

Assessing the vulnerability of plant functional trait strategies to climate change

Samuel C. Andrew¹  | Rachael V. Gallagher^{2,3}  | Ian J. Wright^{2,3} | Karel Mokany¹ 

¹CSIRO Land and Water, Canberra, Australian Capital Territory, Australia

²Hawkesbury Institute for the Environment, Western Sydney University, Penrith, New South Wales, Australia

³Department of Biological Sciences, Macquarie University, Sydney, New South Wales, Australia

Correspondence

Samuel C. Andrew, Land & Water, CSIRO, Acton, ACT, Australia.
Email: sam.andrew@csiro.au

Funding information

RVG was supported by an Australian Research Council DECRA Fellowship (DE170100208). All authors acknowledge the hard work of data custodians who made their trait observations available via the AusTraits database.

Handling Editor: Arndt Hampe

Abstract

Aim: Our ability to understand how species may respond to changing climate conditions is hampered by a lack of high-quality data on the adaptive capacity of species. Plant functional traits are linked to many aspects of species life history and adaptation to environment, with different combinations of trait values reflecting alternate strategies for adapting to varied conditions. If the realized climate limits of species can be partially explained by plant functional trait combinations, then a new approach of using trait combinations to predict the expected climate limits of species trait combinations may offer considerable benefits.

Location: Australia.

Time period: Current and future.

Methods: Using trait data for leaf size, seed mass and plant height for 6,747 Australian native species from 27 plant families, we model the expected climate limits of trait combinations and use future climate scenarios to estimate climate change impacts based on plant functional trait strategies.

Results: Functional trait combinations were a significant predictor of species climate niche metrics with potentially meaningful relationships with two rainfall variables ($R^2 = .36$ & $.45$) and three temperature variables ($R^2 = .21$, $.28$, $.30$). Using this method, the proportion of species exposed to conditions across their range that are beyond the expected climate limits of their trait strategies will increase under climate change.

Main conclusions: Our new approach, called trait strategy vulnerability, includes three new metrics. For example, the climate change vulnerability (CCV) metric identified a small but important proportion of species (4.3%) that will on average be exposed to conditions beyond their expected limits for summer temperature in the future. These potentially vulnerable species could be high priority targets for deeper assessment of adaptive capacity at the genomic or physiological level. Our methods can be applied to any suite of co-occurring plants globally.

KEYWORDS

Australian plants, future climates, hierarchical GAMM, life history traits, plant communities, threatened species

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2022 Commonwealth Scientific and Industrial Research Organisation. *Global Ecology and Biogeography* published by John Wiley & Sons Ltd.

1 | INTRODUCTION

Preventing the loss of biodiversity and the degradation of ecosystems is an urgent challenge for scientists and governments (Bergstrom et al., 2021; Díaz et al., 2019). The impacts of climate change are already being felt and timely action is needed to help protect the most vulnerable species (Coleman & Bragg, 2021; Coleman et al., 2020). The proactive management of species vulnerable to climate change should result in improved conservation outcomes (Drechsler et al., 2011). Therefore, methods for assessing biodiversity to identify potentially vulnerable species for pre-emptive monitoring and management are essential in a world with abundant diversity and limited resources for conservation.

Climate change is perhaps the most challenging anthropogenic threat to manage given the global scale of its impact, the uncertainty around future climate projections, and the unknown capacity of species and ecosystems to adapt (Hoffmann & Sgrò, 2011). Yet, pre-emptive assessments of species vulnerability to climate change will help to focus conservation management and could also be used to improve our ability to forecast secondary extinctions after the loss of vulnerable species, due to knock-on effects upon ecosystem function (Foden et al., 2019). A number of methods exist to assess species vulnerability, with each approach having different advantages and limitations for their varied data types and methodologies. For example, species distribution modelling (SDM) has been extensively applied to estimate climate change exposure to novel conditions and shifting species distributions, for large numbers of species (Austin, 2002; Renner & Warton, 2013). However, standard SDMs do not account for factors such as species interactions, population dynamics or the capacity of species to tolerate or adapt to conditions beyond their realized climate niche (Davis et al., 1998).

In contrast, SDM approaches have been developed that incorporate aspects of species adaptive capacity by harnessing information on physiological limits, phenotypic plasticity, trait heritability and dispersal ability (Bush et al., 2016; Catullo et al., 2015). These approaches are undoubtedly more comprehensive than traditional SDMs and should in principle provide more accurate estimates of the impacts of climate change. However, accurate parameterization of plasticity and heritability requires well-designed experiments with robust sample sizes (Kellermann et al., 2012). Detailed measurements of adaptive capacity have only been undertaken for a small number of species. Adaptive capacity could potentially be estimated for species using functional traits and phylogenetic information, because these attributes are associated with parameters of species responses to their environment (Catullo et al., 2015).

Measurements of functional traits that capture variation in species life history strategies could provide an alternative to direct measures of adaptive capacity in terms of species fundamental climate limits. There are already a number of trait-based SDM approaches that use clinal variation and plasticity in functional traits to estimate species capacity to adapt to varied climates (as synthesized by Garzón et al., 2019). However, one limitation of some trait-based SDM approaches is they require trait data from across

the species distribution, which will not be available for most species. Additionally, methods for assessing species vulnerability based on exposure to threats, the sensitivity of the ecological system and the adaptive capacity of the target species (Foden et al., 2019) have also been expanded to use functional trait data. These methods often require categorization based on human decision making and assumptions about interactions between traits and environments, and about the suitability of combination of traits in different environments (Gallagher et al., 2021).

Many plant functional traits show marked geographic variation, suggesting they reflect adaptation of species to site climate and soil properties (Lamont et al., 2005; Moles et al., 2014; Westoby et al., 2002; Wright et al., 2017). Used in combination, functional traits can summarize plant life history strategies that are crucial to species survival and competitiveness in different environments (Díaz et al., 2016; Westoby, 1998). Here, we use information from the correlations between functional trait combinations and the realized climate limits of species to estimate the expected climate limits of the varied trait strategies of plants. With this method we turn the normal approach of explaining variation in functional traits with climate on its head and use functional traits to predict suitable climate ranges for these trait strategies.

If the viability of plant functional trait combinations can be influenced by climate (Dwyer & Laughlin, 2017), then statistical relationships between realized climate limits and trait strategies could be used to assess how well species are suited to their local environment, based on their traits. Species with potentially vulnerable trait strategies could be identified by finding outlier species that have a realized climate niche that is not correlated with the climate niche of related species with similar trait strategies. Alternatively, species with restricted climate niches that have similar trait combinations to more broadly distributed species, would have an estimated climate range that is broader than their current/realized range. How well a species' functional traits match its realized climate limits could also be combined with other surrogate measures of adaptive capacity, such as population size, genetic diversity, range size and environmental niche width (Razgour et al., 2018). Species with potentially vulnerable trait strategies should be the focus of further investigation to better understand their capacity to tolerate climate change.

Here we use generalized additive models (GAMs) to assess if the current climate niche of species covaries with their functional trait strategies, so that outlier species whose trait strategies do not match their current climate limits can be identified. We expect that we can identify plant species that are potentially vulnerable to climate change using readily accessible data, including functional traits, occurrence data, habitat condition, climate data and future climate projections. We test our approach using Australian plant species because this continent includes a broad range of climates and there is good coverage for both functional traits and spatial occurrence data (Andrew et al., 2021). We focus on three traits that have clear functional significance and are available for a large proportion of species in the flora: maximum height at maturity, leaf area and seed mass (Westoby, 1998). We present a method developed to work for

a large proportion of plant species but flexible enough to use different combinations of functional traits or environmental variables. We also aimed to explore if using traits in combination can prove more informative than when assessed individually. We use the modelled climate limits of species trait strategies to calculate species level vulnerability metrics (Figure 1). In addition, vulnerability metrics were also calculated per locality (10 km × 10 km grid cell) for local species to identify locations that have a high proportion of species with trait strategies that are expected to be poorly adapted to current and future climates. Creating a continuum from which we can identify the outlier species and localities with the greatest differences between their observed and predicted climate niche, allowing potentially vulnerable species and localities to be identified for further assessment, using this data driven method. The overall approach proposed here can be referred to as trait strategy vulnerability. Finally, we explore how trait strategies vary between species that were assessed to have high versus low vulnerability to climate change.

2 | METHODS

Figure 1 provides a schematic of the analytical steps described below for the trait strategy vulnerability approach. Our overarching goals were to: (a) describe the functional trait combinations – based on height (m), leaf area (mm²) and seed mass (mg) – exhibited by a subset of species in the Australian flora; (b) apply, a novel modelling approach for this field by using functional trait combinations as the predictor variable to assess how the realized average climate conditions and climatic limits of species change across functional trait space; and (c) project which species may experience climate conditions outside those currently occupied by their functional strategies by 2070. The analysis focuses on native Australian plant species included in the Australian Plant Census (APC). Only accepted species in the APC that are not naturalized (or naturalized outside their native Australian range) were retained for analysis (as defined by APC data from: <https://biodiversity.org>).

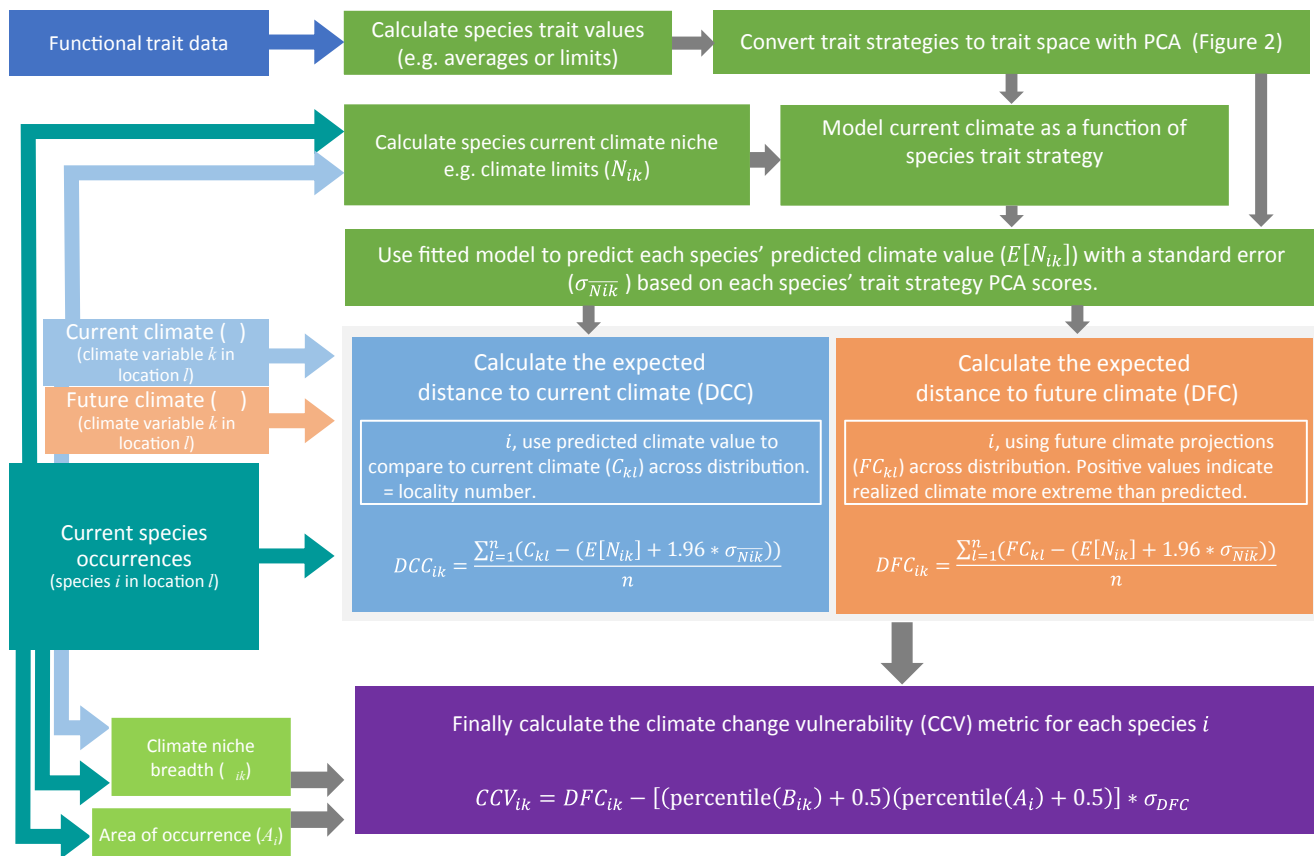


FIGURE 1 The analytical framework for calculating species level vulnerability metrics. The inputs are shown on the left-hand side of the figure and the order of the steps is shown with arrows starting at the top left. The trait, climate and occurrence data are combined to model species predicted climate limits, which were used to obtain preferred climate ranges based on confidence intervals around predictions ($E[N_{ik}] + 1.96 \times \sigma_{N_{ik}}$). Distance to current climate (DCC) and distance to future climate (DFC) were calculated for species predicted distributions and separately for plant assemblages using all species expected at localities. For location average DCC and DFC calculations n represents species number and i would represent each locality. The DCC and DFC distance metrics were calculated using the predicted limits extreme confidence interval (predicted limit + or $-1.96 \times$ standard error) to account for variability around predictions that could represent a broader or narrow range of climates occupied by species in different areas of trait space. Species predicted distributions were used to calculate area of occurrence and also combined with current climate layers to calculate climate niche breadth. See full details of vulnerability metrics in Methods section. PCA = principal components analysis

au/nsl/services/export/index). All non-vascular plants were also excluded.

2.1 | Distribution data

Input occurrence data were overlaid with climate layers to extract climate data for each species' realized climate niche. Occurrence data were downloaded from the Atlas of Living Australia (ALA) in 2020 and cleaned to remove records with obvious spatial errors and taxonomic issues. Only occurrences with herbarium specimens that were of non-cultivated origin were retained (c. 2.9 million occurrence records from 22,062 species out of the c. 25,000 listed native Australian species). Species distribution models (SDMs) produced for these species, using the same occurrence data were used in later stages (see details for SDMs in Andrew et al., 2021). In brief, species distributions were modelled using three methods, to ensure analyses were based on the likely full distribution of species, including areas not represented in herbarium collections. For taxa with greater than 10 occurrence records ($n = 17,479$ species), cleaned occurrence data were combined with climate and soil variables in Poisson point process modelling (Renner et al., 2015). For 3,044 taxa with 3–9 occurrences, range bagging was used, which is a machine learning method that uses an ensemble of convex hulls created from a reduced set of niche parameters and refined via bootstrap aggregation, or bagging (Drake, 2015). A final set of 1,539 species with 1–2 occurrences had their area of occupancy mapped using known occurrences within each 10 km × 10 km grid cell. These modelled distributions were used for generating vulnerability metrics for each species. The SDM outputs and all climate layers used the same resolution (10 × 10 km) and were converted to the Lambert azimuthal equal-area projection. Data from modelled distributions were also used to identify a list of species likely to be present in each 10 km × 10 km grid cells (herein, called local species lists). All species names follow the Australian Plant Census (APC).

2.2 | Climate variables

Our expectation was that the realized/current climate limits of species will covary with their functional trait strategies. To test this idea, we extracted the average climate conditions and upper/lower climate limits for each species by intersecting occurrence records (latitude-longitude coordinates of herbarium specimens) with WorldClim climate layers (Fick & Hijmans, 2017). We focus on three current climate limits across species occurrences (summer maximum temperature at the hottest location, winter minimum temperature at the coldest location, and annual rainfall at the driest location) and two average climate niche values (average annual temperature and average annual precipitation across species occurrences). These climate metrics focus on temperature and water availability because these environmental factors are very important to plant function

and are likely to show the most rapid change in the near future. For the current climate limits across each species distribution, we use the locality with the highest value for Maximum Temperature of Warmest Month (BIO5) hence referred to as 'summer maximum', the locality with the lowest value for Minimum Temperature of the Coldest Month (BIO6) hence 'winter minimum', and the locality with the lowest value for Annual Precipitation (BIO12) hence 'rainfall minimum'. For climate average metrics for each species, the average across all localities with occurrence records was taken for Mean Annual Temperature (BIO1) hence 'average temperature', and Annual Precipitation (BIO12) hence 'average rainfall'. Annual precipitation was \log_e transformed for all analyses.

We used the output of the SDMs to calculate species area of occurrence (A) and climate niche breadth (B) for deriving vulnerability metrics. For A, the number of 10 km × 10 km equal area grid cells (hence referred to as 'localities') expected to be occupied by each species was summed. The area of each grid cell was adjusted based on the estimated habitat condition, from the Australian Habitat Condition Assessment System: HCAS (Harwood et al., 2016), that is, a cell with condition of .5 contributes only 50% of the 100 km² area to A because the condition value represents the capacity for supporting the native species occurring originally in each location. For climate niche breadth, the difference between the localities with the highest and lowest values was calculated for each climate variable.

Gridded outputs from five Global Change models (GCMs), for the four WorldClim layers (BIO1, BIO5, BIO6 and BIO12), were used as estimated projections of future climate: ACCESS1.0, CESM1-CAM5, GFDL-ESM2M, HadGEM2-CC and MIROC5. All models used Representative Concentration Pathway (RCP) 8.5 for years 2061–2080 and were accessed via the CHELSA climate data repository (Karger et al., 2017, 2018). These five models were selected based on recommendations from the Climate Change in Australia website (<https://www.climatechangeinaustralia.gov.au/en/support-and-guidance/faqs/eight-climate-models-data/>), because they are representative for Australia and cover a range of scenarios (e.g. the GFDL-ESM2M model has a hotter and drier projection than the MIROC5 model that has lower warming and increased precipitation). We report the mean response across the five GCMs for each climate variable.

2.3 | Plant functional trait data

All trait values were sourced from the AusTraits database (Falster et al., 2021, version 3.0.1). We accessed data on plant height ($n = 14,749$ species), leaf area ($n = 3,806$) and seed mass ($n = 8,822$), as well as leaf length ($n = 12,127$), leaf width ($n = 11,689$) and seed length ($n = 7,115$). Leaf and seed dimensions were used to gap fill leaf area and seed mass, respectively (see details below). Where species had multiple values for the same trait, the maximum value was used for height, while a mean value was used for leaf area, length and width and for seed mass and length. Averaging was conducted with *plyr* in the statistical software environment R version 3.6.1 (R Core

Team, 2016). The natural log was taken for all traits before taking species maximums or averages.

Leaf area was estimated from length and width measurements using a linear mixed model (LMM) with leaf length and leaf width as fixed effects and taxonomic family as a random factor interacting with leaf length so random factor levels had independent intercepts and slopes, using *lme4* (Bates et al., 2015). Seed mass was similarly estimated from a separate LMM that used seed length (fixed effect) with an interaction with taxonomic family (see details in supplementary R code and also described in Andrew et al., 2021). Estimated leaf area and seed mass values were only used to fill missing values in the original matrix. After combining the estimated values, the number of species with trait data increased for leaf area ($n = 11,990$ species) and seed mass ($n = 11,905$ species) up from 3,806 and 8,822, respectively.

2.4 | Modelling climate of trait strategies

The 'trait space' occupied by all species combined was projected into two dimensions using principal components analysis (PCA), following the methods presented in Díaz et al. (2016). The PCA was performed with the `princomp()` function in R using the options 'cor = TRUE' and 'scores = TRUE'. We particularly wanted to work with traits in combination by using ordination because there is a large potential to explore how species that are similar for one trait might predictably occupy different climates based on other traits. The first two PCA coordinates of each species in trait space were used to quantify the average functional trait strategy for each species. To model how the realized climate limits and climate averages of species covaried with trait space we used generalized additive models (GAMs) with the `gam()` function from the *mgcv* package (Wood, 2017). GAMs were conducted separately for each of the five climate dependent variables. A thin plate spline smoother was used by fitting an interaction between the axes of PC1 and PC2 (Wood, 2003). The models were hierarchical GAMs with random factor levels for families. After combining PCA results with climate data only families with more than 50 species with trait data ($n = 27$ families) were included to avoid modelling families with limited sample size. For these 27 families 6,747 species had trait data for all three traits as well as spatial distribution data. The random factor levels for each family had individual smoothers that had independent shapes but fixed wiggleness penalizing terms across all levels (global smoother plus group-level smoothers method, see Pedersen et al., 2019). This model structure allowed the native plant families that differ from the overall global trend to be adjusted for. Prediction of the expected climate limits and climate averages of each species' functional trait strategy was done using the `predict()` function (Wood, 2017). The standard errors around these predicted values for species were also obtained from the posterior distribution of the model coefficients.

To assess how well the predictions of expected climate limits of plant functional trait strategies match the climate that species

currently occupy in the landscape, all localities across each species' distribution were compared to the expected climate values for the trait strategy of the species. For this mapping task, the SDM predictions of species current distributions were used for a more consistent representation of species expected occurrences in areas with low sampling effort. Comparisons between the expected climate limits of functional trait strategies and species realized climate range led to the development of several new metrics described below. These metrics aim to rank species by how well the expected climate range of their trait strategies matches the climates they do or might experience. The first of these metrics is distance to current climate (DCC_{ik}), which is the average gap between the expected climate niche of species trait strategies and the current conditions across a species' range. The DCC_{ik} was calculated for species i and climate variable k , using all n localities l in which species i was predicted to occur. For the summer maximum climate niche metric (N_{ik})

$$DCC_{ik} = \frac{\sum_{l=1}^n (C_{kl} - (E[N_{ik}] + 1.96 \times \sigma_{N_{ik}}))}{n} \quad (1)$$

where the predicted climate niche value ($E[N_{ik}]$) and associated standard error for the predicted value ($\sigma_{N_{ik}}$) are based on each species' trait strategy PCA scores. The climate value at each locality (C_{kl}) is compared to the positive 95% confidence interval (CI) of the predicted climate value ($E[N_{ik}] + 1.96 * \sigma_{N_{ik}}$), to account for the likely range of climates that species with similar trait strategies are observed to occupy. Species with positive values will on average occupy locations that are hotter than their upper 95% CI and are expected to have functional trait strategies that are not well matched to their current distribution.

To ensure a consistent meaning of positive DCC values indicating species occupying areas beyond their expected climate extreme, for winter minimum temperature and rainfall minimum the lower limit of the 95% CI was used and the values were negated

$$DCC_{ik} = \frac{\sum_{l=1}^n - (C_{kl} - (E[N_{ik}] + 1.96 \times \sigma_{N_{ik}}))}{n} \quad (2)$$

Then for average temperature and average rainfall, distance to current climate was calculated as

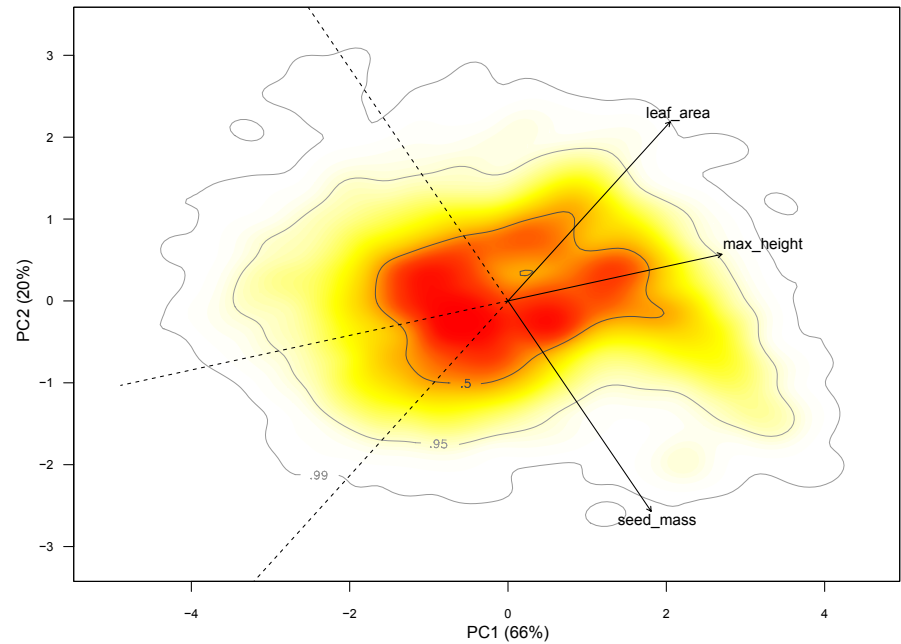
$$pDCC_{ik} = |(C_{kl} - E[N_{ik}])| - 1.96 \times \sigma_{N_{ik}} \quad (3)$$

$$qDCC_{ik} = \begin{cases} 0, & \text{for } pDCC_{ik} < 0 \\ pDCC_{ik}, & \text{for } pDCC_{ik} \geq 0 \end{cases} \quad (4)$$

$$DCC_{ik} = \frac{\sum_{l=1}^n qDCC_{ik}}{n} \quad (5)$$

The absolute difference between local climate and the predicted average climate was compared to the CI and for difference ($pDCC_{ik}$) values less than $1.96 \times \sigma_{N_{ik}}$, differences were rounded to 0 before

FIGURE 2 The principal components analysis (PCA) trait space of Australian plants. The distribution of plant functional trait strategies is projected on a plane with PC1 and PC2. Arrows show the strength and direction of the vectors for the three traits. The colour gradient represents the probability of species occurrence in the trait space (red = high probability; white = low probability) while the contour lines show the .5, .95 and .99 quantiles for proportion of species (as applied in Diaz et al., 2016). The first two principal components explain 86% of the variance in trait strategies (PC1 = 66% and PC2 = 20%)



averaging because these values are within the confidence interval and therefore 'within' the climate niche average.

The same procedures were repeated for each climate variable using future climate projections, hence distance to future climate (DFC). For DFC the climate value at each locality (C_{ik}) is replaced by the value from the future climate projection.

The difference between DFC and DCC was calculated for individual species, with positive values indicating the species being exposed to more extreme conditions across their range under climate change, based on their trait strategy, and negative change values indicating conditions becoming less severe

$$\text{Change}_{ik} = \text{DFC}_{ik} - \text{DCC}_{ik} \quad (6)$$

The above metrics were calculated for each species' distribution by averaging across localities that species are expected to occupy. A second option for calculating DCC and DFC was also applied per location l , using lists of all j species expected at each location (based on SDM predictions), by taking the average of difference between local climate and the predicted climate CI of species, that is, the difference between the predicted climate CI of each species and the local climate was average across all local species. These species differences (summarized as: $s\text{Diff}_{ik}$) are calculated as above for each climate variable (k), varying depending on the climate niche metric. These per location DCC and DFC calculations can be expressed as

$$\text{DCC}_{ik} \text{ or } \text{DFC}_{ik} = \frac{\sum_{i=1}^j s\text{Diff}_{ik}}{j} \quad (7)$$

A final metric that was only calculated for individual species was the climate change vulnerability (CCV) metric. For each species i , the species' DFC scores were adjusted by using information on species climate niche breadth (B_{ik}) and area of occurrence (A_i) to create a continuum of 'potential vulnerability', where species with large areas

of occurrence and niche breadth are assumed to have higher adaptability to varied climates. The potential vulnerability was adjusted in proportion to the variability in range of DFC (σ_{DFC}) scores from across all species

$$\text{CCV}_{ik} = \text{DFC}_{ik} - [(\text{perc}(B_{ik}) + 0.5)(\text{perc}(A_i) + 0.5)]\sigma_{\text{DFC}} \quad (8)$$

The use of percentiles (e.g. 'perc(B_{ik})') in this approach is to rank species so a species in the top percentile for both niche breadth and range size would have 2.25 SD of the DFC variation subtracted from their DFC score and a species with the most restricted ranges for both niche breadth and range size would have only a small adjustment of 0.25 SD subtracted. In this way species overall exposure to climate change based on functional traits (expressed as DFC) was adjusted by species rankings in terms of niche breadth and range size at a scale that is relevant to the range of all DFC values (σ_{DFC}). This vulnerability metric includes aspects of species adaptive capacity based on functional traits and range size, as well as exposure to future climates. Because the calculation of DFC is adjusted between climate metrics so that positive DFC indicates exposure to conditions beyond the species' expected climate niche based on its trait strategies, species with the highest CCV values will have the highest potential vulnerability.

Finally, expected climate limits were used to predict the least and most vulnerable trait strategies at each location. The method aims to identify the most vulnerable species and we would expect the phenotypes of the most and least vulnerable species to contrast. To do this the $s\text{Diff}_{ik}$ differences for all species by location combinations were normalized between the range of 0 and 1 for each climate variable. To identify the least vulnerable trait strategies, the normalized differences were summed for all five climate variables, and the 10 species with the lowest summed normalized DCC were selected in each location, and the mean height, seed mass and leaf area was taken for these least vulnerable species. To identify the most

vulnerable trait strategies at each locality, the maximum normalized DCC score was taken for each species, meaning the most stressful climate variable was used to identify vulnerability at each location. The top 10 species with the highest maximum DCC score were used to get the mean trait values across these most vulnerable species.

3 | RESULTS

The trait space for Australian plant species shows a central nucleus with a higher density of species (Figure 2). The relationships between our five current climate statistics and the trait space displayed in Figure 2 were moderate to strong (Figure 3 and Figure S1, Table S1). Of the environmental variables considered, functional trait combinations were most strongly associated with average rainfall ($R^2 = .45$) and then minimum rainfall ($R^2 = .36$) with the three temperature variables having slightly weaker relationships, with R^2 ranging between .21 and .30 (Figure 3 and Figure S1). However, traits in combination did explain more variation in these climate metrics than individual traits. In a majority of cases trait combination models had R^2 values

that were more than double that of linear models for individual traits (Table S2). The global model fit across all families showed the species with high PC1 values and low PC2 values ($PC1 > 2$ and $PC2 < 0$), generally occupy distributions with a wet tropical climate of high minimum rainfall, high winter minimum and moderate summer maximum temperatures (Figure 3b,d,f) and also having high average annual temperatures and annual rainfall (Figure S1). Tall species with moderate sized leaves and small seeds (high PC1 and PC2 values) were associated with colder and drier climates compared to tall species with larger seeds (i.e. lower PC2 scores). Shorter plants with small leaves (low PC1 values) were associated with both arid and colder climates but of this group those with larger seeds were generally found in hotter and drier climates (Figure 3 and Figure S1).

From these models, climate limits and climate averages were predicted for the trait combination of each species. The standard errors around these predictions for climate limits (Figure S2a–c) are generally small and < 0.5 °C for summer maximum and winter minimum models and less than 0.1 for \log_e transformed minimum rainfall model (on the \log_e scale an increase of 0.1 is about a 10% increase). Positive DCC and DFC scores indicate that on average

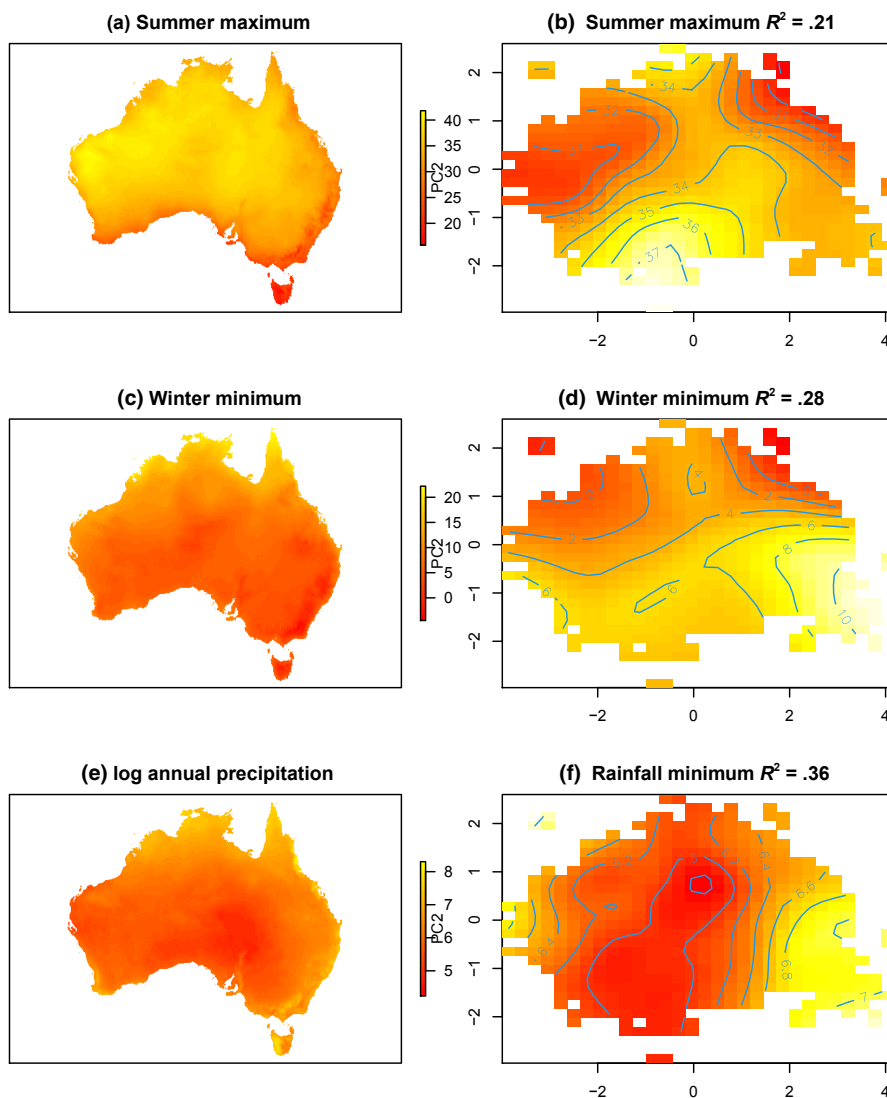


FIGURE 3 Global generalized additive model (GAM) thin plate spline smoothers for current climate limits of Australian plant species. Shown in the left column are maps of the climate variables used to extract species climate values for each model. The right column plots contour maps of the global smoothers with shading to match relief [principal component 1 (PC1) on the x axis and PC2 on the y axis]. These contour maps show how the climate niche metrics of species vary across trait space, highlighting possible signatures of adaptation. These global smoothers show variation in current climate limits across trait space for all species after random factor levels for families are accounted for. The R^2 values for these highly significant relationships are included in panel headings and are for the full model including family level smoothers. The first row is for the summer maximum model (a, b, units °C), the second row is for the winter minimum model (c, d, units °C), and the third row is for the rainfall minimum model (e, f, units mm on \log_e scale)

a species will experience conditions beyond its expected range of preferred climates, modelled on the climate ranges of species with similar functional trait strategies. The species range-wide distance to current climate (DCC) scores were mostly negative with a normal distribution for the three climate limits (Figure S2d–f). The distance to future climate (DFC) species scores were still mostly negative for summer maximum (72% negative) and rainfall minimum (82% negative), but with a moderate positive shift compared to DCC. These results indicate that species will experience more extreme conditions in the future that will still be within the expected suitable range for most species that have negative DFC values. The DFC scores for winter minimum showed the opposite trend with a clear negative shift (Figure S2e, 99.6% of species with negative DFC values). The change between DFC and DCC scores for species range averages (Figure S2g–i) are mostly positive for the summer maximum and rainfall minimum models and the winter minimum change values are all negative with a range between -2 and -7 °C. For all climate variables positive change values indicate future climate conditions becoming more extreme within the species' current distribution and negative values indicate conditions becoming less extreme. Due to temperatures increasing, winter minimum temperatures are becoming less extreme. Similar histograms for climate average models are shown in Figure S3. Because species distributions are likely to shift due to climate extremes, we focus on calculating our CCV index for only the three climate limit models. The CCV scores (Figure S2j–l) for all three climate limits have a normal distribution with nearly all species having negative values, with the small proportion of species with positive values (summer maximum = 4.3%, winter minimum = 0.05% and rainfall minimum = 3.1%) expected to be the most vulnerable species based on trait combination, on average for the five future climate projections assessed.

To visualize vulnerable plant communities, the second option for calculating DCC and DFC was used. For this option differences between local climate and species expected climate niche were averaged across all species at each locality, predicted from distribution models. The DCC maps for climate limits (Figure 4a,d,g) show that the communities in more extreme climates have functional trait strategies that are more likely to be exposed to conditions beyond their expected climate limits (e.g. the central arid areas for summer maximum and rainfall minimum, and the alpine areas in south-east Australia and Tasmania for winter minimum). The DFC for winter minimum shows a clear negative shift and DFC for summer maximum and rainfall minimum show a less strong positive shift (Figure 4b,e,h). Worryingly, we show a shift to higher DFC values across most of Australia for summer maximum (95% increasing) and rainfall minimum (66% increasing). The climate change vulnerability (CCV) scores were averaged for plant communities (Figure 4c,f,i) and show clear spatial variation with the highest values for summer maximum in north-western Australian, in southern Australia for winter minimum, and south-western and central Australia for rainfall minimum. Communities with high mean CCV are expected to be more strongly stressed under future

climate conditions. For the average climate variables (Figure S4) we see DFC increasing the most in the monsoon tropics in northern Australia for average temperature and the arid centre and western Australia for average rainfall. To test the sensitivity of the above GAM method to the use of model-based predictions we include in the supplementary results file a second method based on similar related species in trait space that found comparable results (Figures S5–S7).

Finally, we expect the phenotypes of the most vulnerable species (i.e. the candidates for closer monitoring) to contrast with the least vulnerable species. These contrasts for localities are summarized by the mean phenotype of the 10 most and least vulnerable species (Figure 5). These maps show patterns that are similar to what we might expect based on plant life history trade-offs, in that taller species and species with large leaves are more vulnerable across large areas including south-east and northern Australia with a major exception to this pattern being the wet tropics (see Discussion). Interestingly, the least vulnerable species had relatively small seeds across all of Australia.

4 | DISCUSSION

We have shown that the current climate conditions that species occupy varies across the multivariate trait space of plant height, seed mass and leaf area, with a meaningful proportion of the variance in realized climate ranges being explained. This link between species functional trait strategies and climate could mean that the functional diversity of plant communities will be reshaped if species shift their distributions to adapt to climate change. The trait strategies of Australian plants were significantly related to all five chosen climate response variables, selected for their relevance to plant growth and survival (adjusted- R^2 range .21–.45, Table S1). These relationships highlight how these three functional traits can reflect plant adaptation to varied climates (Figure 3 and Figure S1). In a local adaptation context the strength of these relationships could represent significant differences in fitness for trait strategies across climates, and although this is yet to be fully tested, these relationships could prove valuable for informing conservation. Climate provides multiple challenges for plants and functional traits are not only important to species thermal tolerance (Dwyer & Laughlin, 2017) but also a species' capacity to compete for resources and to reproduce (Díaz et al., 2016). Therefore, the strength of the relationships we observe from this exploratory analysis with just three traits indicates that trait strategies contain potentially meaningful information for assessing species climate preferences. Similar relationships between climate and functional traits have been noted previously, especially for individual traits (e.g. Lamont et al., 2005; Westoby et al., 2002; Wright et al., 2017). However, our method highlights that, for example, tall species with large leaves and seeds will likely occupy very different climate niches to tall species with small leaves and seeds, demonstrating that considering traits in combination can be more informative.

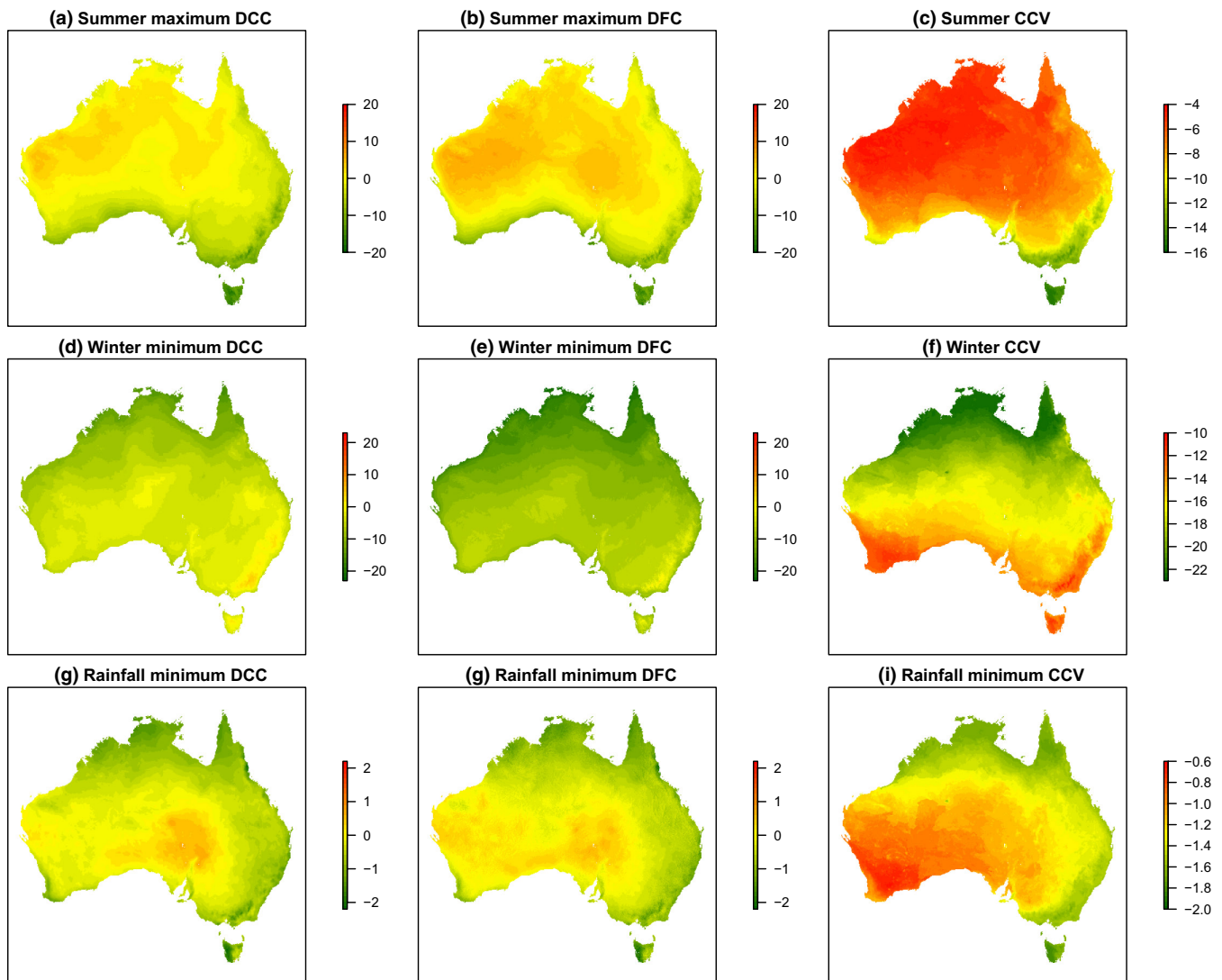


FIGURE 4 Local species mean vulnerability for predicted limits models. These location means for distance to current climate (DCC) and distance to future climate (DFC) are calculated per location using the local climate values and the expected climate limits of each local species. The maps for mean location DCC are in the first column and the maps for mean location DFC are in the second column. The third column has the mean climate change vulnerability (CCV) for the list of species predicted to be present at each locality; these mean CCV values average the CCV values calculated for species distributions. The first row is for the summer maximum model (a, b, c, units °C), the second row is for the winter minimum model (d, e, f, units °C), and the third row is for the rainfall minimum model (g, h, i, units mm on \log_e scale)

Based on relationships between climate and functional traits we find that under climate projections for the next 50–60 years, the majority of species will continue to inhabit the range of climates commonly occupied by related plant species with similar trait strategies. Species living in more extreme climates are more likely to be exposed to conditions beyond their predicted climate limits (Figure 4), partly because the most extreme locations act as an upper bound to current climate limits of species trait strategies. However, the purpose of the DCC, DFC and CCV metrics is that they can use data from a large proportion of species and rank species to identify those that are potentially vulnerable to climate change and could have been overlooked previously in other assessments of vulnerability (see Table S3 for candidate species). Of the 6,747 species analysed here, 400 (5.9%) were already included in the current 1,383 species listed as threatened under the Environment Protection and Biodiversity

Conservation Act 1999 (EPBC Act); the remaining listed species were not included in the analysis. Of our 150 top candidate vulnerable species, 15 (10%) are listed as threatened under the EPBC Act. The mean CCV scores for EPBC listed species were higher than non-listed species (summer maximum = 17.2%, winter minimum = 31.5% higher and rainfall minimum = 27.6% higher); differences between the two groups were significant for all three metrics when tested. We would not expect a strong overlap a priori due to the substantial differences between our method and the methods used for assessing species under the EPBC Act [e.g. International Union for Conservation of Nature (IUCN) analogous criteria]. Our method aims to identify new candidate species based on functional traits, when there is an absence of data on species adaptive capacity and fundamental climate limits. Further investigations of candidate species will hopefully provide better estimates of vulnerability after accounting

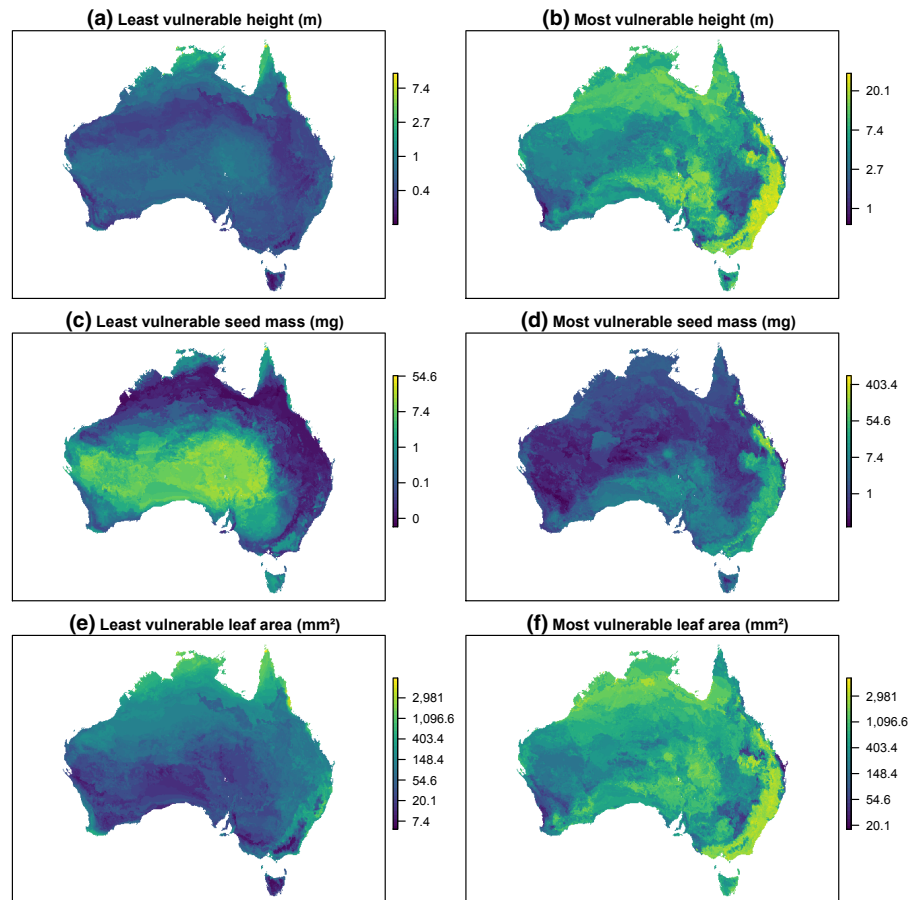


FIGURE 5 Phenotypes of least and most vulnerable trait strategies by locality. Normalized distance to current climate (DCC) scores for all five climate variables were summed for each species to find the 10 species with the lowest total DCC at each location. These 10 species with the lowest combined DCC were used to calculate an average height, seed mass and leaf area for the least vulnerable trait strategies at each locality. The maximum normalized DCC for each species was used to rank species to find the top 10 species with the most vulnerable phenotypes at each location. (a) Least vulnerable height, (b) most vulnerable height, (c) least vulnerable seed mass, (d) most vulnerable seed mass, (e) least vulnerable leaf area, (f) most vulnerable leaf area. All traits are on the natural \log_e scale with legends back transformed to be on the original scale

for other traits or the existence of microclimates that species are occupying. The mismatches between trait strategies and climate limits could also be a legacy of past conditions and dispersal limitations in combination with a limited capacity to adapt functional traits. However, if links between trait strategies and fitness are strong then these mismatches can still have a cost that influences vulnerability.

Anticipated shifts toward hotter and drier conditions under future climate projections for Australia were reflected in mean DCC and DFC scores across the continent (Figure 4 and Figure S4). The exception to this pattern was for winter minimum temperature, which sees a negative shift to warmer and therefore, less extreme winter temperatures. These large shifts between winter DCC and DFC may not be trivial and could mean species turnover across the landscape as winter conditions become less extreme (Alexander et al., 2018). Average CCV scores were also high in many locations characterized by extreme climate conditions (i.e. arid regions) and in areas of high plant endemism, such as the south-west of Western Australia (Figure 4c,f,i). On a more positive note, mapping for average climate conditions (Figure S4) exhibit many areas of low DFC

(e.g. southern Australia for average temperature, northern and eastern Australia for average rainfall). These regions with both low DCC and DFC indicate species assemblages that are expected to remain within their preferred climate niche for their trait strategies.

4.1 | Which trait combinations are the most (and the least) vulnerable to climate change?

The phenotypes of the least vulnerable species with the lowest normalized DCC scores largely follow previously identified trait combinations from global studies into trait–environment relationships (e.g. Laughlin et al., 2010; Liu et al., 2010; de la Riva et al., 2016). For instance, taller plants with larger leaves were characteristic of areas with higher water availability, whereas shorter-statured plants with small leaves were typically found to be less vulnerable in arid and alpine environments (Figure 5, climate variation Figure 3). Interestingly, in the arid central parts of Australia, the least vulnerable species had clearly larger seeds, perhaps reflecting the previously

observed pattern that species with larger seeds have higher survival in environments with lower water availability (Leishman & Westoby, 1994; Metz et al., 2010). In general, the most vulnerable phenotypes under future climates in most areas are species that are relatively tall (> 15 m) with large leaves (> 1,500 mm²) and also with relatively large seeds in the south-east (Figure 5). These phenotypes occur along the southern and eastern coastline where climates are currently temperate due in part to the influence of maritime conditions, but the incidence of extreme events – in particular sustained heatwaves – is increasing (Trancoosa et al., 2020). Tall species with large leaves are common in the rain forests and tall closed eucalypt forests of this region. One possible result of reduced water availability and increased heatwaves might be the loss of these tall, large-leaved species from the landscape if their range changes in order to persist within their current climate niche. The removal of these canopy species would likely change both the composition and function of vegetation in affected areas. Rain forests are also at risk from the combined effects of land clearing and fragmentation, weed invasion and post-logging incursions of flammable species such as eucalypts, which increase the risk of fire intruding into these sensitive communities (Fox et al., 1997; Lindenmayer et al., 2009).

4.2 | Caveats for the application of trait-modelling to climate change predictions

Our ability to predict aspects of the climate niche of plant trait strategies is dependent on the performance of the GAMs that we used. The standard errors around the predicted climate values for our GAMs were generally relatively small (Figure S2a–c), indicating broad convergence in the alignment of trait strategies with climate conditions. The standard errors for temperature models were around 0.5 °C indicating that the CI around the trends is relevant to the range of expected climate change (average temperature increases of 1.5–2 °C) and should be sensitive enough to assess expected changes in temperature. Models that used combinations of functional traits also explained a much larger proportion of the variance in species climate niche metrics than individual traits (Table S2). However, the current climate niche of some species showed large divergence from predicted values indicating these species are potentially at a disadvantage in terms of their trait combination (see DCC range in Figure S2d–f). These outlier species likely possess other adaptations not considered here that increase their capacity to survive in current climate conditions. For example, density of woody tissues may more closely approximate hydraulic strategies revealing information about whole-plant water use efficiency (Anderegg et al., 2020), or root traits likely vary depending on prevailing environmental conditions (Laughlin et al., 2021). Traits like these and many others could be easily added to our method, given data availability. Our approach can also be easily adapted to any group of species or set of functional traits, with the selection of the best available data influenced by knowledge of species biology. The use of ordination to reduce the dimensionality of any set of traits to two dimensions allows the

method to be consistent for any number of multiple traits, but the interpretation of the trait space will likely become more difficult with higher numbers of traits. Our technique allows outlier species to be easily identified for closer evaluation of their vulnerability to climate change with either experimental manipulations or through genomic approaches (Razgour et al., 2018). Future studies of the functional traits of species in decline due to climate change could also help confirm the usefulness of the results presented here.

The methods presented here for identifying vulnerable plant species focus on functional trait strategies and distribution data that are available for many species, but these data are not able to fully replace other measures of thermal tolerance and drought tolerance that are not commonly available but, in principle, are more directly relevant to understanding the climatic limits of species distributions. However, functional traits and life history will affect species competitiveness and survival in different environments and because it is logistically viable to gather these data for a large portion of plant species these traits provide an opportunity to develop a data driven process for identifying potentially vulnerable species that can be the focus of more detailed assessments of vulnerability. Experimentally testing adaptive capacity is not viable for all species but stress tolerance data for a representative sample of trait strategies could help validate the patterns between trait strategies and realized climate limits we have presented.

Our methods also focus on species' capacity to track climate change within their home range rather than the alternative of species' capacity to shift their distribution with climate change. If a plant species shifts its distribution it may be exposed to more familiar climates but will likely face other challenges such as different soils, symbionts, competitors, pathogens, and human land use. Range shifts represent a different set of scenarios to be assessed (Trisos et al., 2020) and it may not be necessary to look at these for species that are not likely to be pushed beyond their fundamental climate limits.

4.3 | Conclusions

Climate change is already having appreciable impacts on species (Coleman & Bragg, 2021). Efforts to understand these impacts require techniques that identify species and regions most at risk. Here we present results using trait data for 6,747 species from the c. 25,000 native Australian plant species, suggesting that trait coverage needs to expand to provide a comprehensive overview across the flora. Gaps in the availability of trait data are not unique to Australia (Cornwell et al., 2019), and efforts to complete a global inventory of plant traits must continue to expand through both regional campaigns and global synthesis of data. Not only are the traits we focused on in this study in need of better coverage, but several other physiological traits that relate to how plants respond to extreme climatic events or drought would further improve our trait-based platform for identifying species vulnerable to climate change. Combining information on species traits, distributions and environment offers a powerful approach for understanding climate change vulnerability in global vegetation and assessing the consequences for species in coming decades.

CONFLICT OF INTEREST

The authors state no conflict of interest.

AUTHOR CONTRIBUTIONS

SCA, RVG and KM had the initial idea for the paper and methodology. SCA produced results and figures with recommendations from other authors. All authors contributed to drafting the paper and reviewed the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Plant trait data are publicly available through AusTraits. Species occurrence records are available from the Atlas of Living Australia. Data for cleaned occurrence records and modelled species distributions are available from the corresponding author upon reasonable request. The models and data needed to replicate results are published on Dryad (<https://doi.org/10.5061/dryad.qz612jmhd>).

ORCID

Samuel C. Andrew  <https://orcid.org/0000-0003-4589-2746>

Rachael V. Gallagher  <https://orcid.org/0000-0002-4680-8115>

Karel Mokany  <https://orcid.org/0000-0003-4199-3697>

REFERENCES

- Alexander, J. M., Chalmandrier, L., Lenoir, J., Burgess, T. I., Essl, F., Haider, S., Kueffer, C., McDougall, K., Milbau, A., Nuñez, M. A., Pauchard, A., Rabitsch, W., Rew, L. J., Sanders, N. J., & Pellissier, L. (2018). Lags in the response of mountain plant communities to climate change. *Global Change Biology*, 24, 563–579. <https://doi.org/10.1111/gcb.13976>
- Anderegg, L. D. L., Loy, X., Markham, I. P., Elmer, C. M., Hovenden, M. J., HilleRisLambers, J., & Mayfield, M. M. (2020). Aridity drives coordinated trait shifts but not decreased trait variance across the geographic range of eight Australian trees. *New Phytologist*, 229(3), 1375–1387.
- Andrew, S. C., Mokany, K., Falster, D. S., Wenk, E., Wright, I. J., Merow, C., Adams, V., & Gallagher, R. V. (2021). Functional diversity of the Australian flora: Strong links to species richness and climate. *Journal of Vegetation Science*, 32, e13018. <https://doi.org/10.1111/jvs.13018>
- Austin, M. P. (2002). Spatial prediction of species distribution: An interface between ecological theory and statistical modelling. *Ecological Modelling*, 157, 101–118. [https://doi.org/10.1016/S0304-3800\(02\)00205-3](https://doi.org/10.1016/S0304-3800(02)00205-3)
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-8. <http://CRAN.R-project.org/package=lme4>
- Bergstrom, D. M., Wienecke, B. C., Hoff, J., Hughes, L., Lindenmayer, D. B., Ainsworth, T. D., Baker, C. M., Bland, L., Bowman, D. M. J. S., Brooks, S. T., Canadell, J. G., Constable, A. J., Dafforn, K. A., Depledge, M. H., Dickson, C. R., Duke, N. C., Helmstedt, K. J., Holz, A., Johnson, C. R. ... Shaw, J. D. (2021). Combating ecosystem collapse from the tropics to the Antarctic. *Global Change Biology*, 27(9), 1692–1703. <https://doi.org/10.1111/gcb.15539>
- Bush, A., Mokany, K., Catullo, R., Hoffmann, A., Kellermann, V., Sgrò, C., McEvey, S., & Ferrier, S. (2016). Incorporating evolutionary adaptation in species distribution modelling reduces projected vulnerability to climate change. *Ecology Letters*, 19, 1468–1478. <https://doi.org/10.1111/ele.12696>
- Catullo, R. A., Ferrier, S., & Hoffmann, A. A. (2015). Extending spatial modelling of climate change responses beyond the realized niche: Estimating, and accommodating, physiological limits and adaptive evolution. *Global Ecology and Biogeography*, 24, 1192–1202. <https://doi.org/10.1111/gcb.12344>
- Coleman, M. A., & Bragg, J. G. (2021). A decision framework for evidence-based climate adaptation interventions. *Global Change Biology*, 27, 472–474. <https://doi.org/10.1111/gcb.15429>
- Coleman, M. A., Wood, G., Filbee-Dexter, K., Minne, A. J. P., Goold, H. D., Vergés, A., Marzinelli, E. M., Steinberg, P. D., & Wernberg, T. (2020). Restore or redefine: Future trajectories for restoration. *Frontiers in Marine Science*, 7, 1–12. <https://doi.org/10.3389/fmars.2020.00237>
- Cornwell, W. K., Pearse, W. D., Dalrymple, R. L., & Zanne, A. E. (2019). What we (don't) know about global plant diversity. *Ecography*, 42, 1819–1831. <https://doi.org/10.1111/ecog.04481>
- Davis, A. J., Jenkinson, L. S., Lawton, J. H., Shorrocks, B., & Wood, S. (1998). Making mistakes when predicting shifts in species range in response to global warming. *Nature*, 391, 783–786. <https://doi.org/10.1038/35842>
- de la Riva, E. G., Tosto, A., Pérez-Ramos, I. M., Navarro-Fernández, C. M., Olmo, M., Anten, N. P. R., Marañón, T., & Villar, R. (2016). A plant economics spectrum in Mediterranean forests along environmental gradients: Is there coordination among leaf, stem and root traits? *Journal of Vegetation Science*, 27, 187–199. <https://doi.org/10.1111/jvs.12341>
- Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönsch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., ... Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, 529, 167–171. <https://doi.org/10.1038/nature16489>
- Díaz, S., Settele, J., Brondizio, E., Ngo, H., & Guèze, M. (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. IPBES.
- Drake, J. M. (2015). Range bagging: A new method for ecological niche modelling from presence-only data. *Journal of the Royal Society Interface*, 12, 20150086. <https://doi.org/10.1098/rsif.2015.0086>
- Drechsler, M., Eppink, F. V., & Wätzold, F. (2011). Does proactive biodiversity conservation save costs? *Biodiversity and Conservation*, 20, 1045–1055. <https://doi.org/10.1007/s10531-011-0013-4>
- Dwyer, J. M., & Laughlin, D. C. (2017). Constraints on trait combinations explain climatic drivers of biodiversity: The importance of trait covariance in community assembly. *Ecology Letters*, 20, 872–882. <https://doi.org/10.1111/ele.12781>
- Falster, A. D., Gallagher, R., Wenk, E., Wright, I., Indiarito, D., Andrew, S. C., Lawson, J., Allen, S., Fuchs, A., Adams, M. A., Collin, W., Alfonzetti, M., Angevin, T., Atkin, O. K., Auld, T., Baker, A., Buckton, G., Burrows, G., Caldwell, E., ... Ziemińska, K. (2021). AusTraits – A curated plant trait database for the Australian Flora. *bioRxiv*, 1–62.
- Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37, 4302–4315. <https://doi.org/10.1002/joc.5086>
- Foden, W. B., Young, B. E., Akçakaya, H. R., Garcia, R. A., Hoffmann, A. A., Stein, B. A., Thomas, C. D., Wheatley, C. J., Bickford, D., Carr, J. A., Hole, D. G., Martin, T. G., Pacifici, M., Pearce-Higgins, J. W., Platts, P. J., Visconti, P., Watson, J. E. M., & Huntley, B. (2019). Climate change vulnerability assessment of species. *Wiley Interdisciplinary Reviews: Climate Change*, 10, e551. <https://doi.org/10.1002/wcc.551>
- Fox, B. J., Taylor, J. E., Fox, M. D., & Williams, C. (1997). Vegetation changes across edges of rainforest remnants. *Biological Conservation*, 82, 1–13. [https://doi.org/10.1016/S0006-3207\(97\)00011-6](https://doi.org/10.1016/S0006-3207(97)00011-6)
- Gallagher, R. V., Butt, N., Carthey, A. J. R., Tulloch, A., Bland, L., Clulow, S., Newsome, T., Dudaniec, R. Y., & Adams, V. M. (2021). A guide

- to using species trait data in conservation. *One Earth*, 4, 927–936. <https://doi.org/10.1016/j.oneear.2021.06.013>
- Garzón, M. B., Robson, T. M., & Hampe, A. (2019). Δ TraitSDMs: Species distribution models that account for local adaptation and phenotypic plasticity. *New Phytologist*, 222, 1757–1765.
- Harwood, T. D., Donohue, R. J., Williams, K. J., Ferrier, S., McVicar, T. R., Newell, G., & White, M. (2016). Habitat Condition Assessment System: A new way to assess the condition of natural habitats for terrestrial biodiversity across whole regions using remote sensing data. *Methods in Ecology and Evolution*, 7, 1050–1059. <https://doi.org/10.1111/2041-210X.12579>
- Hoffmann, A. A., & Sgrò, C. M. (2011). Climate change and evolutionary adaptation. *Nature*, 470, 479–485. <https://doi.org/10.1038/nature09670>
- Karger, D. N., Conrad, O., Böhrer, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, 4, 1–20. <https://doi.org/10.1038/sdata.2017.122>
- Karger, D. N., Conrad, O., Böhrer, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2018). Data from: Climatologies at high resolution for the earth's land surface areas, Dryad, Dataset. [Dryad, Data set].
- Kellermann, V., Overgaard, J., Hoffmann, A. A., Fløjgaard, C., Svenning, J.-C., & Loeschcke, V. (2012). Upper thermal limits of *Drosophila* are linked to species distributions and strongly constrained phylogenetically. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 16228–16233.
- Lamont, B. B., Warton, D. I., Falster, D. S., Garnier, E., Poorter, H., Wright, I. J., Cornelissen, J. H. C., Oleksyn, J., Hikosaka, K., Westoby, M., Osada, N., Reich, P. B., Villar, R., & Lee, W. (2005). Assessing the generality of global leaf trait relationships. *New Phytologist*, 166, 485–496. <https://doi.org/10.1111/j.1469-8137.2005.01349.x>
- Laughlin, D. C., Leppert, J. J., Moore, M. M., & Sieg, C. H. (2010). A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora. *Functional Ecology*, 24, 493–501. <https://doi.org/10.1111/j.1365-2435.2009.01672.x>
- Laughlin, D. C., Mommer, L., Sabatini, F. M., Bruelheide, H., Kuyper, T. W., McCormack, M. L., Bergmann, J., Freschet, G. T., Guerrero-Ramírez, N. R., Iversen, C. M., Kattge, J., Meier, I. C., Poorter, H., Roumet, C., Semchenko, M., Sweeney, C. J., Valverde-Barrantes, O. J., van der Plas, F., van Ruijven, J., ... Weigelt, A. (2021). Root traits explain plant species distributions along climatic gradients yet challenge the nature of ecological trade-offs. *Nature Ecology and Evolution*, 5, 1123–1134. <https://doi.org/10.1038/s41559-021-01471-7>
- Leishman, M. R., & Westoby, M. (1994). The role of seed size in seedling establishment in dry soil conditions – Experimental evidence from semi-arid species. *The Journal of Ecology*, 82, 249. <https://doi.org/10.2307/2261293>
- Lindenmayer, D. B., Hunter, M. L., Burton, P. J., & Gibbons, P. (2009). Effects of logging on fire regimes in moist forests. *Conservation Letters*, 2, 271–277. <https://doi.org/10.1111/j.1755-263X.2009.00080.x>
- Liu, G., Freschet, G. T., Pan, X., Cornelissen, J. H. C., Li, Y., & Dong, M. (2010). Coordinated variation in leaf and root traits across multiple spatial scales in Chinese semi-arid and arid ecosystems. *New Phytologist*, 188, 543–553. <https://doi.org/10.1111/j.1469-8137.2010.03388.x>
- Metz, J., Liancourt, P., Kigel, J., Harel, D., Sternberg, M., & Tielbörger, K. (2010). Plant survival in relation to seed size along environmental gradients: A long-term study from semi-arid and Mediterranean annual plant communities. *Journal of Ecology*, 98, 697–704. <https://doi.org/10.1111/j.1365-2745.2010.01652.x>
- Moles, A. T., Perkins, S. E., Laffan, S. W., Flores-Moreno, H., Awasthy, M., Tindall, M. L., Sack, L., Pitman, A., Kattge, J., Aarssen, L. W., Anand, M., Bahn, M., Blonder, B., Cavender-Bares, J., Cornelissen, J. H. C., Cornwell, W. K., Díaz, S., Dickie, J. B., Freschet, G. T., ... Bonser, S. P. (2014). Which is a better predictor of plant traits: Temperature or precipitation? *Journal of Vegetation Science*, 25, 1167–1180. <https://doi.org/10.1111/jvs.12190>
- Pedersen, E. J., Miller, D. L., Simpson, G. L., & Ross, N. (2019). Hierarchical generalized additive models in ecology: An introduction with mgcv. *PeerJ*, 7, e6876. <https://doi.org/10.7717/peerj.6876>
- R Core Team (2016). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org>
- Razgour, O., Taggart, J. B., Manel, S., Juste, J., Ibáñez, C., Rebelo, H., Alberdi, A., Jones, G., & Park, K. (2018). An integrated framework to identify wildlife populations under threat from climate change. *Molecular Ecology Resources*, 18, 18–31. <https://doi.org/10.1111/1755-0998.12694>
- Renner, I. W., Elith, J., Baddeley, A., Fithian, W., Hastie, T., Phillips, S. J., Popovic, G., & Warton, D. I. (2015). Point process models for presence-only analysis. *Methods in Ecology and Evolution*, 6, 366–379. <https://doi.org/10.1111/2041-210X.12352>
- Renner, I. W., & Warton, D. I. (2013). Equivalence of MAXENT and poisson point process models for species distribution modeling in ecology. *Biometrics*, 69, 274–281. <https://doi.org/10.1111/j.1541-0420.2012.01824.x>
- Trancoso, R., Syktusa, J., Toombs, N., Ahrens, D., Wong, K.-K.-H., & Pozza, D. R. (2020). Heatwaves intensification in Australia: A consistent trajectory across past, present and future. *Science of the Total Environment*, 742, 140521. <https://doi.org/10.1016/j.scitotenv.2020.140521>
- Trisos, C. H., Merow, C., & Pigot, A. L. (2020). The projected timing of abrupt ecological disruption from climate change. *Nature*, 580, 496–501. <https://doi.org/10.1038/s41586-020-2189-9>
- Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, 199, 213–227.
- Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A., & Wright, I. J. (2002). Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, 33, 125–159. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150452>
- Wood, S. N. (2003). Thin plate regression splines. *Journal of the Royal Statistical Society. Series B: Statistical Methodology*, 65, 95–114.
- Wood, S. N. (2017). *Generalized additive models: An introduction with R* (2nd ed.). CRC Press.
- Wright, I. J., Dong, N., Maire, V., Prentice, I. C., Westoby, M., Díaz, S., Gallagher, R. V., Jacobs, B. F., Kooyman, R., Law, E. A., Leishman, M. R., Niinemets, Ü., Reich, P. B., Sack, L., Villar, R., Wang, H., & Wilf, P. (2017). Global climatic drivers of leaf size. *Science*, 357, 917–921. <https://doi.org/10.1126/science.aal4760>

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Andrew, S. C., Gallagher R. V., Wright I. J., & Mokany K. (2022). Assessing the vulnerability of plant functional trait strategies to climate change. *Global Ecology and Biogeography*, 31, 1194–1206. <https://doi.org/10.1111/geb.13501>