The highest-ranked models of dioecy incorporated the additive effects of the relative proportion of woody species and either annual temperature ranges, January to March rainfall or average annual daily maximum temperature. **Conclusions.** Dioecy was associated with woodiness, abiotic pollination and endozoochory, in line with studies of other flora, with the model of stable temperature range and woodiness being the highest-ranked model of dioecy. **Implications.** Areas with higher proportions of dioecy can be targeted for future investigations into dioecious plant ecology to aid conservation and ecosystem management.

Keywords: arid zones, climate, dioecy, environmental adaptation, life-history traits, plant reproduction, proportions.

Introduction

Dioecy, the separation of sexes to create separate male and female individuals, occurs in approximately 6% of flowering plant species (Renner 2014), but despite being a relatively rare mechanism of plant reproduction, dioecious plant species display a diversity of life histories across numerous habitats. Studies of dioecious plants have also identified correlated characteristics (see Sakai and Weller 1999 for review), including a perennial, woody habit (Renner and Ricklefs 1995; Renner 2014; Wang *et al.* 2020), fleshy fruits (Bawa 1982; Renner and Ricklefs 1995; Webb *et al.* 1999) and generalist insect- (Bawa 1980; Renner and Feil 1993; Bawa 1994) or wind-pollination (Freeman *et al.* 1979; Renner and Ricklefs 1995; Renner 2014) mechanisms.

Many of the characteristics that correlate with dioecy are related to reproductive characters associated with the separation of sexes. For example, wind pollination obviates reliance on biotic vectors transporting pollen from male to female flowers and is more common in dioecious species than in hermaphroditic species (Renner 2014), whereas generalist insect pollination of small, unspecialised dioecious flowers is another correlate of dioecy, which theoretically reduces the need for potentially rare specialised pollinators (Bawa 1982) and may also reduce the costs of geitonogamous pollination (Kohn and Casper 1992; Snow *et al.* 1996), especially for mass-flowering trees (Hessing 1988; Ishii and Sakai 2001). Correlates of fleshy fruit production and biotic seed dispersal also enable wider seed dispersal, reducing competition among seedlings and their female parents, which is typically exacerbated by dioecy (Heilbuth *et al.* 2001; Vamosi *et al.* 2007). The fleshy fruits of dioecious females can also be aggregated in larger displays, which may improve frugivore visitation and removal rates (Vamosi *et al.* 2007).

High levels of dioecy are often found in tropical to subtropical habitats such as the coastal plains of south-eastern Brazil (14%; Matallana *et al.* 2005) and the dry rainforests of northern Queensland (21%; Hansman 2001) and the Northern Territory (17.5%; Russell-Smith and Lee 1992) in Australia. Dioecy is also more common on some islands (Bawa 1982; Matallana *et al.* 2005; Renner 2014) such as Hawaii (14.7%; Bawa 1980; Sakai *et al.* 1995*a*; Sakai and Weller 1999), the Ogasawara Islands (13%; Abe 2006), Madagascar (18.4%; Vary *et al.* 2011), New Caledonia (16%; Bawa 1992) and the Barro Colorado Island, Panama (9%; Bawa 1980). The high proportion of dioecious species in island flora was suggested by Carlquist (1974) to be because dioecy was an advantage in such habitats, because the separation of sexes was thought to protect small island populations from inbreeding depression. However, recent research suggests that the dioecy–tropical habitat nexus is confounded partially by the correlation of tropical habitats with abundant woody and climbing species (Gentry 1991; Bernardello *et al.* 2001) and fleshy fruit production (Chen *et al.* 2017). Nevertheless, 31.8% of dioecious Hawaiian species arose *in situ*, rather than by dispersal to the islands (Sakai *et al.* 1995*b*), suggesting that tropical island environments favour the evolution of dioecy. Dioecy is also associated with islands in non-tropical climates, as reflected in proportions of some southern oceanic islands (10.2%; Lord 2015) and the high proportion of dioecy in New Zealand (13%; Godley 1979; McGlone and Richardson 2022), although this figure is confounded by the high proportion of colonising dioecious species, suggesting that dioecy in many instances did not arise *in situ* in New Zealand (Godley 1975, 1979; Lloyd 1985; Webb and Kelly 1993; Webb *et al.* 1999).

The proportion of dioecious species in arid habitats is much lower than that in tropical or mesic habitats, as evident from the proportions of dioecy for the Iberian Peninsula (2.2%; Amich *et al.* 2004), California (2.8%; Fox 1985) and Israel (1.7%; Rottenberg 1998). However, despite these proportions being low relative to the world average (6%), dioecious plant species reproduce successfully and are prevalent in the native floras of semi-arid and arid regions. For example, in Australia, dioecious Casuarinaceae (Wilson and Johnson 1989), Sapindaceae (Reynolds and West 1985) and Amaranthaceae subfamily Chenopodiodeae (Wilson 1984) are prominent in temperate, coastal and arid habitats. In tropical habitats of Australia, proportions of dioecious species are comparable to those of other countries, at 21.5% of northern Australian tree species (Gross 2005), 17% of northern New South Wales rainforest trees (Adam and Williams 2001), 21% of species in Queensland rainforests (Hansman 2001) and 17.5% for Northern Territory rainforests (Russell-Smith and Lee 1992); however, the prevalence of dioecy in drier, more temperate regions of Australia is less well understood.

Only three studies could be identified reporting the proportion of dioecy spanning non-tropical regions of Australia; two for south-western Australia at 4.4% (Mccomb 1966) and 5% (Lamont and Groom 2015) respectively, and one for South Australia at 3.9% (Parsons 1958). However, Parsons' (1958) state-wide study may have missed finer-scale differences in the proportion of dioecy among habitat types, because the study region included arid deserts and grasslands (<200 mm year^{-1} rainfall), denser riparian and temperate woodlands, higher-rainfall mountainous forests (>600 mm year^{-1}) and coastal regions. The proportion of dioecy reported by Parsons (1958) was therefore averaged across multiple habitat types, each with different evolutionary pressures. Additionally, although the study conducted by Mccomb (1966) encompassed a smaller area, it featured a latitudinal gradient largely defined by the coastline of Western Australia. The area covered would likely have variation in climate and abiotic stresses along the gradient and may also have missed nuances in shifts in the proportion of dioecy between climate and habitat types. Studies are rarely conducted on continuous distributions and thus may fail to account for how the proportion of dioecy might change with habitat and climate conditions across a heterogenous landscape (Fox 1985).

Understanding how dioecious plants are distributed on a larger, continuous scale of diverse habitat and climate conditions may improve our understanding of the habitats in which dioecy is most prevalent. For central southern Australia, such an investigation would also be in the absence of known correlates linked with tropical and small island habitats. Central southern Australia also provides a suitably large and climatically diverse case study area, given its habitat heterogeneity and having been the subject of previous reports of the proportion of dioecious species (Parsons 1958). We make use of the Interim Biogeographical Regionalisation of Australia (IBRA) subregions, which offer an existing framework of habitat types, to achieve this more easily. Use of the IBRA system may also allow for findings to be integrated back into the framework for conservation planning and the direction of future research. In contrast to other, broader studies of sexual systems, this study focuses specifically on dioecious plants to understand this under-researched group better. However, it is acknowledged that monoecy is another important sexuality-based reproductive strategy, particularly in Australian rainforest habitats where families with high proportions of monoecy, such as Euphorbiaceae, are abundant (Gross 2005).

Our study therefore sought to (1) quantify the number of dioecious species in central southern Australia and determine whether dioecy is associated with particular growth forms, pollination mechanism or seed-dispersal life-history characteristics, (2) use these lists of identified dioecious species to map dioecious species as a proportion of total species richness (proportion of dioecy) occurring within the 66 IBRA subregions encompassing central southern Australia, and (3) identify whether spatial variation in the proportion of dioecious species between IBRA subregions may be linked to distributions of life-history traits, climate variables, or a combination of both. Our study aimed to characterise the life-history traits of dioecious species in central southern Australia that may enable their survival there, and to identify any potential dioecious 'hotspots' for further investigation into dioecious plant evolution in central southern Australia.

Materials and methods

Identification of dioecious species

A review of the Australian Herbarium databases was undertaken to map the distribution of dioecy in the terrestrial native flora of central southern Australia, as defined by 66 contiguous IBRA subregions covering the region and spanning Mediterranean to arid climates (Fig. 1, inset map). The electronic Flora of South Australia 4th edition (eFloraSA; Barker *et al.* 2005) was also used to help determine the likely breeding systems of the native plants within the search region, supplemented with information from the online Flora of South Australia 5th edition, online floras of Victoria, New South Wales, Western Australia, Flora of Australia and The Families and Genera of Vascular Plants series (ed. Kubitzki 1993–2016), as well as some taxon-specific publications (Supplementary Table S1). Species without, or with unclear breeding-system determinations were excluded from the analyses, and where reports of breeding systems were contradictory, the eFloraSA was followed for consistency. Species were classified as dioecious so long as they were described as predominantly dioecious, or where multiple sexual systems were listed, dioecy was the first mentioned. For example, for a species described as 'dioecious, with some instances of monoecious plants' (e.g. *Allocasuarina*), or 'dioecious, or rarely polygamodioecious'

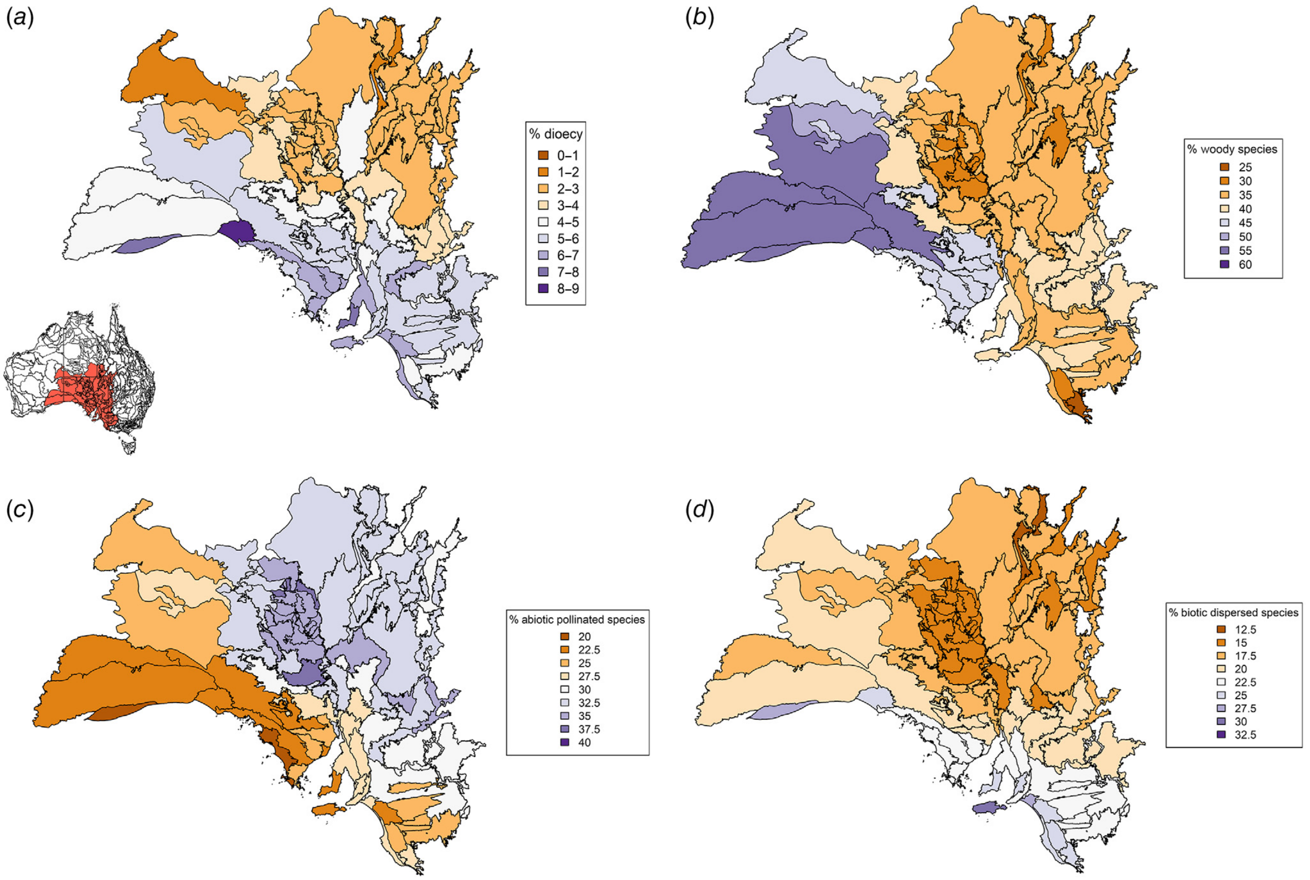

Fig. 1. Map of study region in context to Australia (filled in red, inset), and (*a*) study region coloured by the proportion of dioecious species, (*b*) species with woody growth, (*c*) species with abiotic pollination mechanisms and (*d*) species with biotic seed-dispersal mechanism of total native species richness by Interim Biogeographical Regionalisation of Australia subregions (main). Legend boxes are: (*a*) percentage dioecy from 0 to 9; (*b*) percentage woody species from 25 to 60; (*c*) percentage abiotically pollinated species from 20 to 40; (*d*) percentage biotically dispersed from 12.5 to 32.5.

(e.g. *Dodonaea*), species were classified as dioecious on the assumption that if monoecious individuals were common, the description would have classified these species as polygamodioecious. Examples of species not classified as dioecious in this study are those described as exclusively 'polygamodioecious', 'temporally dioecious' or 'monoecious or dioecious'. Finally, as the study focused on in-land species, dioecious marine plants were excluded.

Dioecious species characteristics data collection and analysis

All dioecious species were categorised by growth form (annual herb, perennial herb, shrub, tree, climbing), pollination mechanism (anemophilous, entomophilous, ornithophilous, ambophilous) and seed-dispersal method (biotic, abiotic), as determined by species descriptions of eFloraSA, other online herbaria, research articles or the Kubitzki series (Kubitzki 1993–2016), where possible, or inferred from other members of the genus or family with similar morphology. Initially, plants that were reported to have multiple trait variations (e.g. climbing or shrub growth forms; anemophilous pollination with some recorded of entomophily) had all variations recorded. Following this, trait outcomes were reduced into binary traits of woody versus non-woody, biotic versus abiotic pollination and biotic versus abiotic seed dispersal. Where species fell into both binary categories, the species was allocated to its primary mechanism, being the more prevalent and frequently occurring mechanism noted in the literature, or that most aligned with morphology. For example, although a species may initially disperse seeds ballistically (abiotically), if the most significant seed-dispersal mechanism was by ants (biotically), the species was classified as biotically dispersed. The same process was undertaken for non-dioecious species in the study area.

Species counts were cross-classified by whether they were dioecious or not and the occurrences of each of these binary traits were counted separately. The homogeneity of counts across categories was assessed using a chi-squared test of association, based on 2 × 2 contingency tables in R (ver. 4.2.1; R Core Team 2022).

Several additional chi-squared contingency analyses were also conducted to investigate the impact of large taxonomic groups and prevalent features of the Australian flora on associations of life-history traits. Because of the abundance of dioecious species within certain Australian plant families, an analysis of all life-history traits in the absence of the primarily wind-pollinated and wind-dispersed taxa of Amaranthaceae subfamily Chenopodiodeae, Sapindaceae and Casuarinaceae was undertaken. Another two analyses were also conducted, one where species with the prominent arid-zone seed-dispersal mechanism, myrmechory (Berg 1975), were removed from the dataset, whereas in the other, only species with specifically endozoochoric biotic dispersal were retained to compare rates between dioecious and non-dioecious species.

Data collection and analysis were conducted at species, and not subspecies, level, to avoid taxonomic uncertainty, because subspecies are often difficult to recognise definitively and may not have been fully investigated using morphological as well as molecular techniques.

Regarding the potential impact of phylogenetic constraints, dioecy is not considered to be constrained phylogenetically for a number of reasons. First, within many lineages, dioecy is known to be a dynamic state equally capable of being gained or lost multiple times (Goldberg *et al.* 2017); hence, it is not a dead end in evolutionary terms (Käfer *et al.* 2017). Second, transitions to dioecy occur independently from clades possessing the traits typically associated with dioecy (Vamosi *et al.* 2003), so it is unlikely that a species from a non-dioecious clade would be inhibited from transitioning to dioecy if it conferred an advantage in their habitat (Barrett 2014). Finally, and importantly in context to this study, because phylogenetic effects were found to be absent in a similar recent study of dioecy in arid zones (Ramírez 2022), a formal phylogenetic study of the species in the region was not undertaken in the current study.

Proportions of dioecious species in IBRA subregions and correlations with life-history and climate variables

Dioecy and climate

Data for dioecious species were gathered from the Australasian Virtual Herbarium database (AVH, https://avh.chah.org.au/), which includes only verified collections. These dioecious-species location data were then downloaded through the Atlas of Living Australia spatial data portal (ALA, https://www.ala.org.au/; Atlas of Living Australia 2021*a*). Species lists of all non-dioecious species occurring in the study region were also obtained using IBRA subregion filters within the AVH database and downloaded from ALA (Atlas of Living Australia 2021*b*) using species-level distributions to eliminate taxonomic uncertainty. So as to exclude non-native species, native or non-native establishment status was determined for plants from their listing in the AVH, eFloraSA, or other online herbaria if not recorded for South Australia. Dioecy percentage per subregion was calculated as the proportion of native dioecious species relative to the total number of native species in that subregion.

Raster layers of 11 climate variables pertaining to rainfall and temperature (average daily maximum, mean, and minimum temperature, annual minimum mean temperature, annual average temperature range (Bureau of Meteorology 2011*a*), average annual rainfall, average rainfall from January to March (Bureau of Meteorology 2020*a*), average number of days with rainfall >1 mm (Bureau of Meteorology 2011*b*), rainfall variability (Bureau of Meteorology 2020*b*), average precipitation, precipitation seasonality, i.e. minimum difference between months (Harwood 2019); see Table S2 for further details) were obtained from Australia's Terrestrial Environment

Research Network data portal (TERN Landscapes, https://portal.tern.org.au/) and imported into ArcGIS ver. 10.8.1.14362 (ESRI 2011). The shapefile of IBRA subregions was obtained from the Department of Agriculture Water and the Environment (2020). Using ArcGIS, 30 random points within each IBRA subregion were selected using the create-random-points tool to find a suitable average value for each subregion, because subregions varied in size and raster resolution was either 30 or 90 km. The single averaged value for each variable within each subregion was then used in subsequent analyses.

Generalised linear mixed models (GLMMs) of the proportion of dioecy for each IBRA subregion were fitted using the IBRA subregion average values of each of the 11 climate variables separately as explanatory variables. Because of the expectation of non-linear patterns of proportion of dioecy across environmental gradients, each climate variable was either included in the models as a linear term only, or as a linear plus polynomial quadratic term. As IBRA subregions are defined from vegetation characteristics, which are influenced by climate variables, it is also reasonable to expect positive spatial autocorrelation in dioecy, because neighbouring IBRA subregions may be more likely to have similar proportions of dioecy owing to proximity than are more distant subregions. Therefore, exponential spatial autocorrelation was integrated into the model as a structured spatial factor by using the package glmmTMB (Brooks *et al.* 2017) in R. Models were fitted with a Gaussian distribution rather than a binomial distribution for the variance, because despite the response variable measuring a proportion of the trait of interest, the proportion values were through the middle of the proportion range and were not towards the lower or upper boundaries (i.e. no dioecious species or all dioecious species). Hence, a Gaussian distribution appropriately explained the pattern of variance.

Life-history traits

Because dioecy, life-history traits and climate are likely to be interrelated, we also sought to understand whether climate could inform overall patterns of the life-history traits of woodiness, abiotic pollination and biotic seed dispersal at the scale of IBRA subregions. These GLMMs were fitted with life-history traits, measured as the proportion of species within each IBRA subregion with the specific life-history trait as the response variable and each of the climate variables described above being included separately as an explanatory variable.

Additionally, because the three life-history traits of woodiness, abiotic pollination and biotic seed dispersal are known correlates of dioecy in other flora, the spatial distribution of the proportion of these traits may be able to explain variation in the proportion of dioecy. Hence, we also fitted GLMMs with dioecy as the response variable and each life-history trait separately as the explanatory variable.

Dioecy–climate–life-history models

Finally, to determine whether dioecy–climate models could be improved by incorporating the effects of life history, we constructed GLMMs with explanatory variables as pairwise combinations of each climate and life-history trait variable. For these models, single life-history traits were added as linear terms; non-linear partial effects could not be explored because the sample size (restricted to the number of IBRA subregions) precluded additional model complexity.

To compare the effectiveness of the models explaining variation in the proportion of dioecy, particularly those incorporating life-history traits compared with those that did not, adjusted R^2 values of the models were used. Models were ranked by Akaike information criterion (AIC) and ordered using the AIC weights to determine which model(s) received the highest support (on the basis of how much variation is explained by the individual model while ensuring parsimony); AIC was calculated using the MuMIn package (Bartoń 2022) in R. Covariates with statistical support were then plotted to visualise the form of the relationship with dioecy by displaying predictions of the model (with confidence intervals). Adjusted R^2 of models that included individual effects of either climate or life history, or models with the additive effects of climate and life history were used to understand the contributions of each variable type.

Results

Life-history characteristics of dioecious species in central southern Australia

In all, 165 dioecious species (3.9%, see Table S1a for species list) and 3945 non-dioecious species were included in the study, for a combined total of 4110 native species within the central southern Australia study region. Of the 27 families with dioecious species, those with the greatest number of dioecious taxa were Amaranthaceae subfamily Chenopodiodeae (25), followed by Sapindaceae (19), Asparagaceae (16) and Casuarinaceae (16).

Of dioecious species within selected central southern Australian IBRA subregions, the shrub growth form was most common (53.9%), with anemophilous and entomophilous pollination systems being nearly equally common (42.4% and 41.2% respectively). The most common seed-dispersal mechanism was by abiotic vectors (47.9%) (Table 1; see Table S1b for all species life-history traits).

Chi-squared contingency analysis showed associations between dioecy and woody growth form and abiotic pollination, but not with biotic or abiotic seed dispersal ($P < 0.05$; Table 2).

The additional analyses found that the removal of the three prevalent dioecious families from the analysis, namely, Chenopodiodeae, Sapindaceae and Casuarinaceae, caused shifts in the life-history correlations of dioecy. Removing these three families from the current analysis caused dioecy to, instead, be associated with biotic pollination and biotic seed dispersal, and neither woody nor non-woody growth

Table 1. Table of dioecious and non-dioecious species counts classified by growth form, pollination mechanism, and seed-dispersal vector from the study region of 66 southern Interim Biogeographical Regionalisation of Australia subregions.

Item	Growth form					Pollination mechanism					Seed-dispersal vector		
	Herb	Perennial	Shrub	Tree	Climber	Ane	Ent	Amb	Hyd	Zoo	Bio	Abio	Both
Dioecious	5 (3.0)	49 (29.7)	89 (53.9)	16 (9.7)	6 (3.6)	70 (42.4)	68 (41.2)	21 (12.7)	6 (3.6)	0 (0)	29 (17.6)	79 (47.9)	57 (34.5)
Non-dioecious	753 (19.1)	1505 (38.1)	1367 (34.7)	291 (7.4)	29 (0.7)	769 (19.5)	2733 (69.3)	122 (3.1)	12 (0.3)	309 (7.8)	509 (12.9)	2665 (67.6)	771 (19.5)

The percentage of total dioecious and non-dioecious species are given in parentheses (see below for the total number of dioecious and non-dioecious species). $N_{\text{species-level}} = 165$; $n_{\text{non-dioecious}} = 3945$; pollination mechanisms are anemophily (Ane), entomophily (Ent), ambophily (Amb), hydrophily (Hyd), and vertebrate zoophily (Zoo); seed-dispersal mechanisms are Bio (any dispersal including a biotic vector; e.g. endozoochory, exozoochory), and Abio (any other dispersal not including a biotic vector; e.g. barochory, hydrozoochory, anemochory).

Table 2. Chi-squared comparisons of life-history traits between dioecious and non-dioecious species within the study region of 66 southern Australian Interim Biogeographical Regionalisation of Australia subregions.

Sexual system	Growth form		Pollination mechanism		Seed dispersal	
	Woody	Non-woody	Biotic	Abiotic	Biotic	Abiotic
Dioecious	**117 (70.9)**	48 (29.1)	68 (41.2)	**97 (57.8)**	54 (32.7)	111 (67.3)
Non-dioecious	1746 (44.3)	2195 (55.64)	3054 (77.3)	891 (77.4)	1089 (27.6)	2856 (72.4)
χ^2_1	45.23		113.7		2.07	
P-value	<0.001		<0.001		n.s.	

Values in parentheses are percentages; bolded values indicate the trait of association for dioecious species.
Woody growth form: trees, shrubs, some perennials and some climbers; non-woody growth form: herbs and some perennials; biotic pollination: entomophilous, ornithophilous, zoophilous; abiotic pollination: anemophilous, hydrophilous, self-pollination.

forms (see Table S3a for chi-squared association test). The removal of myrmechorous species from seed-dispersal association tests resulted in an association between dioecy and biotic seed dispersal (see Table S3b for chi-squared association test). Finally, when the biotic seed-dispersal category was reduced to only endozoochorous species, dioecy was associated with endozoochory (see Table S3c for chi-squared association test).

Proportion of dioecious species for selected central southern Australian IBRA subregions and correlation with climate and life-history variables

The proportion of dioecious species for each of the IBRA subregions varied from 1.68% to 8.52% (Fig. 1), with 11 subregions having proportions above the total angiosperm average of 6% (Table 3).

Proportion of dioecious species was highest along the coastline and decreased towards the northern subregions. The subregion with the highest proportion of dioecious species among total native species was Yalata (8.52%), on the south-western coast of South Australia, along the eastern portion of the Great Australian Bight.

The highest-ranked model identified and supported by AIC was the model with explanatory variables of annual temperature range and woodiness (adjusted R^2 0.64). The next-ranked model was substantially poorer, with a difference in AIC from the highest ranked model of 14 (see Table S4 for rankings of all models).

The additive contribution of each life-history variable relative to a model with only a climate variable was minimal in most instances (Table 4).

The life-history variables provided only marginal increases in the variance in dioecious proportion explained by spatial patterns in climate. This result is expected, given that woodiness (adjusted R^2 = 0.23, non-linear), abiotic pollination (adjusted R^2 = 0.007, linear) and biotic seed dispersal (adjusted R^2 = 0.20, linear) are not strongly associated with dioecy (see Table 4). There were some instances of increases to adjusted R^2 of >0.2 for dioecy–climate models after the addition of a life-history variable (e.g. model of dioecy with annual rainfall variability + biotic seed dispersal). However, in most instances this was due to the association between the climate variable and life-history trait, as opposed to associations with dioecy. Additionally, notable increases to adjusted R^2 did not always result in models that explained large proportions of variation, because the models of dioecy with climate had low explanatory power to begin with (e.g. average annual daily minimum and maximum temperature, average annual minimum temperature).

Seven abiotic variables and two life-history variables were found to be correlated with proportion of dioecy. Proportion of dioecy was negatively correlated with average temperature range (R^2 = 0.54), annual January to March rainfall (R^2 = 0.71) (Fig. 2), annual minimum temperature (R^2 = 0.19), average daily minimum (R^2 = 0.19), mean (R^2 = 0.40) and maximum annual temperature (R^2 = 0.50) and rainfall

Table 3. Number of dioecious species and their percentage of total species richness in each of the 66 selected South Australian IBRA subregion in the study region, with percentages above 6% in bold.

Subregion	Total species richness	Dioecious species richness	Dioecious sp. (%)	Woody sp. (%)	Abiotically pollinated sp. (%)	Biotically dispersed sp. (%)
Yalata (NUL03)	303	26	**8.58**	58.75	24.75	30.36
Hampton (HAM01)	433	34	**7.85**	59.35	21.48	33.03
Southern Yorke (EYB01)	701	50	**7.13**	44.35	23.11	30.53
Bridgewater (NCP01)	774	54	**6.98**	35.54	27.96	28.35
Murray Lakes and Coorong (MDD03)	764	53	**6.94**	42.52	28.98	30.98
Eyre Mallee (EYB05)	954	63	**6.60**	48.90	22.54	28.51
Kangaroo Island (KAN01)	887	57	**6.43**	43.49	24.80	33.71
Tintinara (NCP04)	710	45	**6.34**	43.36	23.63	30.94
Eyre Hills (EYB03)	1090	68	**6.24**	47.61	25.62	29.46
St Vincent (EYB02)	1115	68	**6.10**	43.67	28.02	27.39
Myall Plains (GAW01)	794	47	5.92	47.67	27.30	25.57
Talia (EYB04)	766	45	5.87	47.32	22.03	29.99
Murray Mallee (MDD02)	1387	81	5.84	39.86	30.86	26.59
Yellabinna (GVD06)	671	39	5.81	55.44	23.96	27.08
South Olary Plain (MDD01)	848	49	5.78	40.61	30.78	24.41
Braemer (MDD07)	391	22	5.63	44.25	34.53	24.81
Fleurieu (KAN02)	1243	68	5.47	38.03	27.84	28.48
Lowan Mallee (MDD04)	1125	61	5.42	40.09	25.75	27.71
Mount Lofty Ranges (FLB01)	1342	72	5.37	36.27	28.86	28.04
Gawler Lakes (GAW03)	709	38	5.36	45.84	29.34	22.57
Glenelg Plain (NCP02)	1007	52	5.16	29.22	29.00	27.41
Lucindale (NCP03)	873	45	5.15	31.84	26.40	27.66
Broughton (FLB02)	936	48	5.13	37.93	28.13	27.17
Gawler Volcanics (GAW02)	827	42	5.08	47.88	23.79	25.60
Murray Scroll Belt (RIV06)	795	40	5.03	39.29	31.99	24.31
Mount Gambier (SVP02)	599	30	5.01	28.09	29.38	27.21
Olary Spur (FLB03)	782	39	4.99	40.46	31.11	25.61
Maralinga (GVD03)	563	28	4.97	58.08	26.47	26.11
Central Flinders (FLB06)	894	44	4.92	40.27	28.38	25.14
Southern Flinders (FLB04)	986	48	4.87	38.54	27.59	26.37
Arcoona Plateau (GAW04)	608	29	4.77	35.86	34.65	20.85
Carlisle (NUL01)	360	17	4.72	56.39	24.44	24.17
Nullarbor Plain (NUL02)	565	26	4.60	55.75	24.96	26.19
Commonwealth Hill (GAW08)	343	15	4.37	48.40	34.40	22.16
Wimmera (MDD05)	1385	60	4.33	36.75	26.53	27.99
Bimbowrie (BHC05)	378	16	4.23	37.83	33.07	23.54
Dieri (SSD03)	462	19	4.11	39.61	33.98	22.08
Roxby (GAW07)	521	21	4.03	37.62	39.27	21.07
Northern Flinders (FLB05)	981	39	3.98	39.96	31.29	22.43
Kingoonya (GAW05)	604	24	3.97	44.70	30.46	23.68
Warriner (SSD04)	396	15	3.79	34.34	36.52	17.38
Curnamona (BHC06)	349	13	3.72	36.68	32.95	20.92

(*Continued on next page*)

Table 3. (*Continued*).

Subregion	Total species richness	Dioecious species richness	Dioecious sp. (%)	Woody sp. (%)	Abiotically pollinated sp. (%)	Biotically dispersed sp. (%)
Torrens (GAW06)	499	18	3.61	39.68	33.87	19.44
Murnpeowie (STP03)	753	27	3.59	35.59	35.86	21.12
Barrier Range (BHC01)	726	26	3.58	40.91	33.33	24.93
Barrier Range Outwash (BHC04)	444	15	3.38	40.09	35.59	22.97
Peake-Dennison Inlier (STP04)	304	10	3.29	34.21	36.18	18.09
Tieyon (FIN03)	664	20	3.01	42.77	34.34	22.59
Breakaways (STP01)	734	22	3.00	39.10	34.74	20.71
Kintore (GVD04)	541	16	2.96	51.02	27.73	24.21
Coongie (CHC06)	587	17	2.90	32.37	34.41	19.08
Witjira (STP06)	774	21	2.71	36.30	36.43	19.64
Strzelecki Desert (SSD05)	636	17	2.67	35.69	34.91	20.13
Watarru (CER02)	378	10	2.65	49.21	26.46	26.98
Oodnadatta (STP02)	807	21	2.60	36.06	35.64	19.70
Sturt Stony Desert (CHC02)	933	24	2.57	36.44	32.69	20.90
Lake Pure (CHC07)	511	13	2.54	38.16	33.86	22.50
Baltana (STP07)	642	16	2.49	33.33	36.45	19.94
Tallaringa (GVD05)	499	12	2.40	43.89	33.67	23.05
Cooper-Diamantina Plains (CHC05)	710	17	2.39	36.95	32.07	21.02
Simpson Desert (SSD02)	839	20	2.38	38.02	33.25	21.69
Macumba (STP05)	396	9	2.27	33.59	38.79	19.44
Everard Block (CER03)	574	13	2.26	41.11	34.32	23.87
Pedirka (FIN04)	341	7	2.05	36.07	32.55	22.58
Diamantina-Eyre (CHC04)	333	6	1.80	34.83	34.13	17.72
Mann-Musgrave Block (CER01)	1111	18	1.62	47.61	25.99	26.19

variability ($R^2 = 0.33$). However, whereas the linear model for January to March rainfall had the largest R^2 value, the dioecy–climate model that ranked highest (relatively) by AIC was linear average annual temperature range, where smaller annual temperature ranges were associated with higher proportions of dioecy (see Table S4 for all model AIC rankings and adjusted R^2). A likely reason for the discrepancy between the highest AIC-ranked model and the model with the highest adjusted R^2 (which both have the same number of parameters) may be a difference in the degree of spatial correlation of each abiotic variable, resulting in variance explained by each model being absorbed by the adjustment for spatial autocorrelation to different degrees. Dioecy also correlated positively with woodiness and biotic seed dispersal.

As AVH distribution data were based on collection data, which have been demonstrated to contain locational biases (Haque *et al.* 2017), a regression analysis was performed on a proportion of dioecy against the total number of records per subregion. The regression analysis showed no significant correlation between IBRA subregion proportion of dioecy and the number of sample records, i.e. sampling effort ($P > 0.05$).

Discussion

Life-history characteristics of dioecious species in South Australia and included IBRA regions

In the study region, dioecious species were most prevalent in Chenopodiodeae (*Atriplex*, *Rhagodia*, *Maireana* and *Scleroleana*), Sapindaceae (*Dodonaea*), Asparagaceae (*Lomandra*) and Casuarinaceae (*Casuarina* and *Allocasuarina*). Although being not limited to members of these groups, the prevalence of shrub and woody growth forms, abiotic (particularly anemophilous) pollination and abiotic seed dispersal among them are likely to have contributed to each of these traits being the most common traits among dioecious species in the study. This finding corroborates current understanding of characteristics most associated with dioecy (Renner and Ricklefs 1995; Sakai and Weller 1999; Renner 2014).

Table 4. Table of percentage of variation in proportion of dioecy explained by models of abiotic variables against proportion of dioecious species, abiotic variables against proportion of species with three life-history traits, and for combined models of abiotic variables and proportion of species with three life-history traits against proportion of dioecy, for 66 central southern Australian Interim Biogeographical Regionalisation of Australia subregions.

Abiotic variable	Dioecy ~ climate variable	Woodiness ~ climate variable	Abiotic pollination ~ climate variable	Biotic seed dispersal ~ climate variable	Dioecy ~ climate variable + woodiness	Dioecy ~ climate variable + abiotic pollination	Dioecy ~ climate variable + biotic seed dispersal
Annual temperature range	54	<1	7.9	66	64	57	59
January–March rainfall	71	<1	48	56	65	72	71
Average annual daily minimum temperature (QP)	19	<1	<1	<1	22	<1	45
Annual minimum mean temperature (QP)	19	<1	14	5.3	20	20	49
Average annual daily mean temperature (QP)	40	4	23	47	40	43	57
Average annual daily maximum temperature (QP)	50	5.9	16	53	63	58	62
Annual rainfall variability	25	1.9	47	62	28	27	47

(QP) indicates that climate variable in the model is a quadratic polynomial term: models are written as 'response variable ~ explanatory variable 1 + explanatory variable 2'; dioecy is the proportion of native dioecious species richness of total native species richness for the IBRA subregion; woodiness is the proportion of native species richness of total native species richness for the IBRA subregion that possess woody growth forms; abiotic pollination is the proportion of native dioecious species richness of total native species richness for the IBRA subregion that utilise abiotic pollen vectors (anemophily, hydrophily, etc.); biotic seed dispersal is the proportion of native dioecious species richness of total native species richness for the IBRA subregion that utilise biotic seed-dispersal vectors (endozoochory, exozoochory, myrmechory, etc.).

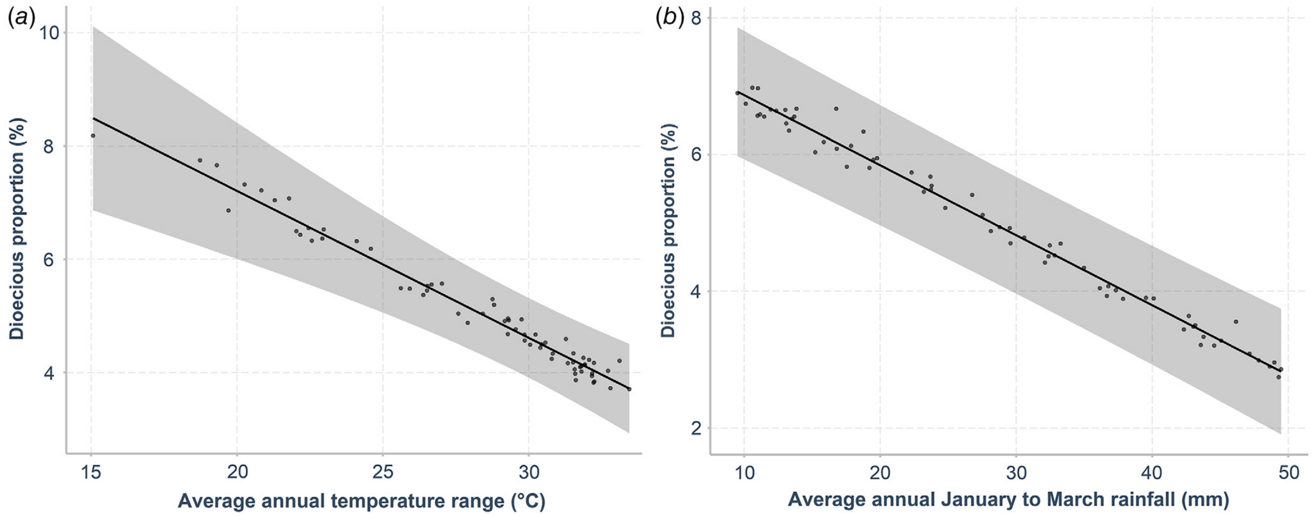

Fig. 2. Effect plots of predicted proportion of dioecious species of native species richness in Interim Biogeographical Regionalisation of Australia subregions against (*a*) annual temperature range, and (*b*) January–March rainfall. Solid lines show relationships, shaded bands are 95% confidence regions, and solid points are partial residuals.

Wind pollination (Renner and Ricklefs 1995; Weller *et al.* 1998) and woody growth forms (Renner and Ricklefs 1995; Webb *et al.* 1999; Renner 2014; Wang *et al.* 2020) have been frequently associated with dioecy in other floras. Wind pollination and dioecy are well paired with each other, because the separation of sexes prevents self-pollination

(Renner 2014). Adaptations favouring abiotic pollination also reduce the reliance on insect populations in pollinator-poor habitats such as arid zones (Freeman *et al.* 1979; Vamosi and Otto 2002). Because of the benefits of wind pollination, combined with dioecy in arid zones, and given the abundance of wind-pollinated Chenopodiodeae, Sapindaceae and Casuarinaceae in arid zones, the finding of an association between dioecy and woodiness and abiotic pollination is unsurprising. Whereas no association was found when comparing biotic and abiotic seed dispersal, biotic seed dispersal is another trait correlated with dioecy (Heilbuth *et al.* 2001; Barot and Gignoux 2004; Vamosi *et al.* 2007). Compared with other native flora, myrmechory is common in arid Australia and is thought to have arisen there in response to aridification during the late Tertiary (Berg 1975). As myrmechory is less prevalent in other native floras (Lengyel *et al.* 2010), the inclusion of this form of biotic dispersal may have affected the investigation of associations of seed-dispersal vector. In the additional tests where myrmechorous species were removed or re-classified as abiotically dispersed, and the tests where biotic seed dispersal is reduced to only endozoochory, dioecy was found to be associated with biotic dispersal and endozoochory in both instances. Hence, the prominence of myrmechory is a feature of the study region (Davidson and Morton 1981) that may have influenced the test and conclusions of associations.

Removing the predominantly woody, abiotically pollinated and/or dispersed Chenopodiodeae, Sapindaceae and Casuarinaceae caused a shift in the life-history associations of dioecy (see Table S3a for chi-squared association test). Such shifts in life-history associations in the absence of large predominantly dioecious groups have been seen before, particularly in the Cape flora in the absence of Restionaceae (Steiner 1988). As dioecy is typically associated with woodiness (Renner and Ricklefs 1995; Renner 2014; Wang *et al.* 2020), the association of dioecy with neither woody or non-woody growth forms after removal may indicate that central southern Australia has more non-woody dioecious species than is typically seen. The association of the remaining dioecious species with biotic pollination by insects, of which dioecious species had non-specialist pollination by a variety of insects, is similar to the findings in other studies of dioecy (e.g. Bawa 1980, 1982; Sakai and Weller 1999; Borkent 2004). Although not analysed statistically in this study, many of the insect-pollinated dioecious species also possess small, pale flowers (e.g. *Lomandra*, *Logania* and *Pimelea* spp.), which is also listed as a potential correlate with dioecy (Bawa 1980; Muenchow 1987; Sakai and Weller 1999).

Proportion and distribution of dioecious species and correlation of abiotic variables

For the central southern Australian IBRA subregions studied here, the overall proportion of dioecious species of native plants was low (3.9%), but were comparable to previous estimates. In particular, Parsons (1958, table 1) reported the proportion as 3.9%, albeit a miscalculation because the percentage of dioecious species in his table calculates to 4.1%; hence, figures are approximately unchanged since previously studied. However, there was considerable variation among subregions in the current study (1.68–8.52%). Notably, 11 subregions had proportions above the world average of 6%, of which 10 were adjacent to coastlines, such as the Eyre and Yorke peninsulas and eastern portion of the Great Australian Bight. In contrast, even the highest subregion proportion seen in our study was considerably lower than those seen in tropical regions of Australia (Russell-Smith and Lee 1992; Adam and Williams 2001; Hansman 2001; Gross 2005).

Overall, higher proportions of dioecious species were associated with climate conditions including stable annual temperature ranges, low summer rainfall, low rainfall variability and overall lower temperatures. This group of significantly correlated variables appears to indicate that higher proportions of dioecy may be associated with habitats where increased temperature and/or rainfall stability, low summer rainfall and lower annual and daily temperatures are apparent.

Dioecy was best explained by the additive effects of annual temperature range and the proportion of woodiness; the proportion of dioecy is predicted to be high where temperature ranges are narrow and proportion of woodiness is high, criteria that commonly occur in coastal IBRA subregions. Also, additive effects of either total rainfall (January–March) or temperature (average daily maximum) and the proportion of woody species ranked lower, but explain the substantial variation in the proportion of dioecious species. Dioecy was also correlated with climate conditions of low January to March rainfall and low maximum daily temperatures, which are also features of coastal areas.

Relatively small increases in variation explained by models with the additive effects of climate and life-history traits are partially informed by the strength of correlation of these variables to dioecy. The distributions of woodiness and biotic seed dispersal were significant spatial correlates of dioecy; however, at best, these models were able to explain only 20% of variation in the proportion of dioecy among IBRA subregions. Hence, in most cases, the increase to the fit of a model through addition of the distribution of a life-history trait was marginal, indicating the existence of relatively weak spatial associations between dioecy and each life-history trait.

Because dioecy is capable of being lost or gained (Goldberg *et al.* 2017; Käfer *et al.* 2017) and whether or not a species becomes dioecious is largely a product of the state being favoured in their current environment (Barrett 2014). Hence, the relatively short scale of time from which the climate variables were averaged (30–100 years) may, nonetheless, be reflective of the conditions under which dioecy may thrive. Our study appears to indicate that coastal environments in the study region support dioecious species compared with inland habitats. Dioecy has often been associated globally with island systems (Bawa 1982; Sakai *et al.* 1995*b*), which naturally contain coastal habitats. Coastal habitats are also prevalent with woody species (Gentry 1991; Bernardello *et al.* 2001), which was correlated with dioecy in this and other studies (e.g. Renner and Ricklefs 1995; Sakai *et al.* 1995*a*; Renner 2014). Comparative studies of dioecy in coastal systems relative to tropical or inland habitats were not able to be found.

It is difficult to determine the underlying drivers of dioecy appearing to be prominent in coastal subregions. Dioecy is proposed to be beneficial in environments that are abiotically stressful because of the advantage of independent development of sexes (Darwin 1877; Bawa and Opler 1975; Freeman *et al.* 1979; Barrett 1992); however, the climate variables associated with dioecy in our study were narrower temperature ranges, less harsh day-time temperatures and less variable rainfall. Inversely, the typically deemed stressful habitats of central Australia, characterised by high temperatures and large ranges in temperature (Smith and Morton 1990), combined with low, variable rainfall (Bureau of Meteorology 2017), had lower proportions of dioecy. Arguably, coastal regions could be considered abiotically stressful environments and competitive environments (Frank 1989; Martinez 2003) owing to factors outside of the climate variables in this study. For example, South Australian coastal areas have highly alkaline soil pH (Department of Environment and Water 2021), low nutrients (although not as low as in arid zones; Viscarra Rossel *et al.* 2014*a*, 2014*b*, 2014*c*), high salinity (Department of Environment and Water 2021) and extensive erosion (Bourman *et al.* 2016). Thus, the elevated abiotic stress present in coastal regions may have contributed to dioecy being a competitive advantage in these systems, potentially resulting in a high proportion of dioecy among species growing in coastal subregions. Further study into the competitive abilities and succession dynamics between dioecious and hermaphrodite species in habitats with high proportions of dioecy would be required to properly evaluate this theory.

Finally, a factor to consider in the calculation of proportions of dioecy by IBRA subregion is that calculations are based on collection data from the AVH. Despite finding no association between the number of records per subregion (sampling effort) and proportion of dioecy, there may still have been an effect of collection bias. Thus, as with the underrepresentation of floristic diversity on remote inlands in Australia (Kier *et al.* 2005), this bias could have exacerbated the apparent coastal effect seen in our study.

Conclusions

As a group, the proportion of dioecious species in central southern Australia was low at 3.9%, similar to findings of Parsons (1958) nearly 50 years ago. Dioecy was also found to be associated with woodiness, abiotic pollination and endozoochory relative to non-dioecious species, in agreement with previous work. However, at a higher-resolution IBRA subregion scale, proportion of dioecy ranges between 1.68% and 8.52%, suggesting spatial variation in the numbers of dioecious taxa amongdifferent regional habitats. Our results demonstrated that using IBRA subregions as a basis for partitioning diverse landscapes can lead to a more thorough understanding of the spatial variation in the proportion of dioecy.

While there were weak to absent associations between proportion of dioecy and the distribution of life-history traits of woodiness, abiotic pollination and biotic seed dispersal of IBRA subregions, stronger associations were found between dioecy and climate variables. Dioecy was also correlated with annual temperature ranges and summer rainfall, where greater proportions of dioecy were more likely to occur in regions with stable temperature ranges and low summer rainfall. The highest-ranked model of dioecy incorporated variables of annual temperature range and woodiness, with low support for all other models tested. The prevalence of a few major dioecious lineages that dominate the landscape, in combination with narrow-range coastal endemics, may be obscuring our understanding of the environments in central southern Australia that may promote dioecy as a competitive advantage.

Further study, focusing particularly on non-climatic abiotic attributes, may help show the factors influencing this variability of dioecy across the study region. The identification of habitats with relatively higher proportions of dioecious species may also be beneficial to future research into the ecology and physiology of dioecious species, so as to understand the drivers of their prevalence in harsh environments.

Supplementary material

Supplementary material is available online.

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