Population decline in a Pleistocene refugium: Stepwise, drought-related dieback of a South Australian eucalypt

Gunnar Keppel [a,b,*], Udo Sarnow [a], Ed Biffin [c], Stefan Peters [a], Donna Fitzgerald [a], Evan Boutsalis [a], Michelle Waycott [c,1], Greg R. Guerin [d,1]

[a] *UniSA STEM and Future Industries Institute, University of South Australia, GPO Box 2471, SA 5001 Adelaide, Australia*
[b] *AMAP, Université de Montpellier, CIRAD, CNRS, INRAE, IRD, Montpellier, France*
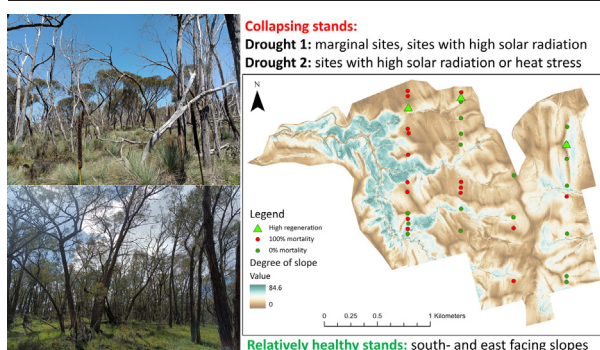[c] *State Herbarium of South Australia, Botanic Gardens and State Herbarium, Department for Environment and Water, Adelaide, Australia*
[d] *School of Biological Sciences, University of Adelaide, Adelaide, SA, Australia*

HIGHLIGHTS

- We confirm a eucalypt population as unique and restricted to a Pleistocene refugium.
- Dieback through two droughts removed >40 % of individuals and biomass
- Dieback occurred mostly in the most marginal sites after the first drought.
- Heat stress was a key driver of dieback after the second drought.
- Ecosystem decline is ongoing, but the population may persist in microrefugia.

GRAPHICAL ABSTRACT

ARTICLE INFO

ABSTRACT

Refugia can facilitate the persistence of species under long-term environmental change, but it is not clear if Pleistocene refugia will remain functional as anthropogenic climate change progresses. Dieback in populations restricted to refugia therefore raises concerns about their long-term persistence. Using repeat field surveys, we investigate dieback in an isolated population of *Eucalyptus macrorhyncha* during two droughts and discuss prospects for its continued persistence in a Pleistocene refugium. We first confirm that the Clare Valley in South Australia has constituted a long-term refugium for the species, with the population being genetically highly distinct from other conspecific populations. However, the population lost >40 % of individuals and biomass through the droughts, with mortality being just below 20 % after the Millennium Drought (2000–2009) and almost 25 % after the Big Dry (2017–2019). The best predictors of mortality differed after each drought. While north-facing aspect of a sampling location was significant positive predictor after both droughts, biomass density and slope were significant negative predictors only after the Millennium Drought, and distance to the north-west corner of the population, which intercepts hot, dry winds, was a significant positive predictor after the Big Dry only. This suggests that more marginal sites with low biomass and sites located on flat plateaus were more vulnerable initially, but that heat-stress was an important driver of dieback during the Big Dry. Therefore, the causative drivers of dieback may change during population decline. Regeneration occurred predominantly on southern and eastern aspects, which would receive the least solar radiation. While this refugial

population is experiencing severe decline, some gullies with lower solar radiation appear to support relatively healthy, regenerating stands of red stringybark, providing hope for persistence in small pockets. Monitoring and managing these pockets during future droughts will be essential to ensure the persistence of this isolated and genetically unique population.

1. Introduction

Large-scale, stand-level dieback of trees is a global phenomenon that is intensifying under global change (George et al., 2022; Hammond et al., 2022; Hartmann et al., 2022). Stand-level tree dieback refers to stands of dead or dying trees, typically occurring in several locations in the landscape (Mueller-Dombois, 1986). Various causes of stand-level dieback have been proposed, including natural causes such as the collapse of dominant species during successional processes, natural or climate-change-enhanced disturbances (such as droughts and heatwaves), introduced or native pathogens or pests, and pollution (Mueller-Dombois, 1986; Wang et al., 2012). Furthermore, anthropogenic impacts, such as landscape-scale habitat transformation and various forms of pollution, can create stress in trees, rendering them more vulnerable to natural disturbances and pest species (Breshears et al., 2005; Carnicer et al., 2011).

Droughts are increasing tree mortality globally and are a trigger for stand-level dieback events (Choat et al., 2018; George et al., 2022; Hartmann et al., 2022). The relationship between drought and mortality is complex and influenced by various factors, including interactions among stressors, inter- and intra-specific interactions, and fine-scale environmental variation (Haberstroh and Werner, 2022; Trugman et al., 2021). The latter often produces patchiness in drought-related dieback (Evans and Lyons, 2013; Stephenson et al., 2018), with higher mortality often found in water-limited sites, such as steeper and equator-facing slopes and in shallow soils (Brouwers et al., 2013; Guarín and Taylor, 2005; Stephenson et al., 2018). Furthermore, the relationship between water availability and mortality is non-linear, meaning catastrophic hydraulic failure may occur at certain thresholds (Brown et al., 2018; Choat et al., 2018) that could be exceeded earlier in more vulnerable locations.

Anthropogenic climate change is causing warmer climates with more extreme events worldwide (IPCC, 2021). Droughts are becoming more prolonged and hotter, a phenomenon that has been termed climate-change-type droughts (Breshears et al., 2005; Carnicer et al., 2011), and are predicted to increase dieback in tree populations (Camarero et al., 2021). Mediterranean biomes are characterized by cold, wet winters and hot, dry summers, with droughts, fires, and heat waves being relatively regular disturbances (Cowling et al., 2005). They are predicted to experience large reductions in precipitation and more intense disturbances (Tramblay et al., 2020), and thus are considered particularly vulnerable to climate change (Klausmeyer and Shaw, 2009; Yates et al., 2010). Although trees in these ecosystems are adapted to fluctuations in temperature and extended droughts, large-scale drought-related mortality is being increasingly reported and there is concern for the persistence of many forests in Mediterranean biomes (De Kauwe et al., 2020; Matusick et al., 2013; Sánchez-Salguero and Camarero, 2020).

Refugia are locations that are buffered to varying degrees from changing environmental conditions, providing a retreat for organisms during adverse conditions and a springboard to recolonize the surrounding landscape should the conditions there become suitable again (Keppel et al., 2012). During the last glacial maximum (LGM) in the Pleistocene, such refugia played a key role in retaining biodiversity and facilitating subsequent recolonization of landscapes (Byrne, 2008; Ordonez and Svenning, 2015; Smith et al., 2022). While refugia are often characterized by high biodiversity (Keppel et al., 2018), molecular approaches are required to conclusively identify refugia and to determine whether they have persisted since the Pleistocene (Byrne, 2008; Molina-Venegas et al., 2017).

The buffered environmental conditions characteristic of refugia may arise due to their geographic location or topographic position. For example,

the Channel Islands of California are providing a safe haven from drought-induced stress on the mainland (Ramirez et al., 2020) and karst depressions offer conditions that facilitate the persistence of cold-adapted plants in the warming landscapes of Central Europe (Bátori et al., 2019). Hence, refugia are potentially important for facilitating in situ survival and regeneration of organisms under ongoing anthropogenic climate change (Keppel and Wardell-Johnson, 2012; Morelli et al., 2020). However, refugia may not be indefinite safe havens because of limits to the amount of environmental change that they can buffer (Keppel et al., 2015). Furthermore, conditions during past climate change, such as the LGM, differed from ongoing and predicted climate change, potentially making populations in Pleistocene refugia vulnerable to extinction (Jiménez-Alfaro et al., 2016; Keppel et al., 2017).

Despite the potentially catastrophic impacts of stand-level dieback and the limits of refugia to facilitating the persistence of biodiversity, our understanding about both remains limited. For the limits to refugial capacity, we urgently need to understand how and when refugia cease to be safe havens for biodiversity under climate change. For dieback events, we need better data on the rates, drivers, and demographic variability of forest mortality and regeneration (Hartmann et al., 2018; Shriver et al., 2022). However, causes of dieback are often complex (Guerin et al., 2022; Trugman et al., 2021) and the progression of dieback is difficult to document because of a lack of long-term data (De Kauwe et al., 2020). This study investigates the impact of successive droughts on the health and dynamics of a refugial tree population,

We document the dieback over 15 years in an isolated population of red stringybark (*Eucalyptus macrorhyncha* F.Muell. ex Benth. subsp. *macrorhyncha*) in the Clare Valley of South Australia through two major drought events, the Millennium Drought (2000–2009) and the Big Dry (2017–2019). Monitoring >400 trees that were tagged within two years of dieback being first reported, we investigate the progression and potential drivers of the dieback through the two drought periods. In particular, we ask 1) Does the population indeed constitute a refugium?, 2) What is the current health status of the population?, 3) How do environmental variables relate to observed mortality after the two drought periods?

2. Materials and methods

2.1. Study species

The red stringybark is a tree with rough, grey bark that comes off in strings. The species is widespread in south-east Australia with an outlying population in South Australia restricted to the Clare Valley, over 500 km west of its major distribution area (Fig. 1). Climatically, summer aridity in the Clare Valley population is greater than in the more eastern populations (Fig. S1). Elevation in the Clare Valley mostly ranges between 400 and 570 m, with red stringybark being mostly restricted to shallow soils at higher elevations on the western ridge, which intercepts weather systems from the west (Boomsma, 1949). The species has medium to high susceptibility to hydraulic failure (Li et al., 2019), especially in the northern parts of its distribution (De Kauwe et al., 2022), and dieback has been observed throughout the species' distribution (see Dead Tree Detective database: https://biocollect.ala.org.au/acsa/project/index/77285a13-e231-49e8-b212-660c66c74bac; accessed 11 November 2022). Red stringybark is relatively slow growing (Blackman et al., 2019), typically single-stemmed (Barker et al., 2016), and can reach 35 m in height (Brooker and Slee, 1996), although in South Australia it rarely exceeds 17 m (Barker et al., 2016).
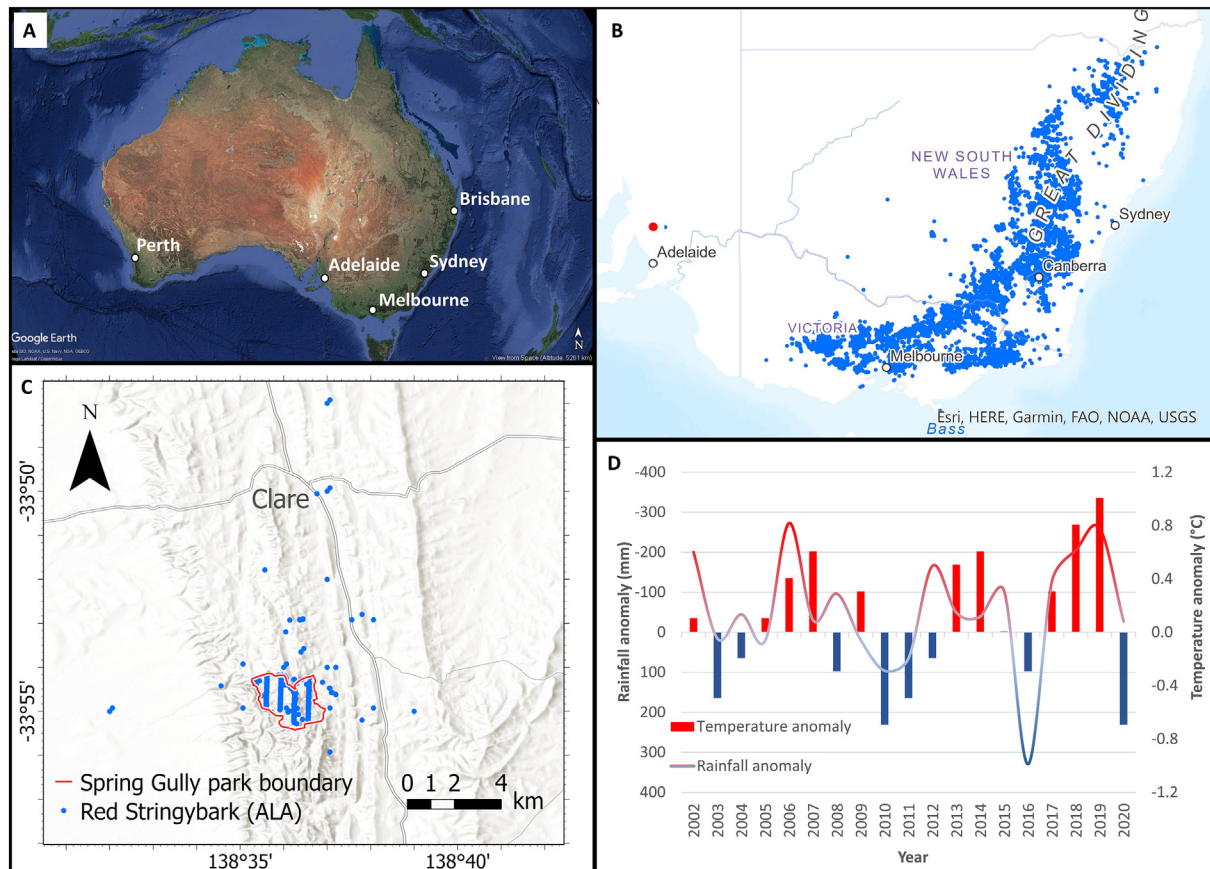
Fig. 1. Distribution of the red stringybark, *E. macrorhyncha*, in Australia and the Clare Valley (inset) and climate anomalies in the town of Clare. A: Map of Australia (source: *Google Earth*; data: SIO, NOAA, U.S. Navy, NGA, GEBCO; image: Landsat / Copernicus) with the location of major cities added. B: Distribution of red stringybark in Australia with the outlying population in the Clare Valley north of Adelaide (red dot) based on records (blue dots) in the Atlas of Living Australia (https://www.ala.org.au/; accessed 29/3/2021 and filtered to spatial uncertainty within 1 km) with records that are doubtful or referring to trees in cultivation removed. C: Distribution of red stringybark in Clare Valley (blue dots) based on the same source as for B and the location of the town of Clare, 7 km North of Spring Gully Conservation Park (SGCP). Boundaries of the SGCP are delineated in orange. D: Anomalies in mean maximum temperature and mean rainfall 2002–2020 for Clare. Note the inverted y-axis for rainfall, with rainfall deficits being shown above the y-axis. Anomalies were determined by comparing values over the last two decades (2000 − 2020) with the average from 1960 to 1990. Data was obtained for the Clare High School station (ID: 021131) and its predecessor, the Clare Post Office station (021014, years included: 1960–1994). Data Source: Bureau of Meteorology (http://www.bom.gov.au/climate/averages/tables/cw_021131.shtml; accessed 15 July 2022).

2.2. Study site

This study took place in Spring Gully Conservation Park (SGCP; 33°54′40.32″S, 138°35′43.44″E; Fig. 1c) within the Clare Valley, a well-known wine region that is on traditional Kaurna and Ngadjuri land. European settlers undertook heavy logging and livestock grazing in this 400 ha reserve before its establishment in 1961 to preserve the only population of red stringybark in South Australia (DENR, 2010). Vegetation in the park is mostly low open forest with monodominant red stringybark, and small areas where the South Australian blue gum, *Eucalyptus leucoxylon* F.Muell. subsp. *pruinosa* (F.Muell. ex Miq.) Boland (hereafter 'blue gum'), and drooping she-oak, *Allocasuarina verticillata* (Lam.) L.A.S.Johnson, are common. In the mid-stratum, *Xanthorrhoea quadrangulata* F.Muell., and *Bursaria spinosa* Cav. subsp. *spinosa* are common. The ground stratum is varied and often dominated by *Hibbertia exutiacies* N.A.Wakef. and *Lissanthe strigosa* subsp. *subulata* (R.Br.) J.M.Powell, and mixed herbaceous species and grasses (Guerin et al., 2014). The soils are acidic (pH = 5.3–5.8) and non-calcareous (TERN, 2018).

The climate is Mediterranean, with hot, dry summers and cold, wet winters (Fig. S2). Generally, winds from the north and west carry warmer, drier air from arid landscapes, while winds from the south and east are cooler and more likely to carry moisture {Al-Obaidi et al., 2021; Pezza et al.,

2012). The last two decades were warmer and drier than the average of 1960 to 1990, with warmer temperatures and lower precipitation during the two climate-change-type droughts, the Millennium Drought and the Big Dry (Fig. 1d). The Millennium Drought appears to have been shorter in the Clare Valley than on the continental scale (2005–2009 versus 2001–2009). The three fires recorded in the park by the South Australian Department for Environment and Water (DEW; http://spatialwebapps.environment.sa.gov.au/firemaps/; accessed 12 October 2022) since 1931 only impacted the edges of the park and not the study sites (Fig. S3). While red stringybark is known to be susceptible to *Phytophthora cinnamomi* (Weste et al., 1973), this pathogen has not been reported north of Gawler, c. 90 km south of the study site (DEW, 2021).

2.3. Molecular analyses

Population samples of red stringybark were collected from SGCP and from the broader range of the species (Fig. 2). Genomic DNA was extracted from the silica dried samples by AgriTech-Intertek (https://www.intertek.com/agriculture/agritech/) using *sbeadex chemistry* developed by LGC Biosearch Technologies (http://info.biosearchtech.com/sbeadex-for-agbio). DNA sequencing libraries were prepared in-house, using a hybrid capture approach to target several low-copy nuclear gene regions
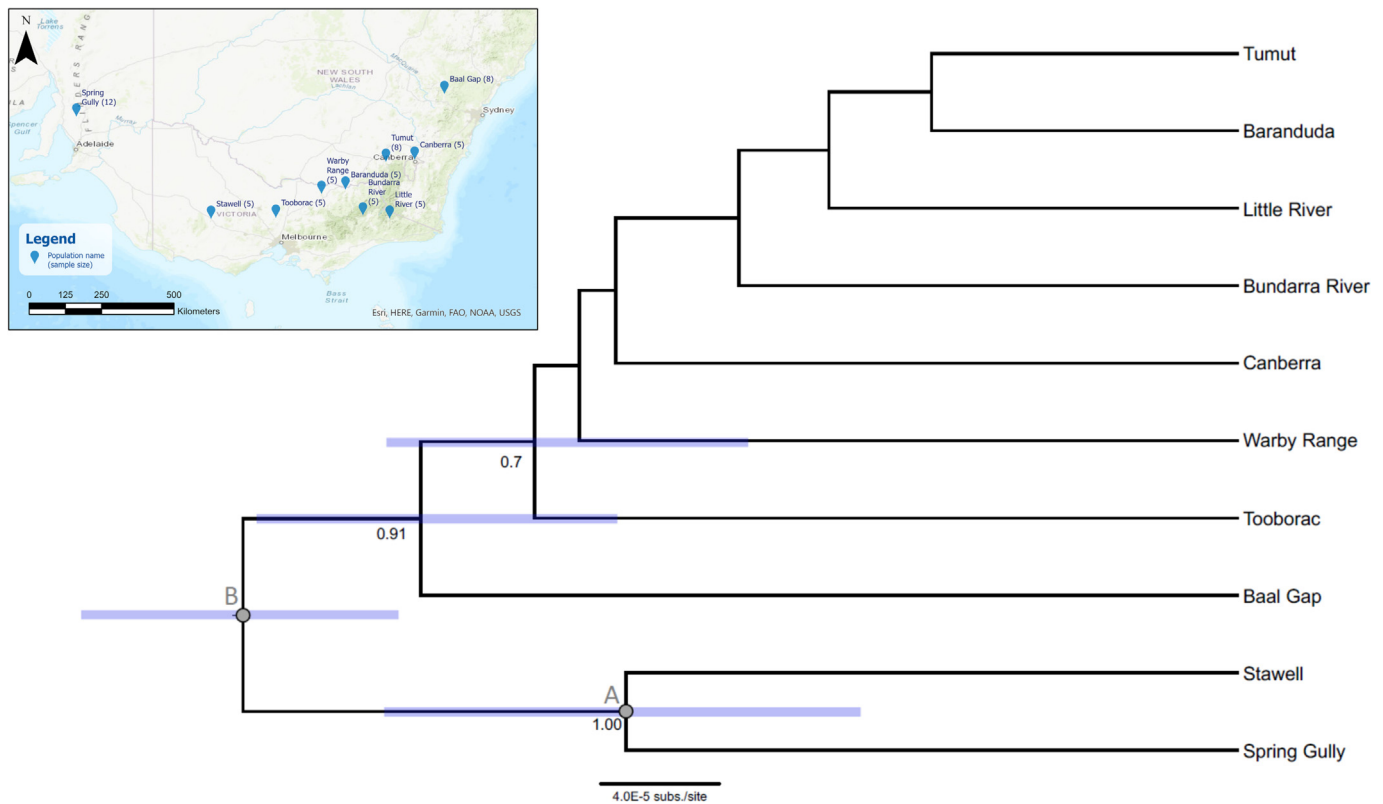
Fig. 2. Sampling locations and maximum clade credibility tree for red stringybark, *E. macrorhyncha*, populations inferred using the AIM model in *BEAST inferred from low copy nuclear gene regions. Note that the 'Spring Gully' population is the focus of this study and was hypothesized to be relictual. Posterior probabilities ≥0.5 are indicated adjacent to the branch and branch lengths (substitutions/site, scale bar indicated) are proportional to time. Blue bars indicate the variation in branch length estimates (95 % highest posterior density) around that node. Nodes marked A and B are referred to in the discussion. The inset map shows the sampling locations and sample sizes (n). All populations represent *E. macrorhyncha* subsp. *macrorhyncha*, with the exception of Baal Gap, NSW, which represents *E. macrorhyncha* subsp. *cannonii* (R.T.Baker) L.A.S. Johnson & Blaxell.

(Table S1) with methods and protocols as outlined in Waycott et al. (2021). The prepared libraries were sent to the Australian Genome Research Facility (AGRF) for Illumina paired-end (2 × 150) sequencing.

The pooled paired-end data were demultiplexed and quality trimmed (Phred-score threshold of 20) using *CLC Genomics Workbench v7.5.1* (https://www.qiagenbioinformatics.com). We used de novo assembly (length and similarity fraction = 0.9) of pooled samples to generate a set of reference contigs for the species. The de novo contigs were converted to a BLAST database and we used reference genomic sequences in *Eucalyptus grandis* (downloaded from *Phytozome v 12.1*, https://phytozome. jgi.doe.gov\) as query sequences. The de novo contigs matching the *Eucalyptus* genes were then used as a reference for each individual to generate a per sample mapping for each locus. The resultant mapping files were exported in BAM format and allele phasing was performed on the BAM files using *SAMTools Phase* (Li et al., 2009). Consensus sequences were generated for each allele per locus and individual using a coverage cut-off of 10. Allele sequences were imported into *Geneious v1.11.5* (Kearse et al., 2012), aligned using the *MUSCLE* (Edgar, 2004) plugin with default parameters and each alignment was manually checked and adjusted.

We used the AIM (Approximate Isolation-with-Migration; Müller et al., 2021) model in * *BEAST* (Heled and Drummond, 2010) to infer phylogenetic relationships between sampled populations. This approach uses the multi-species coalescent model (MSC; Heled and Drummond, 2010; Liu et al., 2009) to infer a species tree while accounting for discordance among gene trees due to incomplete lineage sorting. However, standard implementations of the MSC assume complete isolation of lineage after they have split, while ongoing gene flow can lead to biased estimates of the evolutionary history of the species (Leaché et al., 2014). The AIM model allows the inference of the species tree under the MSC while explicitly modeling gene flow between lineages (Müller et al., 2021). For each

genetic region, we used the HKY + I + G model of sequence evolution with empirical base frequencies and a strict molecular clock model that were linked across gene regions and parameters of the AIM model (effective population size and migration rate) were estimated from the data. Two independent analyses were conducted, each of 2.0 × 108 steps. Convergence between analyses and the appropriate burn-in fraction were assessed using Tracer v1.6.0 (Rambaut et al., 2015) and a summary tree was generated using TreeAnnotator v2.5.1 (part of the *BEAST* package).

2.4. 2009–2014 surveys

Because a sudden dieback of stringybark trees was observed in SGCP from 2007 to 2008 (Clarke, 2021), DEW initiated a tree health monitoring program in 2009, during which four north-south oriented transects were established (Fig. S3). Each transect (between 1.2 and 1.8 km long) had sampling sites every 50 m. At each sampling site, the four closest canopy trees within a 10 m radius were marked with a permanent aluminum tag, their location recorded with a handheld GPS (brand and model unknown), and various measurements relating to their health status taken (see below). In total, 471 trees were surveyed, 30 of which were blue gums and the remainder were red stringybark.

Following the methods outlined by Souter et al. (2010), tree condition assessment parameters were recorded by DEW staff during surveys of all trees in January and February 2009, March 2010, November 2011, August 2012, November 2013, and September 2014. Parameters recorded included tree status (dead/ alive), crown extent (percentage area of assessable crown with live leaves), and crown density (percentage of skylight blocked by the leafy crown). Percentage values were recorded as eight categories: 0 (0 %), 1 (1–10 %), 2 (11–20 %), 3 (21–40 %), 4 (41–60 %), 5 (61–80 %), 6 (81–90 %), and 7 (91–100 %). The assessable crown was

defined as consisting of all living and dead branches of the crown. Crown extent and density are important indicators for water stress (e.g., drought, root rot), as *Eucalyptus* trees tend to respond to water stress by reducing leaf area – initially through reduced density and then reduced extent of the crown, which reduces water demand and thermal stress (Souter et al., 2010).

In addition, epicormic growth and extent of reproductive activity (presence of flowers and/or fruits) was classified as four categories: 0 (absent, not visible), 1 (scarce, present but not readily visible), 2 (common, clearly visible throughout the assessable crown), 3 (abundant, dominates the appearance of the assessable crown). Epicormic growth is the growth of shoots (≤ 3 cm in diameter) from the main trunk or major branches after environmental stress (Souter et al., 2010). All trees were checked for mistletoes, but none were found.

As recommended by Horton et al. (2011), we used a summative index consisting of canopy extent, canopy density, and epicormic growth to indicate tree health – hereafter referred to as the tree health index (THI). We did not include reproductive ability in the THI because reproduction could be seasonal, affecting comparability among surveys. While epicormic growth is an indicator of favourable conditions that allow regrowth, it is also the result of prior medium to high water stress (Souter et al., 2010). We decided to include epicormic growth despite these dual connotations because it avoided the possibility of THI = 0 for trees persisting with epicormic growth only. Because crown extent and density are considered the most important indicators of tree health (Souter, 2019), we retained them at their larger scale (0–7, compared to 0–3 for epicormic growth), giving a maximum value of 17 for the THI. Trees that appeared dead at some surveys but that later resprouted (i.e., epicormic growth or basal sprouts), were retrospectively awarded a THI score of 1 (instead of zero).

2.5. 2021 Resurvey

In September and December 2021, we revisited all trees that had been surveyed and tagged previously. Relocation of trees was achieved with high confidence because of the availability of GPS locations for each tree and because tags remained on, or had fallen directly beneath, at least two of the four trees at each site. Due to potentially high spatial errors of up to 10 m (especially in rugged terrain) and the loss of some tags, sometimes extensive searching was required to locate the four trees at each site. Six sites consisting entirely of blue gum were not resurveyed, as this species was not the focus of our surveys and did not display signs of dieback. Methods for the resurvey focused on replicating the methods used in the earlier surveys (to facilitate comparisons) and on collecting additional information on the size of trees and to provide area-based estimates of dieback. It should be noted that assessment of tree condition may differ between individual observers (Ferretti, 1998; Souter et al., 2010).

To achieve area-based estimates, we determined a center point for each site so that each of the four trees at a site was in a different quarter (delineated using the four cardinal directions). For sites with one or more blue gum trees among the four surveyed trees, blue gums were replaced by the nearest stringybark in the relevant quarter. In one instance, no nearest stringybark neighbour was present within 10 m and this site was excluded from analyses including biomass density. Additional trees were added to four sites that had less than four trees surveyed when transects were established. This resulted in a total of 112 sites with 448 trees of red stringybark. This allowed estimating the tree density per hectare at each site using three steps: 1) measuring the distance of each tree to the center point, 2) averaging the four distances, and 3) multiplying the inverse of the squared average distance by the value of the desired area (in this case 1 ha). This approach follows the point-centered quarter method (Cottam and Curtis, 1956; Mueller-Dombois and Ellenberg, 2002). As 50 sites are considered necessary for accurate estimates of tree density (Khan et al., 2016), our total estimates of tree density should be reliable, while site-based estimates are prone to error.

To estimate biomass, we recorded diameter at breast height (DBH) and tree height for each stem of a tree (trees regularly had multiple stems),

living or dead – note that these parameters were not recorded during previous surveys. As was practiced during the initial surveys, trees with dead stems weres considered alive if there was any epicormic or basal growth present. A stem was considered alive if epicormic growth was present above 1.3 m in height. The height (Ht) was estimated to the nearest meter using a 1.5 m range pole that was held up vertically overhead to provide a reference of approximately 3.5 m height. The DBH was measured using a diameter tape 1.3 m above the ground. A wood density (WD) of 795 (± 19) kg.m^{-3} was assumed for all trees, based on measurements of 15 specimens from east coast populations (Ilic, 2002). We used these values to calculate the above-ground biomass (AGB) following Chave et al. (2014) as: AGB = $0.0673 \times (WD \times DBH^2 \times Ht)^{0.976}$. AGB was determined for every stem and then aggregated per tree, meaning a single individual could be composed of both living and dead biomass. Following the approach by Cottam and Curtis (1956) for basal area, we multiplied the estimate of number of individuals per hectare by the mean AGB per tree to obtain area-based estimates of biomass, i.e., biomass density. These calculations were done for each site (to obtain estimates of biomass density per site) and for all 112 sites combined (to obtain a parkwide estimate).

As an estimate of regeneration, the occurrence of seedlings (< 1 m tall, woody growth lacking) and saplings (< 1 m tall, woody growth present) within a 3 m radius of the center point was recorded. Seedling and sampling numbers for each site were combined to provide an indicator of recruitment. In addition, aspect (in degrees rounded to 10° intervals and determined with a compass) and slope (in degrees using a clinometer) were recorded for each site. We calculated 'northness' and 'eastness' as the cosine and sine of the aspect (in radians), respectively (Fassnacht et al., 2003). Where trees within a site were located on different slopes in a valley, the aspect and slope were recorded for each slope and then averaged.

2.6. Data analysis

To get an indication of trends in the health status of the red stringybark population, the proportion of dead trees and the THI of all 441 stringybark trees surveyed repeatedly since 2009 were determined ('THI' dataset; Keppel, 2022). Note that for THI calculations, 12 trees that were surveyed only during the first (2009) and last (2021) survey were excluded. Mortality rates are considered to be a robust indicator of forest health, while the health status of trees is often difficult to assess objectively (Hartmann et al., 2018). To illustrate changes in the mortality rate between the two droughts, all 441 trees were assumed to have been alive in 2006, which is reasonable because dieback was first reported in 2007 and all trees surveyed in 2009 still had their bark present.

To get an indication of the proportion of trees and biomass lost, we calculated the overall proportion of dead trees and proportion of dead AGB of the 448 stringybark trees surveyed in 2021 ('Biomass' dataset; Keppel, 2022). Data manipulation and basic analyses were undertaken in *Microsoft Excel*. *ArcGIS Pro* was used for spatial analyses and to illustrate the patterns of mortality spatially. Because north-westerly winds draw hot, dry air masses from the inland of the Australian continent, they can considerably increase the intensity of heat waves (Al-Obaidi et al., 2021; Pezza et al., 2012). Therefore, distance to the north-west corner of the population (the area likely to be most affected by hot, dry summer winds) was calculated as the planar distance to each sampling location using the *"Near (Analysis)"* geoprocessing tool.

All subsequent analyses were implemented in the *R statistical environment* (R Core Team, 2021; Table S2). Because the relationship between tree height and drought vulnerability remains unresolved (Trugman et al., 2021), we tested whether indicators of tree size within a site (DBH [using the highest value for multi-stemmed trees], Ht, AGB, number of stems) were related to a tree being alive (0) or dead (1) within a site. We used generalized linear mixed models with a binomial error structure and sampling site as a random effect, implemented for each indicator using the *lme4* package (Bates et al., 2022).

Across sites, we used the 112 sites of the 2021 survey ('Drivers' dataset; Keppel, 2022) but included only trees that were surveyed in 2011 as well,

including a total of 441 trees. We estimated mortality for each site after the Millennium Drought (Mortality 2006–2011), as the proportion of dead trees per site in 2011, which was the first year definitely not affected by this drought that ended in 2009 (Fig. 1d). Mortality after the Big Dry

(Mortality 2014–2021) was estimated by calculating the proportion of dead trees in 2021 of those that were still alive in 2014 (the last year of the last survey before the drought), but only for sites that had a minimum of two living trees in 2014, meaning that 12 sites were excluded. We used

A Mortality Rate

B Tree Health Index (THI)

C Indicators of tree health
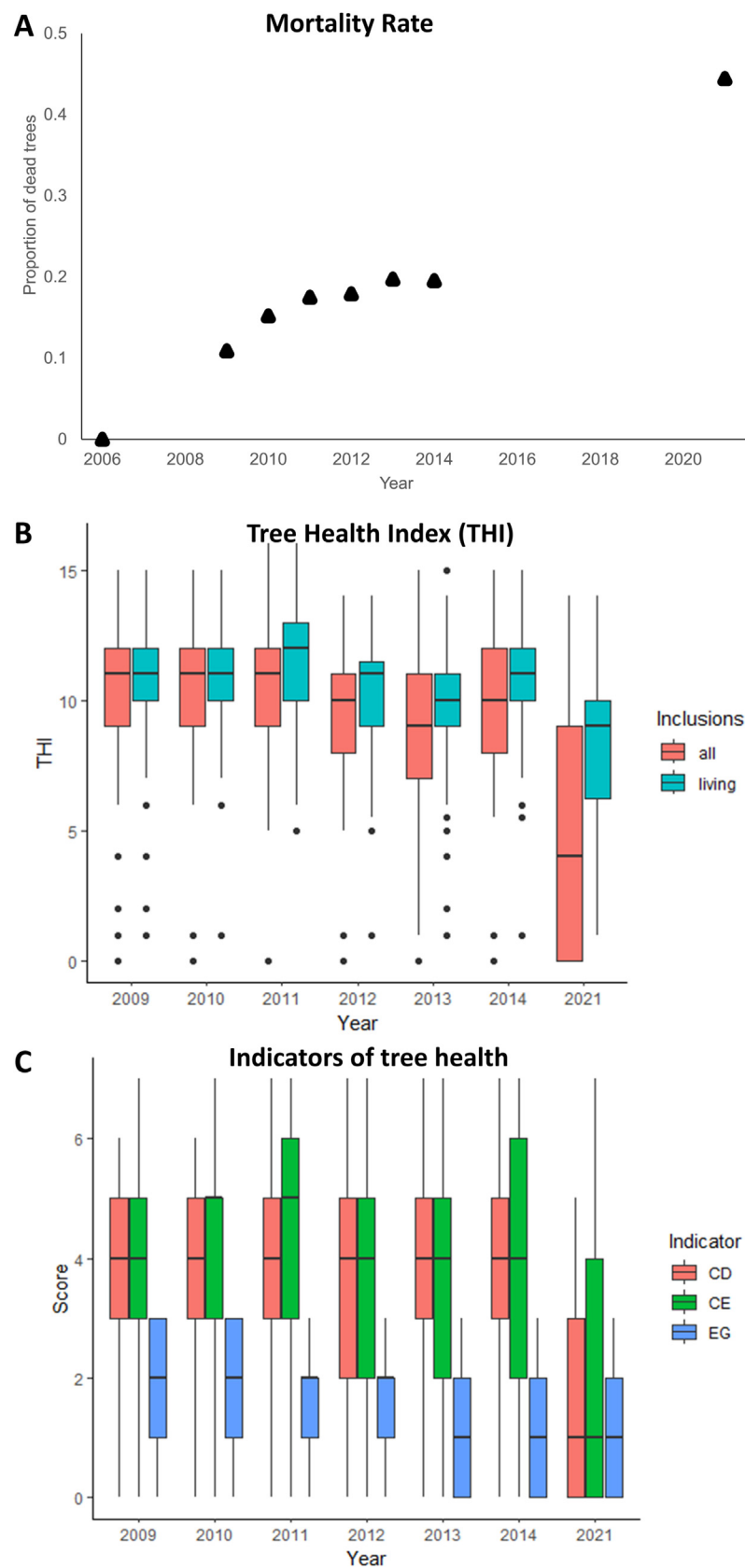
Mortality 2006–2011, Mortality 2014–2021, and regeneration observed in 2021 as indicators of dieback and persistence (response variables). Because the response variables were proportions and count data, we used generalized linear models (GLMs) with quasibinomial and negative binomial error structures using the *MuMin* (Bartoń, 2022) and *MASS* packages (Ripley et al., 2022), respectively. Because regeneration had a high number of zeros, we also implemented a zero-inflated binomial model concurrently using the *pscl* package (Jackman, 2020).

To investigate potential drivers of dieback, we investigated various environmental (northness, eastness, distance to the north-western corner of the population (dNW)) and biological variables (tree density, and biomass density (tons of AGB per ha)) as potential explanatory variables. Based on widely used approaches (Zuur and Ieno, 2016; Zuur et al., 2010) to guide data exploration and analyses, we implemented the following analytical approaches. Because tree density and biomass density were strongly correlated ($r = 0.64$, $p = 2.3 \times 10^{-14}$), we only retained biomass density. Measures of the amount of biomass per unit area, such as biomass density, can be an indicator of sites with growing conditions that are more marginal, as resource limitations can reduce growth rates and maximum height (Klesse et al., 2022; Pan et al., 2013). Because visual exploration revealed the relationships between the response variables and biomass density and dNW to be curvilinear, we transformed these two explanatory variables using $\log_{10}$. All explanatory variables were scaled for effect comparison to a mean of zero with a standard deviation of 1 using the *standardize* package (Eager, 2021).

We scanned for any potentially significant two-way or three-way interactions as predictors of mortality by implementing automated model ranking on all possible three-variable combinations using the *dredge* command of the *MuMin* package (Bartoń, 2022). The following interactions were within a ΔAIC of 2 and were therefore added to the global model; Biomass Density: Northness, Biomass Density: dNW, Northness: Slope, Biomass Density: Slope, and dNW: Slope. We then undertook stepwise model simplification, removing one non-significant variable at a time, beginning with any interactions, and using the Akaike Information Criterion (Akaike, 1974) and ANOVA test (difference needed to be non-significant) between the two models to ensure that the performance of the model did not decrease significantly due to the removal of a variable. The final 'best' model included only significant variables. Where the final model included both eastness and northness, we also ran models with only one of these included, as both are derived from the aspect. The significance of the best models was assessed by calculating the *p*-value associated with X^2 (= Null deviance – Residual deviance) and the respective degrees of freedom. A pseudo-coefficient of determination was calculated as $r^2 = 1 - (\text{residual variance/null variance})$ and used as a measure of model fit (Swartzman et al., 1995). Trends in the variables between surveys were illustrated by plotting the effect sizes of all explanatory variables (without interactions) in relation to mortality from 2006 to 2011 and 2014–2021 using the *jtools* package (Long, 2022).

3. Results

The summary species tree inferred for the red stringybark populations using the AIM model in *BEAST2 (Fig. 2) resolves the SPCP population with strong statistical support as sister to the Stawell population, from western Victoria. These populations are sister to a lineage including *E. macrorhyncha* subsp. *cannonii* from the NSW Central Tablelands (the Baal Gap population), along with all other populations sampled from the eastern part of the species range.

The two major dieback events, broadly corresponding to the Millennium Drought (2000–2009) and the Big Dry (2017–2019) were detected in the red stringybark population at SGCP. Of the 441 trees first surveyed in 2009 (and assumed to be alive in 2006), 44.4 % had died by 2021, including about 17.5 % between 2006 and 2011 and 24.5 % between 2014 and 2021 (Fig. 3a). There was some delayed mortality after the Millennium Drought ended in 2009, with a mortality of 4.5 % between 2010 and 2013.

The droughts also affected the tree health index (THI), with a clear decline in the index after the Big Dry (no data before the Millennium Drought was available or could be inferred). However, during the years of annual surveys (2009–2014), the THI appeared to be relatively stable, with only a minor decline from 2012 onwards and some variability among years. The decline in THI was not solely due to the death of trees but was also evident when only considering trees still alive in 2021 (Fig. 3b). The overall pattern for the THI was reflected in its individual components, canopy density, canopy extent, and epicormic growth (Fig. 3c).

Of the 448 trees surveyed in 2021, about 42.6 % were multi-stemmed, with 854 stems surveyed. Generally, trees had 2, 3, 4 or 5 stems, but three trees had >10 stems (maximum 13 stems). Assuming all trees were alive before the two droughts, these 448 trees would have had an AGB of approximately 162,780 kg (range = 167,468–158,576 kg; based on variation in wood density, see methods) and an average density of about 1464 trees/ha. After the two droughts, 408 stems (47.7 %), 194 trees (43.3 %; Fig. 2b), and about 73,889 kg of biomass (45.5 %) had been lost from the original 448 trees monitored.

While dieback was encountered throughout the population, mortality was not evenly distributed (Fig. 4). Sites with high mortality were more concentrated in the center and the north-west corner of the population, while the north-east was seemingly least impacted. Many areas that did not display mortality after the Millennium Drought were affected by the subsequent Big Dry. The mixed effect models suggested that neither the diameter (DBH; $z = -0.656$, $p = 0.512$), height ($z = -1.552$; $p = 0.121$), number of stems ($z = -1.210$, $p = 0.226$), nor the above-ground biomass (AGB; $z = -1.178$, $p = 0.239$) of trees were significantly related to whether a tree was alive or dead within a site. However, all relationships were negative, indicating a non-significant tendency for dead trees to have smaller stems, shorter heights, less stems, and lower AGB.

There was a shift in the potential causative drivers of mortality (i.e., the environmental variables significantly correlated with the proportion of dead trees per site) identified after each of the droughts (Fig. 5). Northness, biomass density, and slope were significant predictors of mortality from 2006 to 2011 (Table 1). Of these, only northness remained a significant correlate of mortality from 2014 to 2021. Note that slope was negatively correlated with mortality, meaning that mortality was lower on steeper slopes. For mortality from 2014 to 2021, the distance to the north-west corner of the population (dNW) was the only significant variable besides northness. Biomass density and slope were no longer significant correlates of mortality.

Regeneration, which here includes both seedlings and saplings, was observed in just over 30 % of the 112 sites (Fig. S4). It displayed a positive relationship with eastness and a negative relationship with northness, suggesting seedlings and saplings were most frequently observed on south-eastern aspects. However, eastness became non-significant ($p = 0.053$) when being the sole variable in the model, while northness remained significant ($p = 0.018$).

4. Discussion

We found the isolated population of red stringybark in Clare Valley to be genetically unique, suggesting isolation and persistence in this refugium

Fig. 3. Tree health in the red stringybark population in Spring Gully Conservation Park (SGCP) from 2001 to 2006. A: Proportion of dead trees among 441 surveyed red stringybark trees on SGCP during seven surveys from 2009 to 2021, indicated using triangles. The 2006 value assumes that all surveyed trees were alive before the observed dieback in 2007. B: Changes in the tree health index (THI; range: 0 (dead) to 17 (healthiest)) among all 441 surveyed red stringybark trees in SGCP, and for 222 trees that remained alive during seven surveys from 2009 to 2021. C: Changes in the canopy density (CD; range = 0–7), canopy extent (CE; range = 0–7), and epicormic growth (EG; range = 0–3), the three summative components of the THI, from 2009 to 2021. Note that values in B and C are reported annually from 2009 to 2014 and then again for 2021, Boxes in B and C indicate the interquartile range, the bar the median, and the whiskers extend up to 1.5 times the interquartile range.

Fig. 4. Maps showing locations of alive (green) and dead (red) red stringybark trees in 2011 (left) after the Millennium Drought and in 2021 (middle) after the Big Dry and those trees that died between 2011 and 2021 (right). Note that the locations of trees are illustrated using the "disperse markers" technique, which spreads point symbols that are too close for better visualization.

through climatic changes since well before the LGM. Nevertheless, >40 % of individuals and of the AGB have been lost over the last 15 years or so. Our results suggest that stand-level dieback can be a prolonged process, occurring in stages and being related to droughts. Furthermore, the tree health of remaining living trees is declining (Fig. 3b). Interestingly, the importance of environmental variables as correlates of mortality changed during the dieback process. Trees growing in sites with lower biomass and on plateaus, i.e., in sites that are potentially more marginal, had a higher probability of dying during the first drought, while trees close to the north-west corner of the population, i.e., sites potentially subjected to greater heat stress, were more vulnerable during the second drought. Hence, our study provides important insights into the changing dynamics of dieback during successive droughts. Therefore, the only remaining red stringybark forest ecosystem in South Australia is declining and potentially threatened with collapse. However, the persistence of the red stringybark population may not be tied to that of the ecosystem, as there are indications for prolonged survival and regeneration in small pockets, i.e., microrefugia, on south- and east-facing slopes that receive lower solar radiation (Fig. 6).

4.1. Long-term isolation

Inferred phylogenetic patterns among red stringybark populations support the early divergence of the SGCP population, along with the western Victorian (Stawell) population, from those further to the east (Node B,

Fig. 3). Similar patterns of deep divergence have been found in several sclerophyll plant lineages, such as *Callitris* (Worth et al., 2018), *Correa* (French et al., 2016), *Eucalyptus bicostata* (Freeman et al., 2001), *E. behriana* (Fahey et al., 2021), and *Hardenbergia violacea* (Larcombe et al., 2011). These disjunctions and high levels of endemism in the regional flora have been interpreted as evidence for the existence of refugial populations separated by the Lower Murray Basin during Pleistocene (e.g., Byrne, 2008).

The divergence between the SGCP and Stawell populations likely predates the LGM. Although there are no fossil data to calibrate molecular rates and divergence times, a genome wide per generation mutation rate has been recently estimated for *E. grandis* at 4.93×10^{-8} substitutions per site per generation (Silva-Junior and Grattapaglia, 2015). Using this rate, the split between the SGCP and Stawell populations (Node A, Fig. 3) is estimated to have occurred around 4000 generations ago. Assuming a generation time of at least 10 years (Silva-Junior and Grattapaglia, 2015), these estimates suggest population divergence that predates the LGM (c. 22–18 Ka) and that the Clare Valley population is refugial.

The Clare Valley population is also unique in other aspects. Climatically, it experiences higher summer aridity than the more eastern populations (Fig. S1). This may partly explain multi-stemmed individuals being common in the SGCP, despite the species being generally described as single-stemmed (e.g., Barker et al., 2016), as the species may resprout from below-ground epicormic buds when the main stem sustains drought
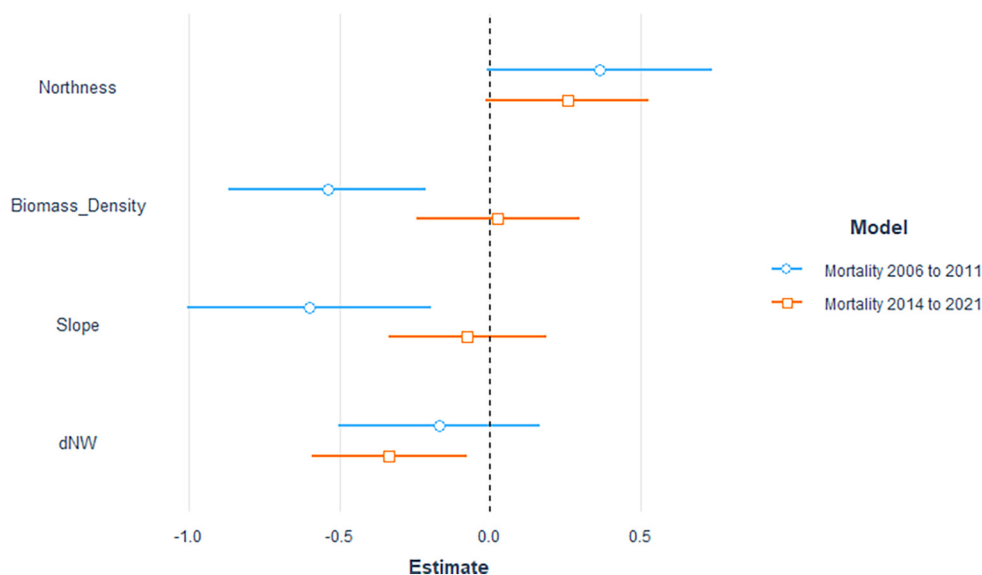

Fig. 5. Effect sizes of explanatory variables explaining site mortality from 2006 to 2011 and from 2014 to 2021. Generalized linear models (GLMs) with quasibinomial error distribution and including all four explanatory variables (eastness was excluded because it was not significant in either model) were used. Coefficient estimates (shapes) for each explanatory variable with 95 % confidence intervals (bars) are shown. dNW = distance to the north-west corner of the population.

Table 1

Best generalized linear models for red stringybark mortality from 2006 to 2011 and 2014–2021 and for regeneration in 112 sites in SGCP, Clare Valley, South Australia, with quasibinomial (mortalities) or negative binomial (regeneration) error distributions. Biomass density and distance to the north-west corner of the population (dNW) were log-transformed and all explanatory variables were scaled and centred.

Variable	Estimate	Std. Error	t value	P-value
Mortality 2006–2011				
Model Parameters: $X^2 = 14.38$, d.f. $= 3$, $p = 0.002$; pseudo-$r^2 = 0.242$				
Intercept	−1.811	0.199	−9.124	4.55×10^{-15}
Biomass density	−0.560	0.167	−3.343	0.001
Slope	−0.643	0.206	−3.114	0.002
Northness	0.387	0.192	2.014	0.047
Mortality 2014–2021				
Model Parameters: $X^2 = 4.13$, d.f. $= 2$, $p = 0.127$; pseudo-$r^2 = 0.090$				
Intercept	−0.795	0.131	−6.089	2.28×10^{-8}
northness	0.277	0.132	2.098	0.039
dNW	−0.336	0.130	−2.587	0.011
Regeneration				
Model Parameters: $X^2 = 10.57$, d.f. $= 2$, $p = 0.005$, pseudo-$r^2 = 0.121$)				
intercept	−0.0417	0.224	−0.186	0.853
northness	−0.559	0.2223	−2.516	0.012
eastness	0.468	0.2205	2.125	0.034

damage. Historical logging and subsequent basal sprouting may also explain the multi-stemmed habit in the Clare Valley. Furthermore, evolution in isolation over long time periods in unique environmental conditions would suggest that the species may have evolved unique adaptations, as has been found for other species of *Eucalyptus* (Steane et al., 2017), and future studies should investigate whether unique adaptations are present in this population.

4.2. Dieback: a prolonged process with shifting drivers

Our study provides further evidence that drought and heat can induce dieback in tree species (Matusick et al., 2016; Sánchez-Salguero and Camarero, 2020; Stephenson et al., 2018). Because the relationship between drought stress and dieback is not linear but related to physiological thresholds being exceeded (Allen et al., 2021; Brown et al., 2018), one would expect a proliferation of dieback events globally as these thresholds are being exceeded (Hammond et al., 2022). Given the predicted increases in extreme weather events because of anthropogenic climate change (Braganza et al., 2013; IPCC, 2021) and the increasing reports of dieback across biomes globally (Hammond et al., 2022), this raises concerns for the persistence of many tree populations (Brown et al., 2018; Hammond et al., 2022).

In the case of red stringybark population in SGCP, our results suggest that dieback is a prolonged process, occurring in stages and with changing causative drivers. During the first drought, the potential drivers associated with dieback were sites that are potentially more marginal (as indicated by low biomass density) or located on north-facing slopes and flat parts of the landscape. While the latter may seem counter-intuitive, the topography of the SGCP is such that flat topography is predominantly found on plateaus that have shallow soils and experience high solar radiation. Hence, sites that present more marginal growing conditions or have lower water availability were apparently the most vulnerable during the first drought. Both the marginality and lower water availability are well-documented drivers of dieback (Brouwers et al., 2013; Brown et al., 2018; Klesse et al., 2022; Stephenson et al., 2018) and red stringybark is potentially vulnerable to long-term water shortages due to a relatively shallow root system (Eberbach and Burrows, 2006).

An alternative explanation for the higher mortality on topographically less complex parts of the park could be historical anthropogenic
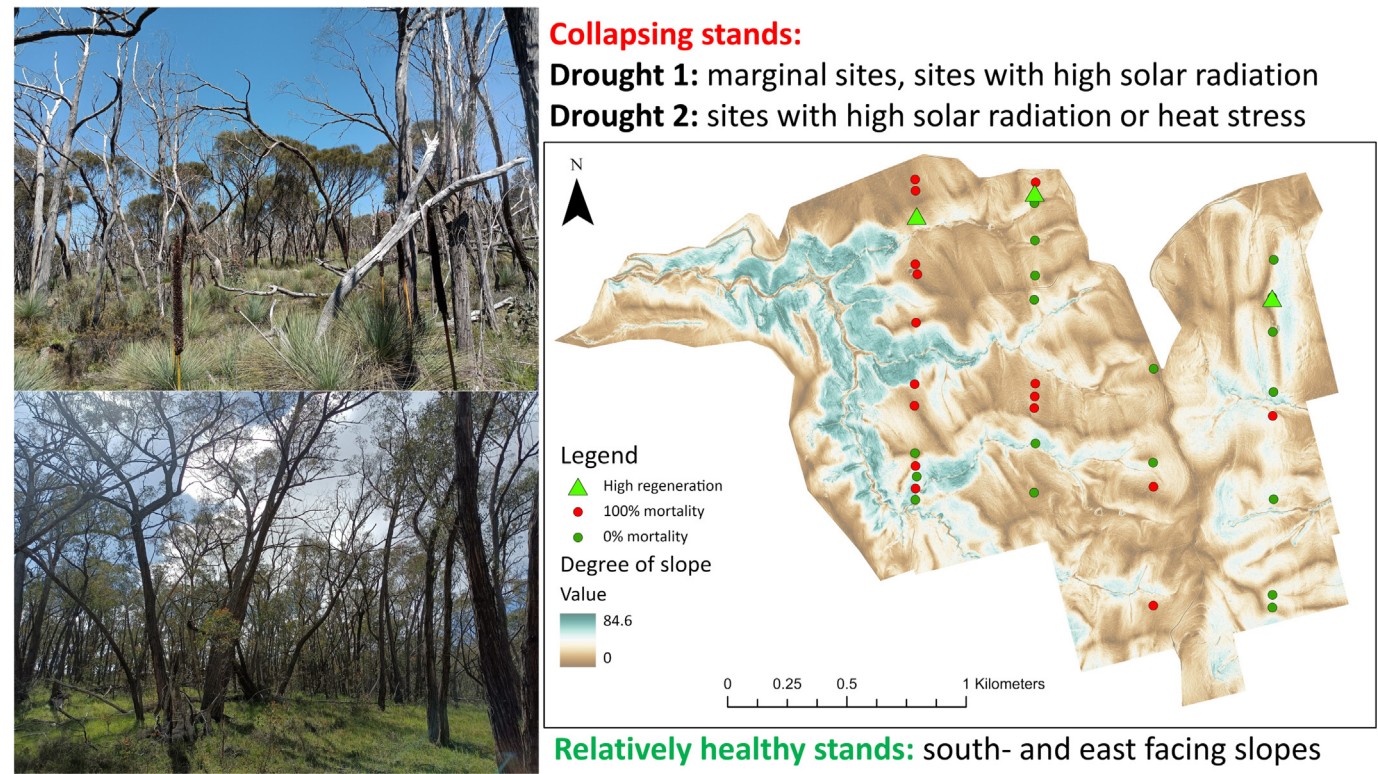

Fig. 6. Summary of the dieback process in the red stringybark population at SGCP, Clare Valley, South Australia. Widespread collapse of stands (100 % mortality of surveyed trees at a site; top picture) is observed at sites exposed to high solar radiation (i.e., excluding south-facing slopes) and sites that are potentially more marginal (i.e., lower biomass density, not shown on map). Relatively healthy stands of red stringybark with 0 % mortality and high regeneration ($\geq$ 10 seedling and saplings per 28.3 m^2) remain on south- and east-facing slopes (bottom picture). The map shows colour-coded terrain slope in % with cyan highlighting steep slopes and brown representing flatter terrain.

disturbance. The SGCP was extensively logged and grazed by livestock before protection (DENR, 2010). Both activities may have persisting legacy effects and were potentially most intensive on the topographically more subdued plateaus. Grazing can compact soils, change soil properties, remove leaf litter cover, cause erosion, and reduce water absorption (Byrnes et al., 2018; Yates et al., 2000). These changes may produce conditions unsuitable for some native species, as has been reported for woodlands dominated by *Eucalyptus salmonophloia* F.Muell. in south-western Australia (Yates et al., 2000). Logging can cause the release of remaining trees, with more rapid growth producing hydraulic tissue with greater conductivity but also higher vulnerability to drought failure (Camarero, 2017).

The second drought, the Big Dry, was seemingly hotter and drier (Fig. 1d). Locations believed to have been subjected to greater heat (north-facing slopes and parts of the park exposed to hot north-western winds) suffered greater mortality. Heat stress is another well-known driver of dieback (Guarín and Taylor, 2005; Matusick et al., 2018) and our results implicate it as a potentially major driver during the second drought. Higher mortality rates during the second drought could also be related to legacy effects persisting from the first drought, a phenomenon reported for interactions between droughts and subsequent heat waves (Matusick et al., 2018). Interactions between major disturbances can indeed have major impacts on ecosystems but can be difficult to document (Ibanez et al., 2022). Our results, therefore, provide important first insights into the impact of successive droughts, which remains a key knowledge gap (De Kauwe et al., 2020).

The differences that we observed between the two droughts with regard to the environmental variables most strongly correlated to tree mortality could have various explanations. One reason could be differences among the droughts, with the Millennium Drought being more prolonged, creating greater water stress, and the Big Dry being hotter, creating greater heat stress. These differences may have been amplified by the high topographic complexity, resulting in trees being exposed to differing stress levels and hence pushed beyond their physiological thresholds at different times. Alternatively, the Millennium Drought may have eliminated trees growing in locations most vulnerable to drought and heat stress and predisposed many less vulnerable to mortality during the Big Dry.

For some *Eucalyptus* species, a complex dieback syndrome has been reported, where drought and heat interact with other drivers such as fungal and insect attacks (Stone et al., 2008; Guerin et al., 2022). Indeed, drought has been repeatedly reported to be followed by attacks of insects or other pests (Carnicer et al., 2011; Trugman et al., 2021). Furthermore, stringybarks are known to be susceptible to the pathogen *Phytophthora cinnamomi* (Kueh et al., 2012). However, no evidence for borer or other significant insect damage was observed on any of the trees surveyed and the current distribution of *P. cinnamomi* does not extend to the Clare Valley. While this does not exclude a potential role of other pathogens, droughts and heat waves are hence the likely primary drivers of the observed dieback.

4.3. An ecosystem in decline

Canopy dieback can have major, long-term consequences for ecosystems, potentially leading to collapse. Because vulnerability to drought differs among tree species, changes in species composition may occur (Chen et al., 2021; Haberstroh and Werner, 2022; Sánchez-Salguero and Camarero, 2020) and shifts to more open ecosystems have been reported globally (Batllori et al., 2020). Field observations suggest that such a shift to a more open ecosystem may be occurring at SGCP, with *Allocasuarina verticillata* being now the dominant species in locations with 100 % mortality of red stringybark in the north-west of the park (see top picture of Fig. 6). However, these observations need to be supported with quantitative data.

Because red stringybark is the only tree species (i.e., monodominant) over large stretches of the park, ecosystem-level impacts are potentially severe, with the consequences of the widespread dieback likely to extend beyond the canopy loss itself. Firstly, dieback of primary producers can have bottom-up effects on higher trophic levels that can result in permanent ecosystem change (Godfree et al., 2019). Furthermore, as the canopy disappears, more solar radiation reaches the ground and increases air and soil

temperatures, producing warmer, drier microclimates (Kopáček et al., 2020; Ruthrof et al., 2016). These changes in microclimates, together with the increased fuel load created by dead biomass, will increase the vulnerability of the ecosystem to fires, which is similar to the effect of cyclones (Ibanez et al., 2022). In addition, higher temperatures and wind gusts after dieback, will produce hotter and faster spreading fires (Ruthrof et al., 2016). Therefore, dieback may impact ecosystem biodiversity, processes, and services (Godfree et al., 2019; Wang et al., 2012).

The studied population of red stringybark is genetically unique and cannot migrate to track cooler climates because it is already restricted to a refugium and surrounded by a highly modified agricultural landscape. It may, therefore, be considered an example of ecosystem collapse, defined as the loss of defining features and replacement by a novel ecosystem (Bland et al., 2018). In this case, the displacement of red stringybark forests by more drought- and heat-tolerant drooping she-oak woodlands as the dominant vegetation in SGCP seems plausible. Such shifts in vegetation towards ecosystems dominated by more resistant species have been reported elsewhere (Haberstroh and Werner, 2022; Mueller et al., 2005). To confirm the extent of red stringybark decline and any shifts in vegetation types, long-term monitoring using and expanded set of ground observations (e.g., including additional species) and remote sensing would need to be implemented.

4.4. Effectiveness of refugia under climate change

The capacity of an area to function as a refugium is often linked to environmental heterogeneity created by topographic complexity (Keppel et al., 2015; Médail and Diadema, 2009). Not only can topographic complexity create a great variety of microhabitats, but it may also create microclimates that remain relatively stable during environmental change through processes such as cool air pooling (Ashcroft et al., 2012; Dobrowski, 2011; Maclean et al., 2015). Compared to its relatively flat surroundings, the Clare Valley displays a rugged topography (Boomsma, 1949) that would create unique microclimates. This topographic heterogeneity is likely important, as even limited topographic complexity can facilitate the persistence of species through environmental change (Keppel et al., 2017).

Our findings suggest that although the SGCP population of the red stringybark is in severe decline, there is potential for persistence on cooler, moister, pole-facing slopes. It is in these microsites that the lowest mortality rates and best regeneration were recorded (Fig. 6). Pockets with higher moisture availability and cooler temperatures have also been shown to be key to the persistence of other species under forecast climatic changes (Bátori et al., 2019; Brown et al., 2018; Maclean et al., 2015). Such microrefugia, small areas that retain favourable climates when the region does not (Ashcroft et al., 2012; Rull, 2009), should be identified and monitored for functionality. Determining demographic parameters that indicate whether regeneration is sufficient to maintain stands of red stringybark in the long-term is particularly important (Shriver et al., 2022).

Microrefugia, therefore, are likely key to the in-situ survival of the genetically unique population of red stringybark in the SGCP and may have functioned in a similar manner to facilitate the persistence of the species in the Clare Valley during the LGM. Considering the likely importance of microrefugia, the extensive anthropogenic impacts in the Clare Valley are of concern. Outside of SGCP, much of the Clare Valley is intensively utilised land for viticulture or other agriculture, implying that at least some potentially suitable habitat for the red stringybark has been converted to anthropogenic landscapes or degraded to varying extents. Some potential microrefugia may therefore have been rendered dysfunctional by anthropogenic impacts.

While our dataset is important in allowing us to estimate the impact of successive droughts on an isolated, genetically unique population, annual monitoring only extended from 2009 to 2014. Therefore, we can at best only infer population trends between 2006 and 2008 and 2015–2020, during which no tree monitoring occurred. For example, while mortality after Big Dry was seemingly higher (by about 7 %, Fig. 3a) than after the Millennium Drought, we lack data from 2015 and 2016 (before the Big Dry) to

confirm this assertion. This highlights the plight for establishing and maintaining long-term monitoring sites to obtain a deeper understanding of tree mortality and the dieback process (Hartmann et al., 2018).

5. Conclusion

Stand-level Dieback in the SGCP red stringybark population is seemingly a process in stages, driven by successive droughts pushing an increasing number of trees beyond critical physiological thresholds. Based on our results, trees growing in more marginal conditions were seemingly more vulnerable during the Millennium Drought, and trees exposed to high heat stress appeared to suffered mortality in the subsequent drought. With the total mortality approaching 50 % and climate change impacts becoming more severe (IPCC, 2021), the unfolding, large-scale decline of the red stringybark forest ecosystem in the SGCP will likely continue. However, there is potential for the red stringybark population to persist in small patches located on cooler, moister, pole-facing slopes. Identifying the locations of, and monitoring red stringybark performance in, these potential microrefugia may be essential for the persistence of this relict population and would allow management intervention should signs of dieback be observed within presumed microrefugia.

CRediT authorship contribution statement

Gunnar Keppel: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Resources; Supervision; Validation; Visualization; Writing – original draft; Writing – review & editing. **Udo Sarnow**: Conceptualization; Data curation; Funding acquisition; Investigation; Methodology; Project administration; Resources; Supervision; Validation; Visualization; Writing – original draft; Writing – review & editing. Data curation, Writing- Original draft preparation. **Ed Biffin**: Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Visualization; Writing – original draft; Writing – review & editing. **Stefan Peters**: Investigation; Visualization; Writing – review & editing. **Donna Fitzgerald:** Investigation; Visualization; Writing – review & editing. **Evan Boutsalis:** Formal analysis; Investigation; Writing – review & editing. **Michelle Waycott:** Funding acquisition; Project administration; Resources; Supervision; Writing – review & editing. **Greg Guerin:** Conceptualization; Formal analysis; Visualization; Writing – review & editing.

Data availability

All data can be accessed in DRYAD repository as the THI', 'Biomass', and 'Drivers' datasets mentioned in the text. Details are in the refeence section under Keppel (2022).

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:
Udo Sarnow reports financial support was provided by Royal Society of South Australia Incorporated.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.162697.

References

Akaike, H., 1974. A new look at the statistical model identification. IEEE Trans. Autom. Contr. 10, 716–723. https://doi.org/10.1109/TAC.1974.1100705.

Allen, K.J., Verdon-Kidd, D.C., Sippo, J.Z., Baker, P.J., 2021. Compound climate extremes driving recent sub-continental tree mortality in northern Australia have no precedent in recent centuries. Sci. Rep. 11, 18337. https://doi.org/10.1038/s41598-021-97762-x.

Al-Obaidi, I., Rayburg, S., Półrolniczak, M., Neave, M., 2021. Assessing the impact of wind conditions on urban heat islands in large australian cities. J. Ecol. Eng. 22, 1–15. https://doi.org/10.12911/22998993/142967.

Ashcroft, M.B., Gollan, J.R., Warton, D.I., Ramp, D., 2012. A novel approach to quantify and locate potential microrefugia using topoclimate, climatic stability, and isolation from the matrix. Glob. Chang.Biol. 18, 1866–1879. https://doi.org/10.1111/j.1365-2486.2012.02661.x.

Barker, W., Barker, R., Jessop, J., Vonow, H., 2016. Census of South Australian Plants, Algae and Fungi. State Herbarium of South Australia, Adelaide.

Bartoń, K., 2022. 'MuMIn': Multi-model Inference. R Package, Version, 1.47.1, 2022.

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R., Singmann, H., Dai, B., Scheipl, F., Grothendieck, G., Green, P., 2022. lme4: Linear Mixed-effects Models Using Eigen and S4. Version 1.1–31.

Batllori, E., Lloret, F., Aakala, T., Anderegg, W.R.L., Aynekulu, E., Bendixsen, D.P., et al., 2020. Forest and woodland replacement patterns following drought-related mortality. Proc. Natl. Acad. Sci. USA 117, 29720–29729. https://doi.org/10.1073/pnas.2002314117.

Bátori, Z., Vojtkó, A., Maák, I.E., Lőrinczi, G., Farkas, T., Kántor, N., et al., 2019. Karst dolines provide diverse microhabitats for different functional groups in multiple phyla. Sci. Rep. 9, 7176. https://doi.org/10.1038/s41598-019-43603-x.

Blackman, C.J., Li, X., Choat, B., Rymer, P.D., De Kauwe, M.G., Duursma, R.A., et al., 2019. Desiccation time during drought is highly predictable across species of Eucalyptus from contrasting climates. New Phytol. 224, 632–643. https://doi.org/10.1111/nph.16042.

Bland, L.M., Rowland, J.A., Murray, N.J., Regan, T.J., Keith, D.A., Murray, N.J., Lester, R.E., et al., 2018. Developing a standardized definition of ecosystem collapse for risk assessment. Front. Ecol. Environ. 16, 29–36. https://doi.org/10.1002/fee.1747.

Boomsma, C.D., 1949. The ecology of the western Clare hills, South Australia. Trans. Roy. Soc. S.Aust. 72, 216–220 Available at: https://archive.org/details/TransactionsRoy72Roya.

Braganza, K., Hennessy, K., Alexander, L., Trewin, B., 2013. Changes in extreme weather. In: Christoff, P. (Ed.), Four Degrees of Global Warming: Australia in a Hot World. Routledge, Abingdon, pp. 33–59.

Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., 2005. Regional vegetation die-off in response to global-change-type drought. Proc. Natl. Acad. Sci. USA 102, 15144–15148. https://doi.org/10.1073/pnas.0505734102.

Brooker, M.I.H., Slee, A.V., 1996. Eucalyptus. In: Walsh, N.G., Entwisle, T.J. (Eds.), Flora of Victoria. Vol. 3, Dicotyledons Winteraceae to Myrtaceae. Inkata Press, Melbourne.

Brouwers, N., Matusick, G., Ruthrof, K., Lyons, T., Hardy, G., 2013. Landscape-scale assessment of tree crown dieback following extreme drought and heat in a Mediterranean eucalypt forest ecosystem. Landscape Ecol. 28, 69–80. https://doi.org/10.1007/s10980-012-9815-3.

Brown, B.J., McLaughlin, B.C., Blakey, R.V., Morueta-Holme, N., 2018. Future vulnerability mapping based on response to extreme climate events: dieback thresholds in an endemic California oak. Divers. Distrib. 24, 1186–1198. https://doi.org/10.1111/ddi.12770.

Byrne, M., 2008. Evidence for multiple refugia at different time scales during Pleistocene climatic oscillations in southern Australia inferred from phylogeography. Quat.Sci. Rev. 27, 2576–2585. https://doi.org/10.1016/j.quascirev.2008.08.032.

Byrnes, R.C., Eastburn, D.J., Tate, K.W., Roche, L.M., 2018. A global meta-snalysis of grazing impacts on soil health indicators. J. Environ. Qual. 47, 758–765. https://doi.org/10.2134/jeq2017.08.0313.

Camarero, J.J., 2017. The multiple factors explaining decline in mountain forests: historical logging and warming-related drought stress is causing silver-fir dieback in the Aragón Pyrenees. In: Catalan, J., Ninot, J.M., Aniz, M.M. (Eds.), High Mountain Conservation in a Changing World. Springer, Cham, pp. 131–154.

Camarero, J.J., Sánchez-Salguero, R., Sangüesa-Barreda, G., Lechuga, V., Viñegla, B., Seco, J.I., et al., 2021. Drought, axe and goats. More variable and synchronized growth forecasts worsening dieback in Moroccan Atlas cedar forests. Sci. Total Environ. 765, 142752. https://doi.org/10.1016/j.scitotenv.2020.142752.

Carnicer, Jj, Coll, M., Ninyerola, M., Pons, X., Sánchez, G., Peñuelas, J., 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. Proc. Natl. Acad. Sci. USA 108, 1474–1478. https://doi.org/10.1073/pnas.1010070108.

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C., et al., 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. Glob. Change Biol. 20, 3177–3190. https://doi.org/10.1111/gcb.12629.

Chen, Y.-J., Choat, B., Sterck, F., Maenpuen, P., Katabuchi, M., Zhang, S.-B., et al., 2021. Hydraulic prediction of drought-induced plant dieback and top-kill depends on leaf habit and growth form. Ecol. Lett. 24, 2350–2363. https://doi.org/10.1111/ele.13856.

Choat, B., Brodribb, T.J., Brodersen, C.R., Duursma, R.A., López, R., Medlyn, B.E., 2018. Triggers of tree mortality under drought. Nature 558, 531–539. https://doi.org/10.1038/s41586-018-0240-x.

Clarke, D.K., 2021. Climate change hits the Clare Valley. http://www.comagecontra.net/Australia/ClareCC.html (accessed 10 Feb 2023).

Cottam, G., Curtis, J.T., 1956. The use of distance measures in phytosociological sampling. Ecology 37, 451–460. https://doi.org/10.2307/1930167.

Cowling, R.M., Ojeda, F., Lamont, B.B., Rundel, P.W., Lechmere-Oertel, R., 2005. Rainfall reliability, a neglected factor in explaining convergence and divergence of plant traits in fire-prone mediterranean-climate ecosystems. Glob. Ecol. Biogeogr. 14, 509–519. https://doi.org/10.1111/j.1466-822x.2005.00166.x.

De Kauwe, M.G., Medlyn, B.E., Ukkola, A.M., Mu, M., Sabot, M.E.B., Pitman, A.J., et al., 2020. Identifying areas at risk of drought-induced tree mortality across south-eastern Australia. Glob. Change Biol. 26, 5716–5733. https://doi.org/10.1111/gcb.15215.

De Kauwe, M.G., Sabot, M.E.B., Medlyn, B.E., Pitman, A.J., Meir, P., Cernusak, L.A., et al., 2022. Towards species-level forecasts of drought-induced tree mortality risk. New Phytol. 235, 94–110.

DENR, 2010. Spring Gully Conservation Park. Visitor's pamphlet available atDepartment for Environment and Natural Resources, Government of South Australia, Adelaide (accessed 10 Feb 2023) https://cdn.environment.sa.gov.au/parks/docs/spring-gully-conservation-park/brochure_spring_gully.pdf?v=1610572472.

DEW, 2021. Locations of Phytophthora infestations. Department of Environment and Water, Government of South Australia, Adelaide (accessed 10 Feb 2023) https://data.sa.gov.au/data/dataset/locations-of-phytophthora-infestations.

Dobrowski, S.Z., 2011. A climatic basis for microrefugia: the influence of terrain on climate. Glob. Chang.Biol. 17, 1022–1035. https://doi.org/10.1111/j.1365-2486.2010.02263.x.

Eager, C.D., 2021. Package 'standardize'. Tools for Standardizing Variables for Regression in R. R Package, Version, 0.0.2.

Eberbach, P.L., Burrows, G.E., 2006. The transpiration response by four topographically distributed Eucalyptus species, to rainfall occurring during drought in south eastern Australia. Physiol. Plant. 127, 483–493. https://doi.org/10.1111/j.1399-3054.2006.00762.x.

Edgar, R.C., 2004. MUSCLE: a multiple sequence alignment method with reduced time and space complexity. BMC Bioinformatics 2004 (5), 113. https://doi.org/10.1186/1471-2105-5-113.

Evans, B.J., Lyons, T., 2013. Bioclimatic extremes drive forest mortality in Southwest, Western Australia. Climate 1, 28–52. https://doi.org/10.3390/cli1020028.

Fahey, P.S., Fowler, R.M., McLay, T.G.B., Udovicic, F., Cantrill, D.J., Bayly, M.J., 2021. Divergent lineages in a semi-arid mallee species, Eucalyptus behriana, correspond to a major geographic break in southeastern Australia. Ecol. Evol. 11, 664–678. https://doi.org/10.1002/ece3.7099.

Fassnacht, S.R., Dressler, K.A., Bales, R.C., 2003. Snow water equivalent interpolation for the Colorado River Basin from snow telemetry (SNOTEL) data. Water Resour. Res. 39, 1208. https://doi.org/10.1029/2002WR001512.

Ferretti, M., 1998. Potential and limitation of visual indices of tree condition. Chemosphere 36, 1031–1036. https://doi.org/10.1016/S0045-6535(97)10167-9.

Freeman, J.S., Jackson, H.D., Steane, D.A., McKinnon, G.E., Dutkowski, G.W., Potts, B.M., Vaillancourt, R.E., 2001. Chloroplast DNA phylogeography of Eucalyptus globulus. Aust. J. Bot. 49, 585–596. https://doi.org/10.1071/BT00094.

French, P.A., Brown, G.K., Bayly, M.J., 2016. Incongruent patterns of nuclear and chloroplast variation in Correa (Rutaceae): introgression and biogeography in south-eastern Australia. Plant Syst. Evol. 302, 447–468. https://doi.org/10.1007/s00606-016-1277-7.

George, J.-P., Bürkner, P.-C., Sanders, T.G.M., Neumann, M., Cammalleri, C., Vogt, J.V., Lang, M., 2022. Long-term forest monitoring reveals constant mortality rise in European forests. Plant Biol. 24, 1108–1119. https://doi.org/10.1111/plb.13469.

Godfree, R.C., Knerr, N., Godfree, D., Busby, J., Robertson, B., Encinas-Viso, F., 2019. Historical reconstruction unveils the risk of mass mortality and ecosystem collapse during pancontinental megadrought. Proc. Natl. Acad. Sci. USA 116, 15580–15589. https://doi.org/10.1073/pnas.1902046116.

Guarín, A., Taylor, A.H., 2005. Drought triggered tree mortality in mixed conifer forests in Yosemite National Park, California, USA. For.Ecol. Manag. 218, 229–244. https://doi.org/10.1016/j.foreco.2005.07.014.

Guerin, G.R., Biffin, E., Jardine, D.I., Cross, H.B., Lowe, A.J., 2014. A spatially predictive baseline for monitoring multivariate species occurrences and phylogenetic shifts in mediterranean southern Australia. J. Veg. Sci. 25, 338–348. https://doi.org/10.1111/jvs.12111.

Guerin, G.R., Keppel, G., Peters, S., Hurren, A., 2022. Dieback of Stringybark Eucalypt Forests in the Mount Lofty Ranges. https://doi.org/10.1101/2022.11.03.515134 bioRxiv 2022, 2022.11.03.515134.

Haberstroh, S., Werner, C., 2022. The role of species interactions for forest resilience to drought. Plant Biol. 24, 1098–1107. https://doi.org/10.1111/plb.13415.

Hammond, W.M., Williams, A.P., Abatzoglou, J.T., Adams, H.D., Klein, T., López, R., et al., 2022. Global field observations of tree die-off reveal hotter-drought fingerprint for Earth's forests. Nat. Commun. 13, 1761. https://doi.org/10.1038/s41467-022-29289-2.

Hartmann, H., Schuldt, B., Sanders, T.G.M., Macinnis-Ng, C., Boehmer, H.J., Allen, C.D., et al., 2018. Monitoring global tree mortality patterns and trends. Report from the VW symposium 'Crossing scales and disciplines to identify global trends of tree mortality as indicators of forest health'. New Phytol. 217, 984–987. https://doi.org/10.1111/nph.14988.

Hartmann, H., Bastos, A., Das, A.J., Esquivel-Muelbert, A., Hammond, W.M., Martínez-Vilalta, J., et al., 2022. Climate change risks to global forest health: emergence of unexpected events of elevated tree mortality worldwide. Annu. Rev. Plant Biol., 673–702 https://doi.org/10.1146/annurev-arplant-102820-012804.

Heled, J., Drummond, A.J., 2010. Bayesian inference of species trees from multilocus data. Mol. Biol. Evol. 27, 570–580. https://doi.org/10.1093/molbev/msp274.

Horton, B.M., Close, D.C., Wardlaw, T.J., Davidson, N.J., 2011. Crown condition assessment: an accurate, precise and efficient method with broad applicability to eucalyptus. Austral Ecol. 36, 709–721. https://doi.org/10.1111/j.1442-9993.2010.02206.x.

Ibanez, T., Platt, W.J., Bellingham, P.J., Vieilledent, G., Franklin, J., et al., Martin, 2022. Altered cyclone-fire interactions are changing ecosystems. Trends Plant Sci. 27, 1218–1230. https://doi.org/10.1016/j.tplants.2022.08.005.

Ilic, J., 2002. Woods of eucalyptus – part 2 distinguishing species from the stringybark group: (E. baxteri, E. globoidea, E. muelleriana, E. macrorhyncha, E. consideniana and E. sieberi). IAWA J. 23, 305–318.

IPCC,n.d.IPCC. n.d.Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change, in: Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S.L., Péan, C., Berger, S., et al. (eds.), Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University, Cambridge.

Jackman, S., 2020. Package 'pscl'. Version 1.5.5. R package.

Jiménez-Alfaro, B., García-Calvo, L., García, P., Acebes, J.L., 2016. Anticipating extinctions of glacial relict populations in mountain refugia. Biol. Conserv. 201, 243–251. https://doi.org/10.1016/j.biocon.2016.07.015.

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., et al., 2012. Geneious basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28, 1647–1649. https://doi.org/10.1093/bioinformatics/bts199.

Keppel, G., 2022]. Population decline in a Pleistocene refugium: stepwise, drought-related dieback of a South Australian eucalypt. during peer review datasets can be accessed via:Dryad https://doi.org/10.5061/dryad.f7m0cfz0z. https://datadryad.org/stash/share/O8QmugxnLpWqKZG_WV9PQHim_hyY2u3QIj_DkkLfUT4.

Keppel, G., Wardell-Johnson, G.W., 2012. Refugia: keys to climate change management. Glob. Chang.Biol. 18, 2389–2391. https://doi.org/10.1365-2486.2012.02729.x.

Keppel, G., Van Niel, K.P., Wardell-Johnson, G.W., Yates, C.J., Byrne, M., Mucina, L., et al., 2012. Refugia: identifying and understanding safe havens for biodiversity under climate change. Glob. Ecol. Biogeogr. 21, 393–404. https://doi.org/10.1111/j.1466-8238.2011.00686.x.

Keppel, G., Mokany, K., Wardell-Johnson, G.W., Phillips, B.L., Welbergen, J.A., Reside, A.E., 2015. The capacity of refugia for conservation planning under climate change. Front. Ecol. Environ. 13, 106–112. https://doi.org/10.1890/140055.

Keppel, G., Robinson, T.P., Wardell-Johnson, G.W., Yates, C.J., Van Niel, K.P., Byrne, M., Schut, A.G.T., 2017. A low-altitude mountain range as an important refugium for two narrow endemics in the Southwest Australian Floristic Region biodiversity hotspot. Ann. Bot. 119, 289–300. https://doi.org/10.1093/aob/mcw182.

Keppel, G., Ottaviani, G., Harrison, S., Wardell-Johnson, G.W., Marcantonio, M., Mucina, L., 2018. Towards an eco-evolutionary understanding of endemism hotspots and refugia. Ann. Bot. 122, 927–934. https://doi.org/10.1093/aob/mcy173.

Khan, M.N.I., Hijbeek, R., Berger, U., Koedam, N., Grueters, U., Islam, S.M.Z., et al., 2016. An evaluation of the plant density estimator the point-centred quarter method (PCQM) using Monte Carlo simulation. PLOS ONE 11, e0157985. https://doi.org/10.1371/journal.pone.0157985.

Klausmeyer, K.R., Shaw, M.R., 2009. Climate change, habitat loss, protected areas and the climate adaptation potential of species in Mediterranean ecosystems worldwide. PLoS One 4, e6392. https://doi.org/10.1371/journal.pone.0006392.

Klesse, S., Wohlgemuth, T., Meusburger, K., Vitasse, Y., von Arx, G., Lévesque, M., et al., 2022. Long-term soil water limitation and previous tree vigor drive local variability of drought-induced crown dieback in Fagus sylvatica. Sci. Total Environ. 851, 157926. https://doi.org/10.1016/j.scitotenv.2022.157926.

Kopáček, J., Bače, R., Hejzlar, J., Kaňa, J., Kučera, T., Matějka, K., et al., 2020. Changes in microclimate and hydrology in an unmanaged mountain forest catchment after insect-induced tree dieback. Sci. Total Env. 720, 137518. https://doi.org/10.1016/j.scitotenv.2020.137518.

Kueh, K.H., McKay, S.F., Facelli, E., Facelli, J.M., Velzeboer, R.M.A., Able, A.J., Scott, E.S., 2012. Response of selected south australian native plant species to Phytophthora cinnamomi. Plant Physiol. 61, 1165–1178. https://doi.org/10.1111/j.1365-3059.2012.02593.x.

Larcombe, M.J., McKinnon, G.E., Vaillancourt, R.E., 2011. Genetic evidence for the origins of range disjunctions in the Australian dry sclerophyll plant Hardenbergia violacea. J. Biogeogr. 38, 125–136. https://doi.org/10.1111/j.1365-2699.2010.02391.x.

Leaché, A.D., Fujita, M.K., Minin, V.N., Bouckaert, R.R., 2014. Species delimitation using genome-wide SNP data. Syst. Biol. 63, 534–542. https://doi.org/10.1093/sysbio/syu018.

Li, H., Handsaker, B., Wysoker, A., Fennell, T., Ruan, J., Homer, N., et al., 2009. The sequence Alignment/Map format and SAMtools. Bioinformatics 25, 2078–2079. https://doi.org/10.1093/bioinformatics/btp352.

Li, X., Blackman, C.J., Peters, J.M.R., Choat, B., Rymer, P.D., Medlyn, B.E., Tissue, D.T., 2019. More than iso/anisohydry: hydroscapes integrate plant water use and drought tolerance traits in 10 eucalypt species from contrasting climates. Funct. Ecol. 33, 1035–1049. https://doi.org/10.1111/1365-2435.13320.

Liu, L., Yu, L., Kubatko, L., Pearl, D.K., Edwards, S.V., 2009. Coalescent methods for estimating phylogenetic trees. Mol. Phylogenet. Evol. 53, 320–328. https://doi.org/10.1016/j.ympev.2009.05.033.

Long, J.A., 2022. jtools: analysis and presentation of social scientific data. R package, version 2.2.0.

Maclean, I.M.D., Hopkins, J.J., Bennie, J., Lawson, C.R., Wilson, R.J., 2015. Microclimates buffer the responses of plant communities to climate change. Glob. Ecol. Biogeogr. 24, 1340–1350. https://doi.org/10.1111/geb.12359.

Matusick, G., Ruthrof, K.X., Brouwers, N.C., Dell, B., Hardy, G.S.J., 2013. Sudden forest canopy collapse corresponding with extreme drought and heat in a mediterranean-type eucalypt forest in southwestern Australia. Eur. J. For. Res. 132, 497–510. https://doi.org/10.1007/s10342-013-0690-5.

Matusick, G., Ruthrof, K.X., Fontaine, J.B., Hardy, G.E.S.J., 2016. Eucalyptus forest shows low structural resistance and resilience to climate change-type drought. J. Veg. Sci. 27, 493–503. https://doi.org/10.1111/jvs.12378.

Matusick, G., Ruthrof, K.X., Kala, J., Brouwers, N.C., Breshears, D.D., Hardy, G.E.S.J., 2018. Chronic historical drought legacy exacerbates tree mortality and crown dieback during acute heatwave-compounded drought. Environ. Res. Lett. 13, 095002. https://doi.org/10.1088/1748-9326/aad8cb.

Médail, F., Diadema, K., 2009. Glacial refugia influence plant diversity patterns in the Mediterranean Basin. J. Biogeogr. 36, 1333–1345. https://doi.org/10.1111/j.1365-2699.2008.02051.x.

Molina-Venegas, R., Aparicio, A., Lavergne, S., Arroyo, J., 2017. Climatic and topographical correlates of plant palaeo- and neoendemism in a Mediterranean biodiversity hotspot. Ann. Bot. 119, 229–238. https://doi.org/10.1093/aob/mcw093.

Morelli, T.L., Barrows, C.W., Ramirez, A.R., Cartwright, J.M., Ackerly, D.D., Eaves, T.D., et al., 2020. Climate-change refugia: biodiversity in the slow lane. Front. Ecol. Environ. 18, 228–234. https://doi.org/10.1002/fee.2189.

Mueller, R.C., Scudder, C.M., Porter, M.E., Talbot Trotter III, R., Gehring III, C.A., Whitham III, T.G., 2005. Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. J. Ecol. 93, 1085–1093. https://doi.org/10.1111/j.1365-2745.2005.01042.x.

Mueller-Dombois, D., 1986. Perspectives for an etiology of stand-level dieback. Annu. Rev. Ecol. Syst. 17, 221–243. https://doi.org/10.1111/j.1365-2745.2005.01042.x.

Mueller-Dombois, D., Ellenberg, H., 2002. Aims and Methods of Vegetation Ecology. Blackburn Press, Caldwell.

Müller, N.F., Ogilvie, H.A., Zhang, C., Fontaine, M.C., Amaya-Romero, J.E., Drummond, A.J., Stadler, T., 2021. Joint Inference of Species Histories and Gene Flow. https://doi.org/10.1101/348391 bioRxiv 2021: 348391.

Ordonez, A., Svenning, J.-C., 2015. Geographic patterns in functional diversity deficits are linked to glacial-interglacial climate stability and accessibility. Glob. Ecol. Biogeogr. 24, 826–837. https://doi.org/10.1111/geb.12324.

Pan, Y., Birdsey, R.A., Phillips, O.L., Jackson, R.B., 2013. The structure, distribution, and biomass of the world's forests. Annu. Rev. Ecol. Evol. Syst. 44, 593–622. https:doi.org/10.1146/annurev-ecolsys-110512-135914.

Pezza, A.B., van Rensch, P., Cai, W., 2012. Severe heat waves in Southern Australia: synoptic climatology and large scale connections. Clim. Dynam. 38, 209–224. https://doi.org/10.1007/s00382-011-1016-2.

R CoreTeam, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Rambaut, A., Suchard, M.A., Xie, D., Drummond, A.J., 2015. Tracer v1.6. 2014 MCMC Trace File Analyser. http://beast.bio.ed.ac.uk/Tracer.

Ramirez, A.R., De Guzman, M.E., Dawson, T.E., Ackerly, D.D., 2020. Plant hydraulic traits reveal islands as refugia from worsening drought. Conserv. Physiol. 8, coz115. https://doi.org/10.1093/conphys/coz115.

Ripley, B., Venables, B., Bates, D.M., Hornik, K., Gebhardt, A., Firth, D., 2022. Package 'MASS'. Version 7.3-58.1. R Package.

Rull, V., 2009. Microrefugia. J. Biogeogr. 36, 481–484. https://doi.org/10.1111/j.1365-2699.2008.02023.x.

Ruthrof, K.X., Fontaine, J.B., Matusick, G., Breshears, D.D., Law, D.J., Powell, S., Hardy, G., 2016. How drought-induced forest die-off alters microclimate and increases fuel loadings and fire potentials. Int. J. Wildland Fire 25, 819–830. https://doi.org/10.1071/WF15028.

Sánchez-Salguero, R., Camarero, J.J., 2020. Greater sensitivity to hotter droughts underlies juniper dieback and mortality in Mediterranean shrublands. Sci. Total Environ. 721, 137599. https://doi.org/10.1016/j.scitotenv.2020.137599.

Shriver, R.K., Yackulic, C.B., Bell, D.M., Bradford, J.B., 2022. Dry forest decline is driven by both declining recruitment and increasing mortality in response to warm, dry conditions. Glob. Ecol. Biogeogr. 31, 2259–2269. https://doi.org/10.1111/geb.13582.

Silva-Junior, O.B., Grattapaglia, D., 2015. Genome-wide patterns of recombination, linkage disequilibrium and nucleotide diversity from pooled resequencing and single nucleotide polymorphism genotyping unlock the evolutionary history of Eucalyptus grandis. New Phytol. 208, 830–845. https://doi.org/10.1111/nph.13505.

Smith, M.L., Wallace, J., Tank, D.C., Sullivan, J., Carstens, B.C., 2022. The role of multiple Pleistocene refugia in promoting diversification in the Pacific Northwest. Mol. Ecol. 31, 4402–4416. https://doi.org/10.1111/mec.16595.

Souter, N.J., 2019. The red gum condition index: a multi-variable tree condition index for visually assessed river red gum (Eucalyptus camaldulensis) trees. Trans. Roy. Soc. S. Aust. 143, 67–85. https://doi.org/10.1080/03721426.2018.1557994.

Souter, N.J., Cunningham, S., Little, S., Wallace, T., McCarthy, B., Henderson, M., 2010. Evaluation of a visual assessment method for tree condition of eucalypt floodplain forests. Ecol. Manag. Restor. 11, 210–214. https://doi.org/10.1111/j.1442-8903.2010.00551.x.

Steane, D.A., Mclean, E.H., Potts, B.M., Prober, S.M., Stock, W.D., Stylianou, V.M., et al., 2017. Evidence for adaptation and acclimation in a widespread eucalypt of semi-arid Australia. Biol. J. Linn. Soc. 121, 484–500. https://doi.org/10.1093/biolinnean/blw051.

Stephenson, N.L., Das, A.J., Ampersee, N.J., Cahill, K.G., Caprio, A.C., Sanders, J.E., Williams, A.P., 2018. Patterns and correlates of giant sequoia foliage dieback during California's 2012–2016 hotter drought. For.Ecol. Manag. 419–420, 268–278. https://doi.org/10.1016/j.foreco.2017.10.053.

Stone, C., Kathuria, A., Carney, C., Hunter, J., 2008. Forest canopy health and stand structure associated with bell miners (Manorina melanophrys) on the central coast of New South Wales. Aust. For. 71, 294–302. https://doi.org/10.1080/00049158.2008.10675048.

Swartzman, G., Silverman, E., Williamson, N., 1995. Relating trends in walleye pollock (Theragra chalcogramma) abundance in the Bering Sea to environmental factors. Can. J. Fish. Aquat. Sci. 52, 369–380. https://doi.org/10.1139/f95-039.

TERN, 2018. Summary of Plots on Spring Gully Conservation Park, 2012-2018. Terrestrial Ecosystems Research Network, Adelaide.

Tramblay, Y., Koutroulis, A., Samaniego, L., Vicente-Serrano, S.M., Volaire, F., Boone, A., et al., 2020. Challenges for drought assessment in the Mediterranean region under future climate scenarios. Earth-Sci. Rev. 210, 103348. https://doi.org/10.1016/j.earscirev.2020.103348.

Trugman, A.T., Anderegg, L.D.L., Anderegg, W.R.L., Das, A.J., Stephenson, N.L., 2021. Why is tree drought mortality so hard to predict? Trends Ecol. Evol. 36, 520–532. https://doi.org/10.1016/j.tree.2021.02.001.

Wang, W., Peng, C., Kneeshaw, D.D., Larocque, G.R., Luo, Z., 2012. Drought-induced tree mortality: ecological consequences, causes, and modeling. Environ. Rev. 20, 109–121. https://doi.org/10.1139/a2012-004.

Waycott, M., van Dijk, K.-j., Biffin, E., 2021. A hybrid capture RNA bait set for resolving genetic and evolutionary relationships in angiosperms from deep phylogeny to intraspecific lineage hybridization. https://doi.org/10.1101/2021.09.06.456727.

Weste, G., Cooke, D., Taylor, P., 1973. The invasion of native forest by Phytophthora cinnamomi. II. Post-infection vegetation patterns, regeneration, decline in inoculum and attempted control. Aust. J. Bot. 21, 13–29. https://doi.org/10.1071/BT9730013.

Worth, J.R.P., Sakaguchi, S., Harrison, P.A., Brüniche-Olsen, A., Janes, J.K., Crisp, M.D., Bowman, D.M.J.S., 2018. Pleistocene divergence of two disjunct conifers in the eastern Australian temperate zone. Biol. J. Linn. Soc. 125, 459–474. https://doi.org/10.1093/biolinnean/bly127.

Yates, C.J., Norton, D.A., Hobbs, R.J., 2000. Grazing effects on plant cover, soil and microclimate in fragmented woodlands in south-western Australia: implications for restoration. Austral Ecol. 25, 36–47. https://doi.org/10.1046/j.1442-9993.2000.01030.x.

Yates, C.J., Elith, J., Latimer, A.M., Le Maitre, D., Midgley, G.F., Schurr, F.M., West, A.G., 2010. Projecting climate change impacts on species distributions in megadiverse South African Cape and Southwest Australian Floristic Regions: opportunities and challenges. Austral Ecol. 35, 374–391. https://doi.org/10.1111/j.1442-9993.2009.02044.x.

Zuur, A.F., Ieno, E.N., 2016. A protocol for conducting and presenting results of regression-type analyses. Methods Ecol. Evol. 7, 636–645. https://doi.org/10.1111/2041-210X.12577.

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x.