



Projected climate change implications for the South Australian flora

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Abstract: South Australia has warmed since 1950 and further temperature increases are forecast this century. We explore the implications of climatic warming for individual plant species and the State's plant biodiversity, which is significant and includes 418 endemic taxa. Environmental constraints and interspecific interactions operate on species to determine which survive in which environment, with resulting compositional signatures. Climate change influences such 'filtering' processes via mechanisms such as altered mortality or recruitment rates and indirectly through fire regimes. While modest environmental changes can be absorbed within a given ecological community, significant change will eventually drive species turnover.

We use the Hopbush, *Dodonaea viscosa* subsp. *angustissima* (DC.) J.G.West as a case study that shows morphological adaptations to arid conditions (narrower leaves and higher stomatal densities), observed in more northern populations in South Australia. Leaves of this species have narrowed through time in conjunction with climatic warming, matching predictions from the spatial cline. Genomic sequencing has also revealed genetic correlations with temperature and aridity, suggesting key climate change variables are impacting the selection of functional genes including those linked to leaf characters. Despite such adaptations in individual species, plant community composition is sensitive to small changes in climate. As a result, predicted climatic changes may ultimately drive complete species turnover, if the more severe scenarios are realised.

Spatial analysis highlights a climatic transition zone, between desert and Mediterranean South Australia, where community composition changes more rapidly with climate and this area is therefore likely to be more vulnerable to climate change. Notwithstanding potential evolutionary adaptation, significant climate change will influence ecophysiology, leading to changes in primary productivity and water stress and is predicted to ultimately lead to lower species richness, altered species composition and more uneven abundances. Although we have an empirical understanding of climate sensitivity for South Australian plant communities, we need sophisticated ecological forecasting that considers complex interactions with fire, habitat configuration and evolutionary adaptation.

Keywords: South Australia, climate change, ecological community, climate sensitivity, ecophysiology, plant biodiversity, functional genes

Introduction

Climate change has emerged as a key threat to global plant biodiversity, exacerbating impacts that include habitat clearance and fragmentation, invasive species, pathogens and eutrophication (Gitay *et al.* 2002; Lawson *et al.* 2010). Changes to fire management regimes are also compounded by climate change and fertilisation from increasing atmospheric carbon dioxide. Managing the resultant heightened fire risk (Hughes 2003; Hennessy *et al.* 2005) for biodiversity outcomes is increasingly difficult in populated and peri-urban landscapes (Gill *et al.* 2014; Bardsley *et al.* 2015). Major historical changes in climate are

implicated in the development of the South Australian flora throughout the Cenozoic period (McGowran & Hill 2015; Hill *et al.* 2018). Major shifts have been documented in the fossil record of wet-tropical forests and *Nothofagus*-dominated warm-temperate forests transitioning through major cooling and drying episodes during the Oligo–Miocene (Hill 2001), finally leading to the more recent expansion of woodlands dominated by *Eucalyptus*. Yet at management-relevant time scales, global species assemblages are changing measurably (Dornelas *et al.* 2014) and studies concentrated in the Northern Hemisphere have found relatively rapid poleward and uphill shifts in terrestrial ecosystems linked to recent global warming

(Peñuelas & Boada 2003; Walther 2010; Grimm *et al.* 2013). Similarly, herbarium records of macroalgae collected since 1940 along the west and east coasts of Australia suggest a significant poleward shift in species assemblages (Wernberg *et al.* 2011; but see also Huisman 2012). Understanding the implications of climate change is critical to appropriate planning and prioritisation for conservation and restoration, leading to informed management decisions that take into account the implications of future climate scenarios. Here, we explore the implications of observed and projected climatic warming on the flora of South Australia, from physiological and morphological consequences for individual species, to regional-scale predictions of changes to biodiversity.

The South Australian flora includes 418 endemic taxa, with plant biodiversity (measured according to various metrics from species richness to more sophisticated measures such as phylogenetic endemism; Rosauer *et al.* 2009) concentrated within a small number of localised centres, notably western Kangaroo Island, the southern Mount Lofty Ranges and the southern Eyre Peninsula (Guerin *et al.* 2016). From a conservation and land management perspective, managers need to know how this native biodiversity will respond to future challenges and where and how to invest in restoring the landscape (Christmas *et al.* 2016b). In addition to the conservation perspective, climatic warming and increasing atmospheric carbon dioxide levels may also create challenges around the management of introduced plant species (Kriticos *et al.* 2003) and is expected to make weed management more challenging in agricultural settings (Hayman & Sadras 2006), with similar challenges likely for conservation areas.

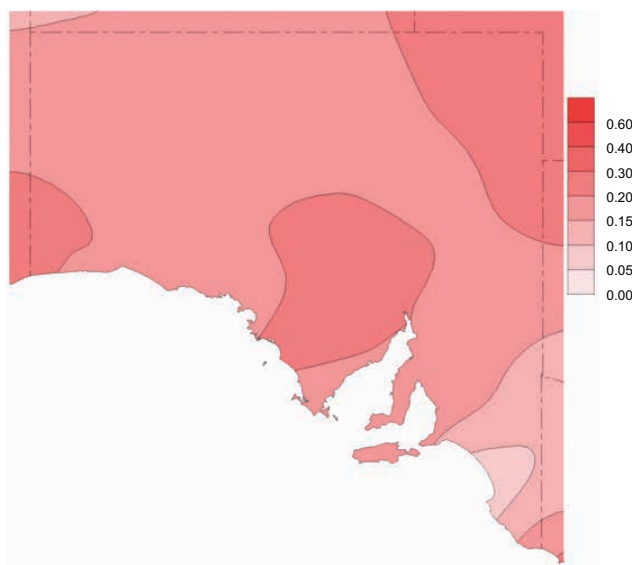


Fig. 1. Map of South Australia showing the trend in mean annual surface temperatures from 1950 to 2016. Legend represents °C per decade. Source: Bureau of Meteorology (<http://www.bom.gov.au/climate/change/#tabs=Tracker&tracker=timeseries>, accessed 21 June 2016 under Creative Commons (CC) Attribution 3.0).

South Australia's climate - recent past and near future

South Australia has experienced a significant warming trend with mean surface temperatures rising regionally by 0.5–1.5°C since 1950 (Fig. 1). Climate forecasts suggest that over the course of this century, the State will experience in the order of two degrees (or more) of warming and a ten percent decrease in rainfall over a 1986–2005 baseline, depending on if, or when, carbon pollution peaks (Charles & Fu 2015). There is predicted to be relatively more warming, but less drying over northern regions of the State. Predicted rainfall decreases will also lead to increased solar radiation due to reduced cloud cover. The South Australian climate is seasonally variable with wild plants needing to persist through periods of drought and heat waves. Underlying this apparent resilience to seasonal and inter-annual climatic variation, though, is emerging empirical evidence of a flora that is sensitive to changes in long-term climate which are small relative to seasonal variation.

A framework for climate change ecology

The composition of plant communities (Community assembly) provides a general context for understanding climate change influences on floral diversity. Community assembly is often visualised as a set of environmental constraints acting to locally filter species out of a regional pool (Hille Ris Lambers *et al.* 2012). At the scale of a habitat patch, species that have passed through these filters are capable of survival and may be present if they can disperse to the patch and compete effectively with other species (Kraft *et al.* 2015). These processes generate particular signatures of composition, functional attributes and relative abundance. Climate change affects which species are able to survive in a given location and their competitive ability, directly via mechanisms such as altered mortality or recruitment rates and indirectly, for example through induced changes to fire regimes (Hughes 2003). Modest changes to community level eco-physiological constraints (such as photosynthetic rates and water balance) can be absorbed within an ecosystem through mechanisms such as shifts in morphology, relative abundance or performance, while more significant environmental change is expected to result in species turnover to meet newly imposed physiological constraints (Suding *et al.* 2008; Guerin *et al.* 2014b).

Climate has associations with geographic range, morphology and evolutionary adaptation

A range of empirical studies have been undertaken to measure climate effects on South Australian plant species and biodiversity (Guerin *et al.* 2012; Crossman *et al.* 2012; Summers *et al.* 2012; Guerin & Lowe 2013a; McCallum *et al.* 2014; Hill *et al.* 2015a, 2015b). Individual species are frequently found to have readily observable responses to climatic regime.

An example is the Hopbush, *Dodonaea viscosa* subsp. *angustissima* (DC.) J.G.West, which, in its more northerly distribution, has leaves that are narrower, but with higher stomatal densities (Guerin *et al.* 2012; Hill *et al.* 2015a; Fig. 2). Such variation indicates adaptation for higher temperatures, because narrower leaves are better for convective heat loss, while dense stomata can be used for rapid evaporative cooling or short periods of rapid growth when moisture is available (Guerin & Lowe 2013b). Indeed, leaves of this species were shown to have become 40% narrower in conjunction with climatic warming in South Australia, matching predictions from the spatial cline in leaf width with maximum temperatures (Guerin & Lowe 2013b).

Analysis of genomic variation in population samples of *D. viscosa* subsp. *angustissima* revealed significant genetic correlations with temperature and aridity along a latitudinal gradient in South Australia (Christmas *et al.* 2016a). Genetic variation among 17 populations distributed along a ~700 km latitudinal transect was identified through sequencing of a set of 970 genes. Gene-environment association analysis of 8,462 single nucleotide polymorphisms (SNPs; a form of genetic variant) identified 55 SNPs that showed significant correlations to temperature and water availability and a further 38 SNPs correlating with elevation, suggesting that allele frequencies of these SNPs have been shaped by environmental selection on these populations.

The functions of the genes containing significant variants were diverse and included genes with products related to aquaporins and abscisic acid (both of which play roles in water transport across cell membranes; Kaldenhoff *et al.* 2008), as well as genes with products related to a variety of environmental stressors such as

water deprivation, salt stress and cold. Interestingly here, a number of genes relating to stomata and leaf shape were found to contain variants that significantly correlated with environmental factors, providing a potential link between genotypic variation and the phenotypic variation observed by Guerin *et al.* (2012) and Hill *et al.* (2015a).

Similar morphological correlations with climate were reported across the spatial range of *Melaleuca lanceolata* Otto in South Australia (Hill *et al.* 2015b), where leaves became narrower, but stomatal density increased north along a latitudinal gradient closely associated with summer maximum temperatures. While climate is clearly involved in shaping morphological patterns within species, it is not yet known how common such responses are among species or whether the capacity to physiologically track climate change via plasticity or evolutionary adaptation is enough to act as a buffer against larger scale changes to species composition.

McCallum *et al.* (2014) combined distribution modelling with population genetic data for the needle bottlebrush (*Callistemon teretifolius* F.Muell. = *Melaleuca orophila* Craven), a shrub endemic to the Mount Lofty and Flinders Ranges, to determine its vulnerability to climate change. Projected climate change had significant impacts on the modelled area of suitable habitat and its intersection with formally protected areas. The area of suitable habitat in the Flinders Ranges National Park was predicted to decline by 41% for a scenario involving 1.5°C warming and 9% decrease in mean annual rainfall (a prediction at the lower end of currently accepted scenarios). Areas of predicted high future habitat suitability coincided with the most abundant and genetically diverse populations in the southern Flinders Ranges, highlighting this region as a potential refugium and hence a priority for management for conservation. Populations elsewhere were predicted to face challenges due to lowering of habitat suitability and low genetic diversity and adaptive capacity, notably in areas such as the northern Flinders Ranges, where the species occurs in fewer numbers, generally only at high altitude and is grazed intensively by feral goats (pers. obs.).

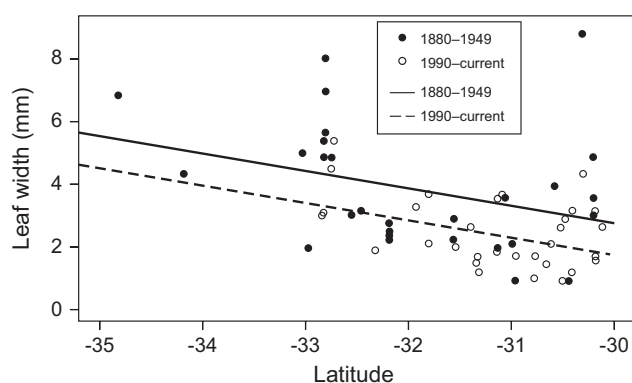


Fig. 2. A shifting latitudinal cline in the leaf width of *Dodonaea viscosa* subsp. *angustissima*, a functional trait linked to performance in convective and evaporative cooling (Guerin *et al.* 2012). Leaves from herbarium specimens collected at more northerly latitudes in the Flinders Ranges are narrower (linear regression lines shown). This spatial pattern has moved approximately three degrees of latitude south. The very strong spatial association of leaf width with summer maximum temperatures, particularly, suggests that this shrinking trend may be linked to warming since 1950 of over 1°C in this region (although involvement of increasing atmospheric carbon dioxide concentration is not ruled out).

Ecological communities in South Australia are sensitive to climate

While projected changes in phenotype and distribution for individual species give detailed insight into the potential climate change responses in the flora, the detection of more general patterns relies on analysis of ecological communities. At a regional level within South Australia, there is evidence that plant community composition is sensitive to changes in climate of a magnitude already experienced or projected for the near future. Transition zones are particularly sensitive to species turnover (Guerin *et al.* 2013) with the highest proportional rate of species turnover occurring in these areas, while temperature increases and rainfall decreases

(in the order of those projected for severe scenarios for example +3.8°C and -30% mean annual rainfall) would drive complete turnover in species composition with associated transitions among dominant families from Ericaceae, Myrtaceae and Proteaceae to Amaranthaceae, Malvaceae and Sapindaceae (Guerin *et al.* 2013). Quantitative field data have further demonstrated that there are climate-related patterns in key community metrics such as species richness. One such pattern is a trend towards more uneven allocation of biomass among species with decreasing rainfall, leading to lower diversity and altered ecosystem processes generally (G.R. Guerin, unpubl. data).

Spatial climate sensitivity analysis at regional and State level has highlighted a major climatic transition zone between desert- and Mediterranean-climate biomes of South Australia where community composition changes more rapidly with climate, along with shifts in family-level composition and vegetation structure (Guerin *et al.* 2013, 2016). This transition zone occurs in a band across the northern side of the Eyre Peninsula, includes much of the Flinders Ranges and extends southward down the eastern side of the Mount Lofty Ranges (Fig. 3). Of the State's plant biodiversity centres, the southern Flinders Ranges has been identified as the most climate sensitive according to this pattern (Guerin *et al.* 2016), whereas the other centres are in areas predicted to be less sensitive, although potentially less resilient due to higher levels of historical habitat loss and modification. This ecotone is expected to be the

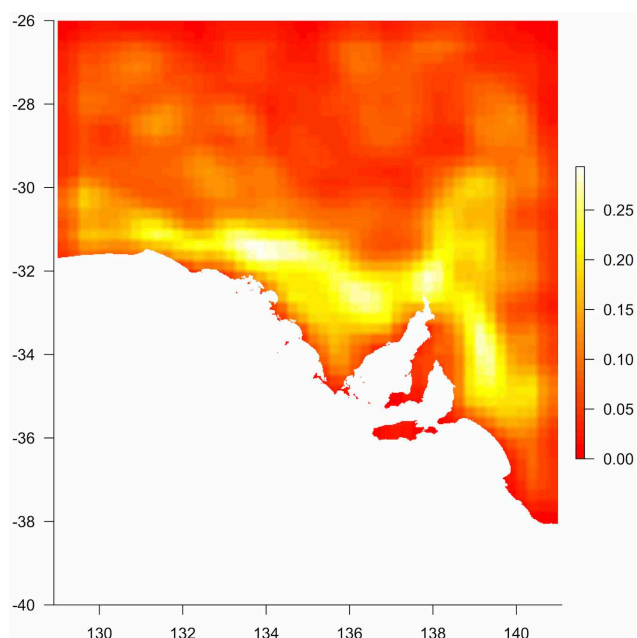


Fig. 3. Modelled spatial sensitivity of regional species composition to climate (mean maximum temperature of the warmest month). The scale shows the relative rate at which composition (represented by position along a constrained ordination axis) changes. Areas with high turnover with respect to spatial differences in climate (northern Eyre Peninsula, Flinders Ranges, eastern side of the Mount Lofty Ranges) have been interpreted as a climatic transition zone. Reproduced from Guerin *et al.* (2016).

most sensitive to climate change, although ecological resilience is a function of other landscape stressors such as levels of habitat fragmentation and grazing pressure and not just climate sensitivity *per se*.

Summers *et al.* (2012), Crossman *et al.* (2012) and Guerin & Lowe (2013a) assessed the combined vulnerability of multiple plant species to climate change for specific regions within South Australia using Species Distribution Modelling, a technique that predicts species distributional responses to environmental change based on the association of recorded occurrences with environmental variables. Summers *et al.* (2012) found a zone of generally higher vulnerability within the Murray Darling Basin Natural Resource Management region along the eastern Mount Lofty Ranges, a transition zone between predominately woodland and mallee growth-form dominated systems.

A similar pattern was found by Guerin & Lowe (2013a), which corroborates the results of community level sensitivity analyses (Guerin *et al.* 2013, 2016), in which turnover patterns across this transition were interpreted as a climatic ecotone. Crossman *et al.* (2012) examined the Mount Lofty Ranges region and identified the central ranges as a high priority area for reducing climate change vulnerability, based on a metric that highlights areas predicted to remain suitable for species that have overall high sensitivity across their range and where habitat is located near to known populations. These cooler, wetter parts of the ranges also contain the least fragmented vegetation in the region and have been shown to be the least sensitive to climate change in terms of species composition (Guerin & Lowe 2013a; Guerin *et al.* 2013). This highlights a difficult dichotomy for climate change conservation planners between on-ground action to increase resilience in regions where change may be the greatest, versus conserving those regions that are potential refugia. Both refugia and transition areas are important, but management may need to focus on maintaining the condition of current ecosystems versus active adaptation for dynamic ecosystems, respectively.

Studies to date on the climate sensitivity of South Australian plant communities have relied on spatial analysis, in which the influence of climate is disentangled from the influence of space and landscape factors. While this 'space-for-time' approach is widely accepted, one of the main limitations is that these models cannot predict the rate at which communities will respond through time, only the rate of change per unit climate, and need validation through longitudinal or experimental studies (Dunne *et al.* 2004). Some changes may occur quite rapidly, as has been observed in northern Hemisphere systems, for example the encroachment of Mediterranean ecosystems into compositionally distinct cold-temperate ecosystems in Europe (Peñuelas & Boada 2003), while larger structural changes may take many years to play out due to time lags, for example due to long-lived trees

persisting even if recruitment is no longer possible (Davis 1986; Svenning & Sandel 2013).

While climate is clearly an important driver of plant communities in terms of attributes such as primary productivity, species composition, vegetation structure and the relative competitiveness of C₃ versus C₄ grasses (Hughes 2003), it is important to note that species turnover, through space in particular, is high generally and driven by a range of factors, including soil chemistry and texture, topography, fire regimes, dispersal limitation, history and chance (such as demographic noise). Similarly, species turnover through time will be influenced by climatic regime, but also factors such as disturbance regimes, demography and chance.

The South Australian flora in a warmer, drier climate

We expect climate change to influence the ecophysiology of individual plants, leading to changes in patterns of primary productivity and water stress. Beyond the limits of evolutionary adaptation, which are still being explored through on-going research, significant climate change in South Australia is predicted to ultimately lead to lower species richness, altered species composition and higher biomass appropriation by dominant species, via differential performance in processes such as mortality, recruitment and growth. The desert–Mediterranean-climate ecotone and landscapes with lowered resilience due to high levels of habitat fragmentation or grazing pressure may be at most risk. This situation will require careful risk management with the flexibility to promote adaptation in native and restored ecosystems to plan for changed conditions (Stein *et al.* 2013).

Focus on the known and potential impacts of climate change on the flora should be tempered by considering the broader conservation situation, particularly across the more heavily impacted southern agricultural regions of the State. In these regions, there has been 70–100% destruction of local native habitats since European settlement (Guerin *et al.* 2016) and fragmented habitats are also highly modified (McIntyre & Hobbs 1999). The resulting impacts on environmental conditions (e.g. light, soil nutrients), population sizes and recruitment can be significant. While climate change is expected to compound both pressures on remnant habitats and challenges for conservation practitioners, the plight of species and habitats threatened now by the impacts of landscape change may be even more urgent than action to deal with potential changes to climate at a decadal scale. Climate change may be most relevant for management of highly climate sensitive transitional zones (Guerin *et al.* 2013) and for longer-term conservation planning, while immediate priorities also include maintaining condition through management of fire and grazing regimes, for example, to maximise general resilience and persistence of populations.

A baseline for on-going monitoring

A network of field plots known as TREND (transect for environmental monitoring and decision-making) has been established along the Adelaide Geosyncline and is supported by the Terrestrial Ecosystem Research Network (TERN) to monitor changes in plant biodiversity due to climate change and to validate spatial models of climate sensitivity (Guerin *et al.* 2014a). Early data include baselines for vegetation composition and structure plus subsequent measures of variability due to seasonal differences and time since fire. We have a good empirical understanding of South Australian plant communities and their sensitivity to climate change. However, we need to be more sophisticated in our approach to forecasting the ecological impacts of climate change because there are complex interactions between biodiversity, biomass and fire (Hennessy *et al.* 2005), habitat fragmentation and evolutionary adaptation, to name just a few of the relevant factors. With a range of information from empirical studies, modelling, monitoring data and spatial information, we are now able to develop process-based landscape models that can project ecological constraints and diversity under a range of future climate and management scenarios.

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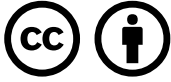
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