Received: 9 January 2025 | Revised: 22 May 2025 | Accepted: 5 June 2025

DOI: 10.1111/csp2.70093

CONTRIBUTED PAPER

Conservation Science and Practice A journal of the Society for Conservation Biology Open Access WILEY

# Using in situ microrefugia to safeguard stringybark eucalypts from hot droughts

**Chloé Bentze**[1] | **Greg R. Guerin**[2] | **Amelia Hurren**[3] | **Gunnar Keppel**[1]

[1]UniSA STEM, University of South Australia, Adelaide, South Australia, Australia

[2]School of Biological Sciences, University of Adelaide, Adelaide, South Australia, Australia

[3]Department of Climate Change, Energy, the Environment and Water, Canberra, Australian Capital Territory, Australia

**Correspondence**
Chloé Bentze, UniSA STEM, University of South Australia, GPO Box 2471, SA 5001 Adelaide, Australia.
Email: chloe.bentze@mymail.unisa.edu.au

**Funding information**
Landscape South Australia - Northern and Yorke Peninsula; Royal Society of South Australia

**Abstract**

Facilitating species persistence under climate change is a pressing issue. Refugia, places where the impacts of climate change may be less severe, can constitute the only option for *in situ* persistence for many taxa. However, refugia will still experience some impacts of climate change. Management approaches that utilize the buffering provided by climate-change refugia, while recognizing their vulnerability, are needed. This increasingly applies to forests impacted by drought-induced dieback, threatening forest ecosystems globally. We established a gradient from good (putative microrefugia) to poor canopy health for a unique population of *Eucalyptus macrorhyncha* in South Australia. Microrefugia were identified in locations that received less solar radiation and were cooler and moister than other habitats. Physiological measurements (percent loss of conductivity) of trees indicate that microrefugia are already impacted by water stress during droughts, but less than more exposed habitats. Strong regeneration was observed in habitats with canopy dieback between 25% and 70%. Therefore, *in situ* persistence and recovery of populations should be feasible but may require interventions during periods of acute stress. Watering of targeted microrefugia and selected adjacent areas of high regeneration during extreme heatwaves and droughts could prevent hydraulic damage that triggers canopy defoliation and maintain a buffer around selected microrefugia.

**KEYWORDS**

drought, *Eucalyptus*, forest dieback, microclimate, refugia

## 1 | INTRODUCTION

Warmer temperatures and extreme weather events worldwide are producing droughts that are more frequent, prolonged, and hotter (Intergovernmental Panel on Climate Change [IPCC], 2021). Such droughts have been termed climate change type droughts (Breshears et al., 2005; Carnicer et al., 2011). In trees, climate change type droughts can lead to hydraulic failure in the vascular system (Choat et al., 2018; Nolan et al., 2021), causing dieback over large areas. Such large-scale dieback of trees is increasingly reported and likely to further intensify as climate change progresses (Choat et al., 2018; Hammond et al., 2022; Hartmann et al., 2022).

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2025 The Author(s). *Conservation Science and Practice* published by Wiley Periodicals LLC on behalf of Society for Conservation Biology.

Current approaches to conservation, such as creating static protected areas, may not afford protection against such long-term changes (Hylander et al., 2022; Maclean & Early, 2023). As a result, novel approaches to protect biodiversity in the face of climate change are being developed (Hylander et al., 2022; Schuurman et al., 2021; Stralberg et al. 2026). One option is to resist the impacts of climate change in locations that provide the best chances for success (Hylander et al., 2022; Keppel et al., 2024). Refugia are such locations, as they are more buffered against the impacts of climate change, promoting survival and thereby forming "bastions" in which biodiversity can persist under anthropogenic climate change (Keppel et al., 2012; Keppel et al., 2024). In the context of drought-related forest dieback, for instance, microrefugia can be created by topographic features, such slopes less exposed to solar radiation, and soils with higher water-holding capacity. Such locations provide greater water availability and lower evaporative demand (Dobrowski, 2011), thus locally reducing the hydraulic stress experienced by vegetation.

Climate change refugia are being increasingly considered to better protect biodiversity (Dreiss & Rice, 2026; Keppel et al., 2024; Morelli et al., 2020). Nevertheless, there is growing recognition that refugia differ in their capacity to buffer the impacts of climate change (Downing et al., 2021; Keppel et al., 2015) and that they are impacted by diverse anthropogenic activities (John et al., 2026; Keppel et al., 2024; Rojas et al., 2022). In some instances, networks of refugia may be required (Morelli et al., 2020) or suitable locations for refugia may need to be actively managed, restored, or newly designed (Backus et al., 2024; Keppel et al., 2024; Morelli et al., 2016). Management frameworks that navigate these and other complexities are currently being developed (Balantic et al., 2021; Keppel et al., 2024; Morelli et al., 2016) but remain in their infancy (Morelli & Mozelewski, 2026).

Trees in the genus *Eucalyptus* L'Hér. dominate many of Australia's forests and woodlands. Many species occur in semi-arid environments and feature drought tolerance traits, such as dense wood with narrow xylem vessel diameters (Bourne et al., 2017). However, some widespread eucalypts tend toward isohydry, that is, regulating water loss predominantly through stomatal conductance to maintain a more stable water potential through drought conditions (Nolan et al., 2018), which renders them vulnerable to hydraulic failure under prolonged drought (Fensham & Fairfax, 2007). Indeed, several species have experienced large-scale, drought-related dieback (Losso et al., 2022; Matusick et al., 2016). Managing dieback in *Eucalyptus* populations will therefore be important to maintain the functioning of many Australian ecosystems under climate change (Fitzgerald et al., 2025).

Determining the locations and quality of refugia for Australian eucalypts will increase our ability to manage the many eucalypt-dominated forest ecosystems and landscapes in Australia under climate change. It will also be key to identifying management solutions that utilize refugia to help prevent irreversible and biodiversity forest loss. In this context, we investigate the potential of refugia to facilitate the *in situ* persistence of a population of Red Stringybark, *Eucalyptus macrorhyncha* ssp. *macrorhyncha* F.Muell. ex Benth., in the Clare Valley, South Australia, vulnerable to climate change type droughts.

This population is a disjunct edge population, being genetically distinct and geographically isolated from other populations of the species to the east (Keppel et al., 2023). Such populations can be highly vulnerable to climate change (Sánchez-Salguero et al., 2017; Vilà-Cabrera et al., 2019). The Red Stringybark investigated here has experienced considerable dieback (ca. 40% mortality and biomass loss) due to climate-change type droughts (Fitzgerald et al., 2023; Keppel et al., 2023). Identifying the refugial capacity and management options for this population of *E. macrorhyncha* may hence be essential for its persistence and may also benefit conservation in the remainder of its distribution in the East.

Remote sensing and field studies have found that topography is a key mediator for dieback, with northern areas and north-facing slopes, exposed to high solar radiation and hot north-westerly winds in summer, experiencing high defoliation and mortality following droughts. Conversely, south-facing slopes were associated with healthier vegetation and relatively intact canopies (Fitzgerald et al., 2023; Keppel et al., 2023). Nevertheless, direct measurements linking hydraulic damage to canopy loss and mortality in this population of *E. macrorhyncha* are lacking. The first aim of this study was to determine the extent to which these topographic microrefugia reduced drought stress (i.e., measure the purported refugial capacity) by quantifying hydraulic damage in trees. We expected trees in microrefugia to display less damage to their hydraulic tissues.

Secondly, we aimed to verify that such potential microrefugia, where healthier canopies are maintained, provide cooler and moister environments during the austral summer period, using ground sensor-based microclimate measurements.

Lastly, we investigated whether regeneration could compensate for mortality by recording the number of seedlings and saplings at study sites. Following Schrieke and Livesley (2017), we hypothesized that seedling germination and success would be optimal at the intermediate

of a gradient between healthy stands of mature trees (where competition for resources is high) and unhealthy stands (where microclimatic conditions would be unfavorable). Finally, we derived potential management approaches based on our findings.

## 2 | METHODS

### 2.1 | Study population

*E. macrorhyncha* is widespread in south-east Australia and dieback has been reported throughout its distribution (Keppel et al., 2023; Losso et al., 2022). The species has medium to high susceptibility to hydraulic failure (Li et al., 2019; Losso et al., 2022). In South Australia, a single, isolated population occurs in the Clare Valley, South Australia, >500 km from the closest con-specific population (Keppel et al., 2023). Currently, nearly half of Spring Gully Conservation Park, where the bulk of the population is protected from land clearing, is dead or dying (Fitzgerald et al., 2023; Keppel et al., 2023). While some regeneration has been noted inside the park, there is concern for the species' persistence in the face of upcoming climate change type droughts (Keppel et al., 2023).

The Clare Valley is formed by two parallel, north–south ranges, located on traditional Kaurna and Ngadjuri indigenous land. It has a semi-arid to sub-humid Mediterranean climate with hot, dry summers and cool, moist winters. Mean annual rainfall at the town of Clare in the northern part of the valley ranges is around 550 mm $yr^{-1}$, with 533 mm $yr^{-1}$ recorded for the Clare High School station (station ID: 021131, 1994–2024) and 632 mm $yr^{-1}$ for the former Clare Post Office station (ID: 021014, 1862–1994), with >55% of that rainfall occurring around the Southern Hemisphere winter from May–September (source: http://www.bom.gov.au; accessed December 6, 2024). The mean maximum temperatures are around 30°C in January and 13°C in July. Higher elevation areas on the western hills intercept weather systems from the east and receive higher rainfall (Bestland et al., 2017).

The area has experienced extensive land clearing for agriculture and most of the remaining native vegetation is restricted to Spring Gully Conservation Park (33°54′40.32″ S, 138°35′43.44″ E). The park has been left relatively untouched since its establishment in 1961, though logging occurred in the area prior (Department for Environment and Natural Resources [DENR], 2010). Evidence of past logging is still visible in flatter, more accessible areas of the park, where clear-cut stumps remain. Red Stringybark is the mono-dominant canopy species in much of this 400-ha reserve located on non-calcareous, mostly shallow soils (Boomsma, 1949). In this location, it often is multi-stemmed (Keppel et al., 2023), and can reach 17 m in height (Barker et al., 2016), unlike the predominantly single-stemmed and taller populations of the species to the East. In relatively restricted areas, the canopy is dominated by the South Australian blue gum *Eucalyptus leucoxylon* subsp. *pruinosa* (F.Muell. ex Miq.) Boland where soils are deeper, and by the drooping she-oak, *Allocasuarina verticillata* (Lam.) L. A. S. Johnson, in some of the most exposed locations. The understorey is varied, and subject to the intrusion of deer and rabbits in the park, alongside native grazers like kangaroos. Generally, it is more sparse and open, with *Xanthorrea quadrangulata* F.Muell., and *Bursaria spinosa* Cav. subsp. *spinosa* in the upper layer, and *Hibbertia exutiacies* N. A. Wakef. and *Lissanthe strigosa* subsp. *subulata* (R.Br.) J. M. Powell commonly found in the ground layer (Guerin et al., 2016).

### 2.2 | Study site selection

Fourteen sites were selected to capture a gradient of health of Red Stringybark stands (from little to no dieback, to almost entirely dead) in the study area. Where possible, sites were selected to include two to three replicates of the various stages of stand dieback (identified by a quick visual estimation of canopy loss at the site). In addition, sites were selected to cover as much of the study area as possible and to allow hydraulic stress measurements (see below).

Potentially suitable stands were initially scoped using previous remote sensing work (Fitzgerald et al., 2023) and field work (Keppel et al., 2023) identifying vegetation health of stands. Maps of the terrain (slope and aspect) and fire tracks were overlaid to ensure accessibility (Figure 1). Potential sites were selected within 200 m of fire tracks and visited to verify suitability. However, sites with little or no dieback were rare among the sites deemed "accessible." Sites were set up at least 20 m from the tracks to avoid local effects on the hydrology (benefits from increased water runoff, downhill of tracks in particular). At each site, data relating to tree health and size, regeneration, hydraulic stress, and microclimate were collected (see sections below). At least one tree with sufficient live material accessible for branch extraction needed to be present, and was designated the center of the survey plot (hereafter referred to as the "PLC tree").

### 2.3 | Hydraulic stress measurements—percentage loss of conductivity

To assess hydraulic damage accumulated in the xylem vessels, native percentage loss of conductivity (PLC) was

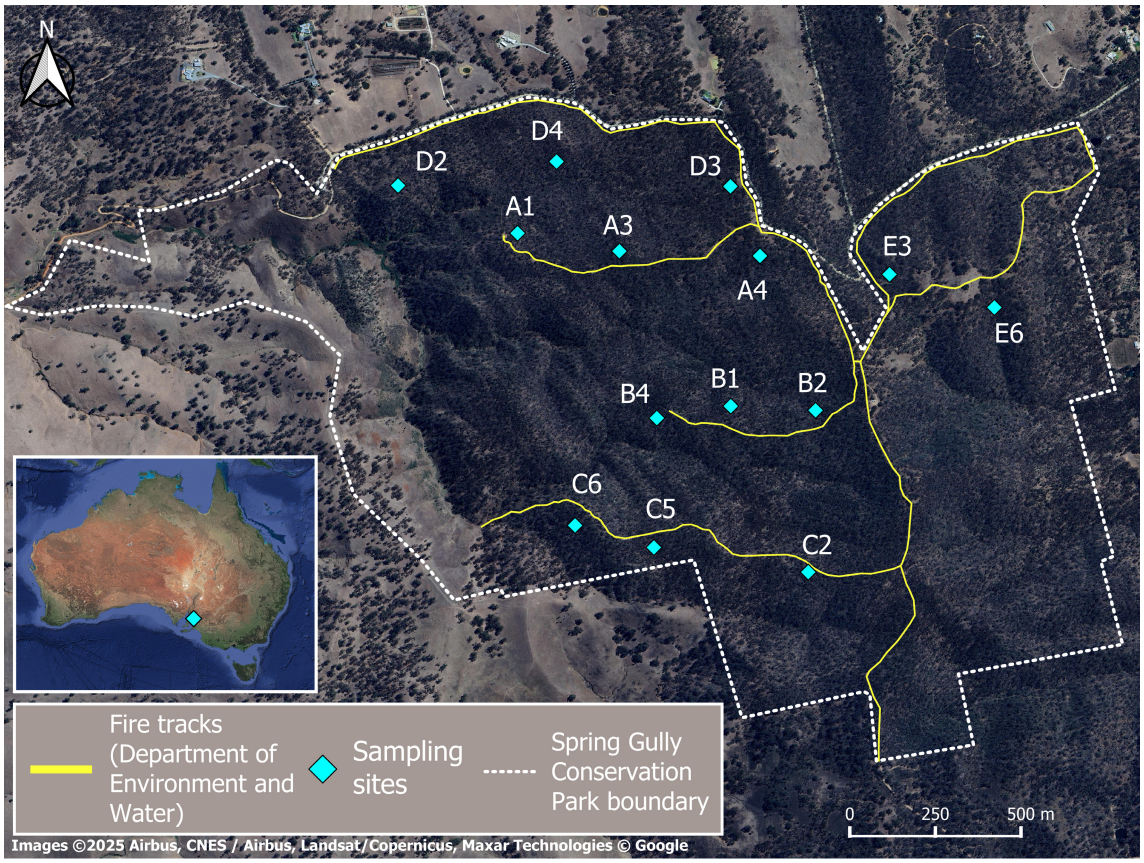



**FIGURE 1** Map of the study area within Australia (*Source*: Google Earth; data: Scripps Institution of Oceanography, National Oceanic and Atmospheric Association, US Navy, National Geospatial-Intelligence Agency, General Bathymetry Chart of the Oceans; image: Landsat/Copernicus). Conservation park boundary, fire tracks, and sampling sites are annotated.

measured from samples collected pre-dawn at each site (Sperry et al., 1988). PLC is an effective method for assessing the proportion of xylem vessels compromised due to episodes of hydraulic stress (Hietz et al., 2008). Specifically, it measures the amount of residual gas bubbles (emboli) caused by the vaporization of sap when trees are under high vapor-pressure deficits in dry soils (Choat et al., 2018).

Samples were prepared following Barigah and Cochard's protocol (2012) developed for the Xyl'EM meter, and implemented following recommendations from Wheeler et al.'s study (2013). One branch was collected from a single tree (the PLC tree, $n = 14$ trees in total) per plot pre-dawn, when water potentials are as close to 0 as possible. This avoids unwanted introduction of air into the sample at the moment of collection. Branches 1.7–2.0 m in length, and 4–5 m aboveground were sawn using a pole-saw. The cut-end was immediately re-cut inside a bucket of water, and left soaking for 20 min to relax tension in xylem vessels. Relaxation steps help prevent artificial embolization and passive refilling of the xylem during and after the cutting process (see Wheeler et al., 2013). To maintain branches in a saturated and dark environment during the trip to the laboratory (ca. 2 h drive), the sample's cut-end was covered with a water-filled balloon, and the canopy wrapped in large black plastic bags with wet paper towels. The branch was further relaxed (i.e., re-cut and placed cut-end in a bucket of water) for 3 h, before being progressively cut back under water at 1-min intervals at least, into 4 to 5 terminal twig sections carrying live foliage, of approximately 1 cm in diameter and 10 cm in length. The twig samples were then prepared for analysis as per Barigah and Cochard (2012)'s protocol.

Twig conductivity measurements were performed by measuring the flow rate of a 100 mM $L^{-1}$ KCl, 10 mM $L^{-1}$ $CaCl_2$, and MilliQ® water solution, degassed and filtered at 0.2 µm, passed through the twig at 2 kPa, and recorded using a digital liquid flow meter (Liqui-Flow; Bronkhorst High-Tech BV, Ruurlo, Gelderland, the Netherlands). Measurements were performed using the FlowDDE and FlowPlot software (Bronkhorst, FlowWare). Initial measurements provide the initial flow rate ($k_{init}$) of the solution through the twigs, before flushing emboli out of twig vessels for at least 15 min at 200 kPa,

and re-measuring the flow rate ($k_{final}$). The PLC was then calculated as:

$$PLC = 100 \times \frac{(k_{final} - k_{initial})}{k_{final}}.$$

Due to time and resource constraints, some samples were kept overnight in a cooler and processed the following morning. Delays in sample measurements, twig and pith diameters and twig length, were noted and analyzed for quality control of the data collected.

## 2.4 | Health and regeneration surveys

Centered around the PLC tree, surveys of mature trees (stems with a circumference >10 cm) and regeneration were undertaken in a circle of 16 m in diameter (a total area of approximately 201 $m^2$). For all standing stems, girth at breast height (GBH) was measured, the maximum height of stems was visually estimated using a 3.5 m tall object as a reference point, and canopy health value was estimated as the percentage of the canopy being defoliated (hereafter referred to as "canopy dieback"). Stand density was calculated as the number of trees with stems >10 cm GBH (alive or dead) within the circular plots. For regeneration surveys, visibly established seedlings (≥20 cm in height) and saplings were counted. Saplings were differentiated from seedlings as being ≥1 m tall and having thicker stems with distinctively corkier bark, and mostly mature leaves (juvenile leaves differ in shape).

## 2.5 | Microclimate measurements

At each site, a microclimate sensor (EasyLogUSB) was placed 2 m north from the centerpoint tree ("PLC tree"), with the location being slightly adjusted to be at least 2 m from any other stem or bushes, if necessary. The sensor was placed 20 cm aboveground under a two-funnel radiation shield (constructed following Hubbart, 2011) on a pole, which records temperatures comparable to commercially available radiation shields. Any large stones were removed if present below the sensor to ensure similar surface albedos and heat retention. Sensors were deployed from 5:00 p.m., October 23, to 4:00 p.m., April 19, 2025, to measure temperature (°C) and relative humidity (%) hourly.

## 2.6 | Analysis

All data were plotted and analyzed in R v. 4.3 (R Core Team, 2023). Pearson correlations between canopy dieback, mean PLC, regeneration, mean maximum temperatures, and solar radiation, calculated over a summer period from a 50 cm resolution Digital Terrain Model (cf. Fitzgerald et al., 2023 for methodology), were calculated using the function *cor()* (Figure S1). Correlations between variables were then tested with the models specified below.

To investigate the relationship between health at the tree/site level and exposure to hydraulic stress, the mean PLC was first modeled against mean canopy dieback at the site (sigmoidal regression) and canopy dieback of the sampled tree (logarithmic regression). This also allowed identification of the extent of hydraulic damage in healthy sites. Secondly, to understand regeneration dynamics in relation to canopy dieback patterns, total recruit counts were modeled according to mean canopy dieback using a generalized additive model (GAM) with the quasipoisson family and log link function.

Microclimates were then characterized according to sites. Mean daytime maximum, night-time minimum temperatures, and temperature fluctuation (standard deviation [SD]) were calculated per day and averaged across the sampling period. The same was calculated for mean maximum, minimum, and SD of relative humidity. Two sites (D2 and B4) were excluded from the analyses because their sensors fell out of the radiation shield. Linear regressions were performed on each microclimate variable independently against mean canopy dieback.

Model performance was assessed using adjusted $R^2$ values, relative standard error values (RSE), and AICc (Akaike Information Criterion for small sample sizes), using the package *MuMin* (Barton & Barton, 2015).

# 3 | RESULTS

A total of 240 trees were sampled for site-level health surveys (canopy health, height, and GBH). At sites with high dieback, often only a single tree retained branches suitable for PLC sampling, and therefore the PLC tree canopy dieback was not necessarily reflective of the site more broadly (Table 1, Figure S2). The majority of sites had a mean canopy dieback between 25% and 70% and only one site had a mean canopy dieback below 20% (C6, Table 1). There was important variation in individual canopy dieback, leading to large SDs (43% at most for a mean canopy dieback value of 51.9% at site C5, Table 1). Tree density was variable, ranging from 5 to 35 trees per site, that is 248.7 to 1740.8 trees per hectare. Signs of logging were observed in multiple sites (A4, A3, A1, B2, C5, and D2). The number of recruits also varied from 0 to 74 in one site (E3, Table 1). PLC measurements varied between branches with means ranging 12%–46%

**TABLE 1** Site characteristics summary.

| Site | Tree density (per ha) | Number of recruits (seedling/sapling) | Mean canopy dieback (%) | PLC tree canopy dieback (%) | Mean maximum temperature (°C) | Mean temperature minimum (°C) | Mean temperature SD (°C) | Mean maximum relative humidity (%) | Mean minimum relative humidity (%) | Mean relative humidity SD (%) | Aspect (°) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| A1 | 895.5 | 0 | 81.7 | 80 | 50.2 | 7 | 9 | 95.7 | 11.5 | 17.5 | 24 |
| A3 | 597 | 7 (5/2) | 39.2 | 15 | 43 | 6.5 | 6.9 | 97.7 | 13.7 | 16.2 | 281 |
| A4 | 547.3 | 25 (14/11) | 43.2 | 15 | 47.7 | 6.2 | 7.8 | 94.7 | 12.5 | 17.3 | 169 |
| B1 | 597 | 4 (1/3) | 64.6 | 25 | 51.7 | 5.2 | 10 | 93.2 | 10.5 | 19.7 | 334 |
| B2 | 845.8 | 6 (3/3) | 66.8 | 55 | 48.7 | 5.2 | 8.9 | 91.7 | 12 | 18.3 | 275 |
| B4 | 497.4 | 4 (4/0) | 55.5 | 10 | *NA* | *NA* | *NA* | *NA* | *NA* | *NA* | 196 |
| C2 | 547.3 | 0 | 79.8 | 10 | 48.7 | 6.2 | 8.8 | 90 | 11.5 | 17.3 | 0 |
| C5 | 1044.8 | 2 (0/2) | 51.9 | 10 | 49.2 | 6.5 | 7.5 | 96.5 | 12.5 | 16.5 | 143 |
| C6 | 248.8 | 0 | 15 | 5 | 44.5 | 6.7 | 6.6 | 96.7 | 14.2 | 15.5 | 247 |
| D2 | 1740.8 | 1 (0/1) | 83 | 5 | *NA* | *NA* | *NA* | *NA* | *NA* | *NA* | 294 |
| D3 | 1343.3 | 26 (14/12) | 53.4 | 80 | 52.5 | 5.7 | 8.6 | 96.5 | 12.5 | 17.5 | 204 |
| D4 | 746.3 | 7 (5/2) | 49.3 | 10 | 43.7 | 6 | 7.3 | 96 | 13 | 16.9 | 188 |
| E3 | 1592 | 74 (52/22) | 57.81 | 10 | 48.5 | 5.2 | 8.9 | 97.2 | 12 | 19.8 | 217 |
| E6 | 696.5 | 12 (3/9) | 37.4 | 10 | 47 | 4.7 | 7.8 | 92.5 | 14.2 | 17.2 | 149 |

Abbreviations: PLC, percentage loss of conductivity; SD, standard deviation.

(Table 1), and notably, within branches with SDs ranging from 4% to nearly 20% (Table 1). Larger mean PLC values also tended to have larger SDs (see Data).

Out of all experimental confounding factors measured during PLC sampling (time between branch collection and measurement, twig size, and twig and pith diameter), only twig size seemed to be associated with higher PLCs. However, the effect was slight, evenly spread between branch samples, and explained a very small fraction of the variation in PLCs ($p$ val = .027, adj. $R^2 = 0.061$, Figure S3).

## 3.1 | Canopy dieback and hydraulic stress

Our data suggest a sigmoidal relationship between canopy health at site and hydraulic damage ($p$ val <.05). Sites with lower canopy dieback generally have lower mean PLC for the tree sampled (Figure 2a). The first inflection point of the sigmoidal model suggests that PLC increases from a baseline value of ca. 20% when mean canopy dieback is about 40%. PLC then plateaus at about 31% with little additional canopy dieback (Figure 2a), suggesting mean canopy dieback of about 40% as a potential threshold for retaining stand health. We note that only a single site with mean canopy dieback <35% could be sampled due to the unavailability of suitable (low canopy dieback and accessible for PLC measurements) sites. Additionally, the PLCs measured for sites with extensive mortality (≥80% mean canopy dieback) were relatively low (some around 20% loss of conductivity, Figure 2a), and likely not representative of the mean PLC in the surrounding trees which were almost entirely defoliated and therefore could not be sampled. The mean PLC was likely to be severely underestimated at those sites, and we discuss the implications of this in Section 4.

A logarithmic relationship between the mean PLC value and canopy dieback of the PLC tree was observed ($p$ val <.05, adj. $R^2 = 63.7\%$). From ca. 24% PLC (23.5% ± 4.3% at 95% confidence interval [CI]), the canopy health of the tree deteriorated more rapidly as cavitation progressed (Figure 2b). Additionally, the logarithmic model predicts complete defoliation from ca. 50% PLC (47.2% ± 8.9% at 95% CI). This threshold is often defined as the point past which trees' hydraulic tissue becomes at risk of critical impairment in woody plants (Choat et al., 2012). Substantial variation among twigs from the same branch (maximum SD of 19.6% in the branch sampled in site D3) was noted, though this variation appears relatively consistent throughout the samples (Figure S3 and Table 1).

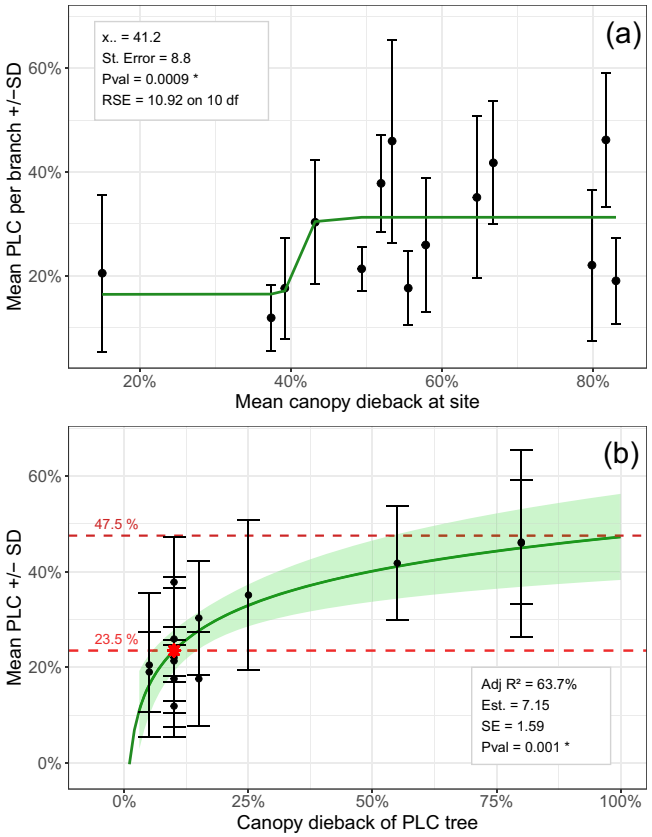



**FIGURE 2** (a) Plot of mean percentage loss of conductivity (PLC) of twigs from a single branch sampled against the mean canopy dieback at each site. $x_0$ is the (PLC) inflection point of the sigmoidal regression (green curve) fitted to the data. (b) Logarithmic regression model (green curve) and 95% confidence interval (green shading) fitted to mean PLC values of twigs in a single branch, against the degree of canopy dieback of the tree the branch was collected from. Dashed red lines indicate thresholds for complete defoliation (predicted at 47.5% loss of conductivity), and where defoliation accelerates drastically as PLC progresses (slope of the derivative dips below 1, predicted at 23.5% loss of conductivity) as predicted by the logarithmic model based on our data. Asterisks refer to statistically significant $p$ values at $\alpha = 0.05$.

## 3.2 | Regeneration

Sites with intermediate levels of canopy dieback (30%–70%) had the highest recruitment (2–74 seedlings or saplings), and sites at the extremes had a single or no seedlings or saplings (Figure 3a, Table 1). This pattern was supported by the GAM model ($p$ val <.05, adj. $R^2 = 54.3\%$, Figure 3a). Site E3 had a large amount of seedlings (52 and 22 saplings, for a total of 74 recruits), which was likely driven by one prolific mature tree located at the edge of a small clearing (Bentze, personal observation; Table 1). There was no obvious pattern in seedling versus sapling counts at sites with intermediate levels of canopy dieback; four sites had an even ratio,

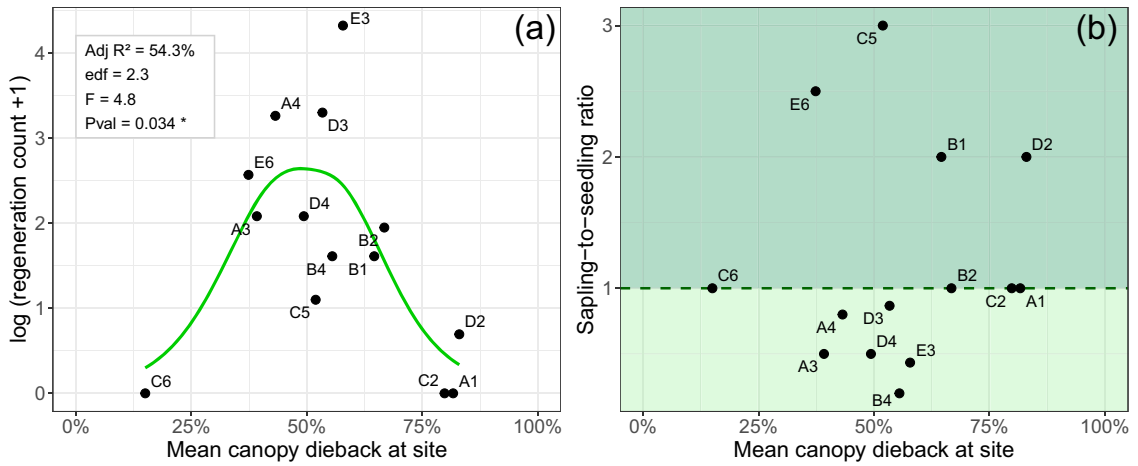



FIGURE 3 (a) Plot of regeneration counts (log + 1) according to canopy dieback, with fitted generalized additive model (green curve) for illustration of general trend. (b) Plot of the ratio of sapling-to-seedling according to canopy dieback. A ratio above 1 (dashed line) reflects the prevalence of saplings over seedlings at the site. Asterisks refer to statistically significant $p$ values at $\alpha = 0.05$.

four sites had more saplings, and six sites had more seedlings (Figure 3b, Table 1).

### 3.3 | Microclimate

Sites with greater canopy dieback were generally hotter and drier during the day, although the highest mean maximum temperature recorded (52.5°C) was at site D3 where the mean canopy dieback was 53.4%. There was almost a 10°C difference between this site and site A3, which had the lowest mean maximum temperature recorded (43°C) and a mean canopy dieback of 39.2%. There was also a near 6°C difference in mean maximum temperature between the site with the lowest mean canopy dieback (15%, mean maximum temperature of 44.5°C) and the site with the highest mean canopy dieback (81%; mean maximum temperature of 50.2°C, Figure 4, Table 1). Overall, mean canopy dieback was positively correlated with the mean maximum temperature ($p$ val <.05, adj. $R^2 = 30.9\%$) and the mean temperature variation (SD, $p$ val <.05, adj. $R^2 = 61.4\%$), and negatively correlated with mean minimum relative humidity ($p$ val <.05, adj. $R^2 = 69.4\%$, Figure 4).

## 4 | DISCUSSION

### 4.1 | Overview

The results of this study confirm putative topographic microrefugia for the Red Stringybark in Spring Gully Conservation Park. In these sites, canopies were in better condition and trees experienced less damage to their hydraulic tissue. These habitats also proved to be cooler and more humid, particularly during the hottest part of the day. These refugial locations therefore provide substantial buffering from warmer, drier conditions expected as global warming intensifies. Healthier sites also proved to have little to no regeneration, as expected, likely due to competition for resources and light. Nevertheless, damage to hydraulic tissue (ca. 20%) in branches of trees growing in microrefugia suggests vulnerability to drought stress. Regeneration was low or absent in the healthiest and unhealthiest sites investigated, and highest at sites displaying intermediate canopy dieback. Collectively, these findings suggest both vulnerability and resilience to dieback in this population.

### 4.2 | Uncertainty on the vulnerability of microrefugia

Though healthier sites displayed lower hydraulic damage, all trees investigated seemed to have experienced some drought stress, suggesting vulnerability to future warming. The strong relationship between PLC and canopy health implicates drought stress as the key driver of dieback observed in the Red Stringybark population of Spring Gully Conservation Park. This strong relationship was also noted for previous drought-related forest dieback of Eucalypts in Australia (Losso et al., 2022; Nolan et al., 2021). Our model also suggests that trees can tolerate some hydraulic damage, until around 25% PLC, where defoliation starts to progress more and more rapidly. Considering that trees with seemingly healthy canopies still had a minimum of around 20% PLC, the buffer before widespread defoliation, that is, dieback, sets in

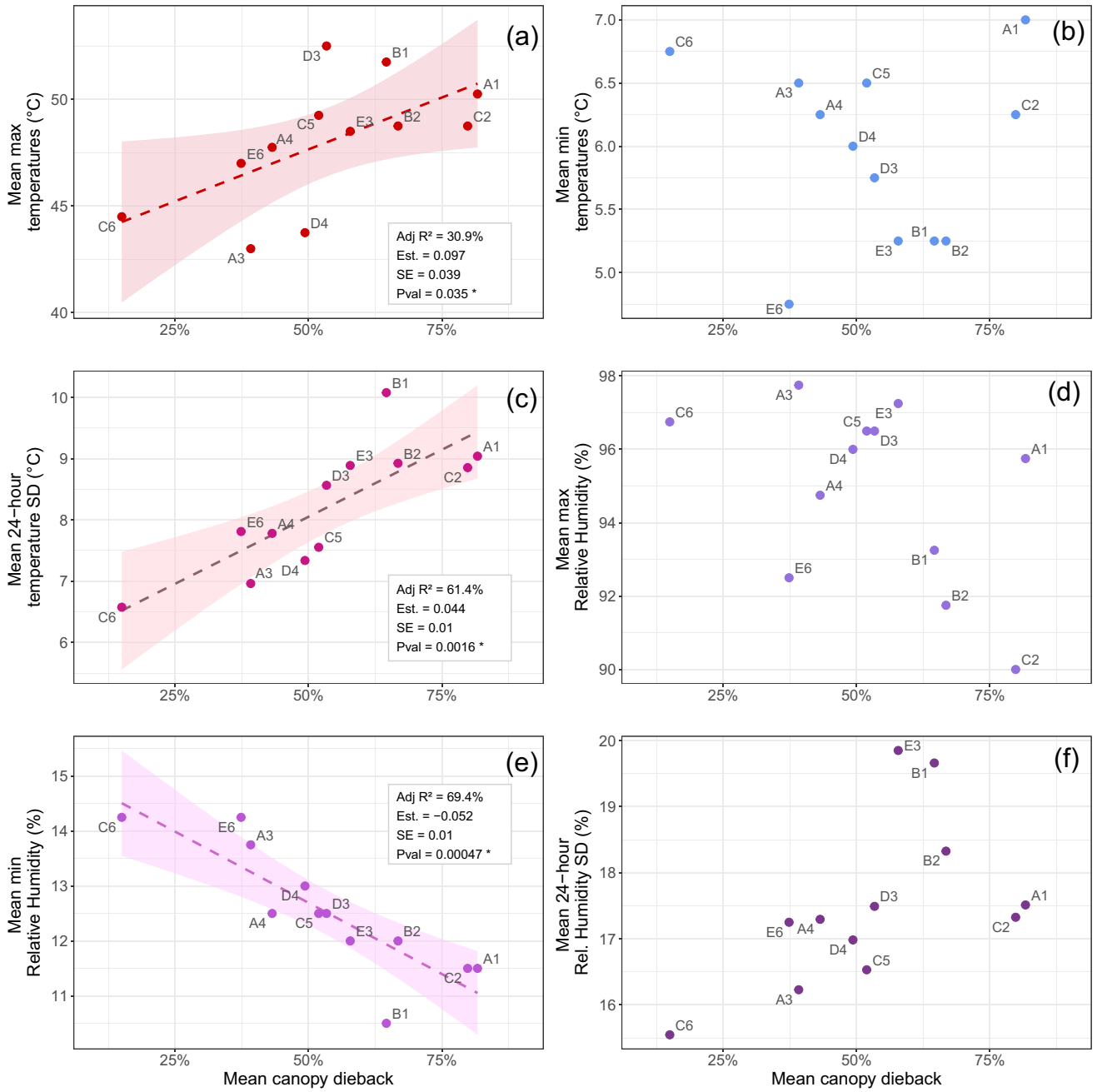



**FIGURE 4** Plots of microclimate variables according to mean canopy dieback at site: (a) mean maximum temperature, (b) mean minimum temperature, (c) mean temperature variation (mean standard deviation [SD]), (d) mean maximum relative humidity, (e) mean minimum relative humidity, and (f) mean 24-h relative humidity variation (mean SD). Dashed lines are statistically significant linear regressions with shaded 95% confidence intervals. SE, standard error. Asterisks refer to statistically significant *p* values at $\alpha = 0.05$.

appears to be low. This minimum value may be due to very steep south-facing slopes in the southern parts of the park being too inaccessible to be sampled, as this excluded trees that could have experienced less drought stress and therefore have had lower PLCs. Nevertheless, PLCs around 20% were also observed in trees with low canopy dieback in drought-affected forests dominated by *Eucalyptus pauciflora*, *Eucalyptus laevopinea*, and *Eucalyptus dalrympleana* in New South Wales during the 2019–2020 austral summer drought (Nolan et al., 2021). Similarly, *E. macrorhyncha* trees assessed post-drought at these sites recorded a minimum of 25% PLC, even after recovery (Losso et al., 2022).

Although this suggests trees with healthy canopies are still vulnerable to further drought stress, the high variation of PLC values within sampled branches point

toward uncertainty in these thresholds. Resprouting is a common coping strategy for eucalypts in response to fire (Pausas & Keeley, 2017) and drought-induced canopy loss (Pausas et al., 2016) and may have contributed to this pattern. Red stringybarks are long-lived and resprout both basally and epicormically, with lignotuber development commencing at the seedling stage (Ashton & Sandiford, 1988). Branchlets sampled from a single branch may hence be of different ages and exhibit differing levels of vascular damage and/or recovery, due to periodic resprouting after stressful periods. Further study of epicormic resprouting patterns and their link with hydraulic damage versus recovery will be particularly useful to better estimate vulnerability to drought-induced mortality.

Adaptations providing resilience to drought stress add further uncertainties to predicting thresholds that lead to population decline. Red Stringybarks have adaptations that allow persistence on shallow soils in regions with limited rainfall (mean annual precipitation throughout its range = 736.3 mm $yr^{-1}$; Blackman et al., 2019). Our study population has been isolated since before the Last Glacial Maximum (Keppel et al., 2023), and such long-term isolation may have led to additional unique adaptations (Steane et al., 2017). Resprouting as a key adaptation to stem damage in this population, which grows on the more arid edge of the species' climatic niche, is further supported by the more frequent occurrence of multi-stemmed trees compared to con-specific populations in other locations (Keppel et al., 2023). The occasional dieback of canopies and stems during drought, and subsequent resprouting, may therefore be a local adaptation and explain why "death of mature trees" at the edges of stringybark forests were also reported when the population was first "discovered" by western scientists (Boomsma 1949).

Furthermore, our results suggest that environmental conditions at finer scales than those investigated here are likely contributing to the amount of drought stress experienced by individual trees. Some of the trees sampled in sites with severe dieback appeared to be coping well, as they retained healthy canopies and displayed relatively low PLCs. A range of factors could contribute to this phenomenon. Firstly, healthier trees could be occurring in more favorable environmental conditions, such as locations with deeper soils and greater water run-on. Fine-scale differences in soil depth have been shown to affect the performance of plant species (e.g., Keppel, Robinson, et al., 2017). Alternatively, trees could be transiently benefitting from the release of competition for resources by neighboring, now extirpated trees. Finally, healthier trees may have physiological traits or strategies allowing them to cope better with drought stress. If the latter is a contributing factor, remnant healthy trees could be better adapted to drought stress, meaning that their propagules would likely perform better in restoration efforts. Further monitoring and investigation would allow determining which processes contribute to the observed phenomenon.

### 4.3 | Regeneration patterns and population resilience

While responses to future extreme climate-change type droughts are uncertain, recruitment observed in response to some dieback suggests resilience. Our results support the hypothesis that sites of intermediate canopy dieback have the highest regeneration, due to reduced recruitment caused by resource competition in healthy sites and unsuitable environmental conditions in sites of high canopy dieback (see Schrieke & Livesley, 2017). Similarly, reduced competition after dieback was suggested to enhance recruitment in the David aspen (*Populus tremula* L.) in Mongolia (Zhao et al., 2018). Such recruitment can potentially compensate for adult mortality (Lloret et al., 2012; Zhao et al., 2018).

The effects of dieback on microclimate may play a key role in determining the overall resilience of the studied population. Previous research has shown that topography affects both the severity of and recovery from dieback in the study population, with stands on south-facing slopes that receive less solar radiation remaining healthier and being more likely to recover canopy (Fitzgerald et al., 2023; Keppel et al., 2023). However, in this study, microclimate measurements are more strongly correlated with the canopy health of stands than with stands directly (Figures S1 and S4), even if topography contributes to canopy health conditions.

Such microclimate effects may be important for continuing recruitment and population persistence. Canopies can buffer against high temperatures and moisture loss at the critical period in the day (i.e., hottest period with the most insolation), creating cooler and more humid conditions (De Frenne et al., 2019; Keppel, Anderson, et al., 2017; McGinn et al., 2023). A severe reduction in canopy density caused by dieback may therefore significantly alter the regulation of temperature and moisture availability in the understorey and in the litter (Keppel, Anderson, et al., 2017). As both suitable microclimates and leaf litter can promote seed germination and seedling persistence (Facelli & Ladd, 1996; Stoneman, 1994), these changes may create environments that are unsuitable for successful seedling establishment. Microclimate may be particularly important for the establishment of Red Stringybark seedlings, which were found to survive for only about a week without water before critical hydraulic

dysfunction in a pot experiment (Blackman et al., 2019). Indeed, sites in Spring Gully Conservation Park with nearly absent canopy cover had little to no regeneration. Therefore, surrounding vegetation and canopies could be essential to modulate the severity of drought stress below a critical threshold, thus allowing Red Stringybark seedlings to survive during summer heatwaves.

### 4.4 | Management implications

Our study confirms the presence of microrefugia for the genetically unique population of Red Stringybark in the Clare Valley, as locations that retain cooler and moister microclimates than the majority of the landscape. Topographically, these microclimates are located on south-facing slopes and in the upper reaches of valleys, and coincide with the healthiest stands of this population. This study highlights that fine-scale heterogeneity in the landscape may provide refugia to woodlands, particularly eucalypts in Australia, threatened by hot drought. Investigating thresholds of resilience and recruitment patterns will also prove useful to determine which, or if, management interventions are needed to maintain this refugial capacity. Results hence confirm the usefulness of refugia for the conservation of species threatened by the impacts of climate change (Keppel et al., 2024; Morelli et al., 2020). However, they also highlight that refugia can be limited in the amount of change they can buffer and that maintaining their capacity to support particular taxa may be dependent on management as climate change intensifies (Keppel et al., 2015, 2024).

Thresholds can be important predictors for the persistence of ecological communities and refugia (Berdugo et al., 2020; Keppel et al., 2024). For the Red Stringybark communities in Clare Valley, mean canopy losses of 40% and 50% appear to be critical thresholds. Canopy losses beyond 40% translate to rapid increases in trees' hydraulic tissue damage, leading to higher chances of tree mortality. Beyond 50% canopy loss, the microclimate seems to become less suitable for seedling establishment, decreasing the potential for sites to recover after moderate canopy dieback. While the details of these thresholds require further investigation, they can provide a rule-of-thumb for management efforts.

The importance of maintaining live canopy to prevent the continuing retraction of the population, and possible future collapse, is further supported by the strong relationships between canopy cover and regeneration and microclimate. Similarly, regeneration, sufficient canopy cover, sufficient seeds, and cooler and wetter microclimates were associated with greater resilience to drought in the piñon-juniper woodlands in the southwestern United States (Redmond et al., 2018). Avoiding excessive dieback is therefore important for successful regeneration to continue, as well as maintaining refugial capacity for wildlife during summer conditions. Regeneration occurring at the margins of potential refugia, where macroclimatic conditions become suboptimal and drive dieback, may be more at risk during severe droughts. Therefore, to prevent severe defoliation and downstream effects on recruitment, active management interventions are recommendable during extreme weather events.

All in all, the Red Stringybark population in Clare Valley seems to be resilient to climate change type droughts. Nevertheless, there is clear evidence that environmental conditions have become unsuitable (high dieback and no regeneration) in areas with the hottest and driest conditions. As a consequence of future climate change, vapor-pressure deficits during hot droughts will likely increase and heighten hydraulic stress in mature trees. Active management interventions to mitigate this stress are required to retain at least parts of the population. Night-time watering within, and at the margins of refugia may help sustain mature trees and avoid loss of recruits during summer heatwaves, where high vapor-pressure deficit may cross a threshold leading to runaway embolism and severe damage for recruits and mature trees alike. Monitoring of water potentials under such conditions will also help tailor the timing and amount of watering which would be sufficient for relieving tension in the xylem and avoiding extensive cavitation. In parallel, temperature in the foliage could also be monitored to identify whether disruption of photosynthesis due to high temperature may also be contributing to canopy dieback during hot droughts (O'Sullivan et al., 2017). Lastly, maintaining or increasing control of grazers in the park will encourage natural regeneration to be successful overall.

## 5 | CONCLUSION

Our findings show that measurements of tree health, regeneration, physiological (drought) stress, and microclimate can provide important insights about the drivers and progression of dieback. Importantly, these measurements identified resilience to drought-related physiological stress and thresholds beyond which resilience begins to erode for the studied population, providing key information on refugial capacity and its management implications. Observed regeneration patterns in conjunction with microclimate suggest that maintaining some canopy cover is an important aspect of seedling establishment. Severe defoliation events may render microclimatic

conditions deleterious for seedling development as well as coping with hot droughts in mature trees. Thus, active interventions such as watering during critical hot-drought conditions in microrefugia and at their periphery may help ensure these microrefugia can persist in a changing climate. In parallel, continued or intensified controls on invasive grazer populations will also increase regeneration's chances of success.

This study shows the potential for harnessing topographic refugia to conserve a population threatened by climate change type droughts. With some management support during critical periods (extreme heat and drought), these refugia should be able to facilitate the persistence of the population. Further investigations to gain a deeper understanding of how microclimates in refugia will change as climate change progresses and of the capacity of *E. macrorhyncha* to cope with and recover from hydraulic stress over time could help further refine critical thresholds and management actions.

## AUTHOR CONTRIBUTIONS

Study design and conceptualization: **CB** and **GK**. Data collection and analysis: **CB** and **GK**. Original draft: **CB** and **GK**. Review and editing: CB, GK, GG and AH.

## ACKNOWLEDGMENTS

The fieldwork was funded by the Landscape South Australia - Northern and Yorke Peninsula Board and the Royal Society of South Australia. The authors thank Paul O'Leary from the Landscape South Australia - Northern and Yorke Peninsula Board for his ongoing support and for facilitating engagement with local stakeholders. The authors also thank Prof. Brendan Choat, Ms. Ellie Nichols, and Dr. Jen Peters for their help and support with percent loss of conductivity measurements. Thanks are also due to the volunteers and rangers of the National Parks and Wildlife Services caring for Spring Gully Conservation Park for their support during fieldwork. The authors acknowledge that this work was undertaken on Kaurna and Ngadjuri land, respect their relationship to country, and their Elders past, present, and emerging. Open access publishing facilitated by University of South Australia, as part of the Wiley - University of South Australia agreement via the Council of Australian University Librarians.

## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## FUNDING INFORMATION

The fieldwork was funded by the Landscape South Australia - Northern and Yorke Peninsula Board and the Royal Society of South Australia.

## DATA AVAILABILITY STATEMENT

Data are available from the corresponding author upon reasonable request. Data will also be made available on the open access University of South Australia Research Output Repository (https://data.unisa.edu.au/dap/default.aspx).

## ORCID

*Chloé Bentze* https://orcid.org/0000-0003-4343-897X
*Greg R. Guerin* https://orcid.org/0000-0002-2104-6695
*Gunnar Keppel* https://orcid.org/0000-0001-7092-6149

## REFERENCES

Ashton, D., & Sandiford, E. (1988). Natural hybridisation between *Eucalyptus regnans* F. Muell. and *E. macrorhyncha* F. Muell. in the Cathedral Range, Victoria. *Australian Journal of Botany*, *36*, 1–22.

Backus, G. A., Clements, C. F., & Baskett, M. L. (2024). Restoring spatiotemporal variability to enhance the capacity for dispersal-limited species to track climate change. *Ecology*, *105*, e4257.

Balantic, C., Adams, A., Gross, S., Mazur, R., Sawyer, S., Tucker, J., Vernon, M., Mengelt, C., Morales, J., Thorne, J. H., Brown, T. M., Athearn, N., & Morelli, T. L. (2021). Toward climate change refugia conservation at an ecoregion scale. *Conservation Science and Practice*, *3*, e497.

Barigah, T. S., & Cochard, H. (2012). *Xylem Embolism Meter (Xyl'EM)*. PrometheusWiki. https://hal.science/hal-00964731/document

Barker, W., Barker, R., Jessop, J., & Vonow, H. (2016). *Census of south Australian plants, algae and fungi*. State Herbarium of South Australia.

Barton, K., & Barton, M. K. (2015). *Package 'mumin'*. Version 1. https://cran.r-project.org/package=MuMIn

Berdugo, M., Delgado-Baquerizo, M., Soliveres, S., Hernández-Clemente, R., Zhao, Y., Gaitán, J. J., Gross, N., Saiz, H., Maire, V., Lehmann, A., Rillig, M. C., Solé, R. V., & Maestre, F. T. (2020). Global ecosystem thresholds driven by aridity. *Science*, *367*, 787–790.

Bestland, E., George, A., Green, G., Olifent, V., Mackay, D., & Whalen, M. (2017). Groundwater dependent pools in seasonal and permanent streams in the Clare Valley of South Australia. *Journal of Hydrology: Regional Studies*, *9*, 216–235.

Blackman, C. J., Li, X., Choat, B., Rymer, P. D., De Kauwe, M. G., Duursma, R. A., Tissue, D. T., & Medlyn, B. E. (2019). Desiccation time during drought is highly predictable across species of *Eucalyptus* from contrasting climates. *The New Phytologist*, *224*, 632–643.

Boomsma, C. D. (1949). The ecology of the western Clare hills, South Australia. *Transactions of the Royal Society of South Australia*, *72*, 216–220.

Bourne, A. E., Creek, D., Peters, J. M., Ellsworth, D. S., & Choat, B. (2017). Species climate range influences hydraulic and stomatal traits in *Eucalyptus* species. *Annals of Botany*, *120*, 123–133.

Breshears, D. D., Cobb, N. S., Rich, P. M., Price, K. P., Allen, C. D., Balice, R. G., Romme, W. H., Kastens, J. H., Floyd, M. L., Belnap, J., Anderson, J. J., Myers, O. B., & Meyer, C. W. (2005). Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 15144–15148.

Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sanchez, G., & Penuelas, J. (2011). Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 1474–1478.

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.

Choat, B., Jansen, S., Brodribb, T. J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S. J., Feild, T. S., Gleason, S. M., & Hacke, U. G. (2012). Global convergence in the vulnerability of forests to drought. *Nature*, *491*, 752–755.

De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B. R., Hylander, K., Luoto, M., Vellend, M., Verheyen, K., & Lenoir, J. (2019). Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution*, *3*, 744–749.

Department for Environment and Natural Resources (DENR). (2010). *Spring Gully Conservation Park*. Visitor's pamphlet available at Department for Environment and Natural Resources, Government of South Australia (accessed 6 Jan 2025). https://cdn.environment.sa.gov.au/parks/docs/spring-gully-conservation-park/brochure_spring_gully.pdf

Dobrowski, S. Z. (2011). A climatic basis for microrefugia: The influence of terrain on climate. *Global Change Biology*, *17*, 1022–1035.

Downing, W. M., Meigs, G. W., Gregory, M. J., & Krawchuk, M. A. (2021). Where and why do conifer forests persist in refugia through multiple fire events? *Global Change Biology*, *27*, 3642–3656.

Dreiss, L. M., & Rice, M. B. (2026). Finding climate refugia on the U.S. National Wildlife Refuge System: A focus on strategic growth values. *Conservation Science and Practice*, *8*(1), e70069. https://doi.org/10.1111/csp2.70069

Facelli, J. M., & Ladd, B. (1996). Germination requirements and responses to leaf litter of four species of eucalypt. *Oecologia*, *107*, 441–445.

Fensham, R., & Fairfax, R. (2007). Drought-related tree death of savanna eucalypts: Species susceptibility, soil conditions and root architecture. *Journal of Vegetation Science*, *18*, 71–80.

Fitzgerald, D. L., Peters, S., Guerin, G. R., McGrath, A., & Keppel, G. (2023). Quantifying dieback in a vulnerable population of *Eucalyptus macrorhyncha* using remote sensing. *Land*, *12*, 1271.

Fitzgerald, D. L., Peters, S., Hurren, A., & Keppel, G. (2025). Vegetation assessment using remote sensing: A systematic review for eucalypts in Australia. *Austral Ecology*, *50*, e70061.

Guerin, G. R., Biffin, E., Baruch, Z., & Lowe, A. J. (2016). Identifying centres of plant biodiversity in South Australia. *PLoS One*, *11*, e0144779.

Hammond, W. M., Williams, A. P., Abatzoglou, J. T., Adams, H. D., Klein, T., López, R., Sáenz-Romero, C., Hartmann, H., Breshears, D. D., & Allen, C. D. (2022). Global field observations of tree die-off reveal hotter-drought fingerprint for Earth's forests. *Nature Communications*, *13*, 1761.

Hartmann, H., Bastos, A., Das, A. J., Esquivel-Muelbert, A., Hammond, W. M., Martínez-Vilalta, J., McDowell, N. G., Powers, J. S., Pugh, T. A. M., Ruthrof, K. X., & Allen, C. D. (2022). Climate change risks to global forest health: Emergence of unexpected events of elevated tree mortality worldwide. *Annual Review of Plant Biology*, *73*, 673–702.

Hietz, P., Rosner, S., Sorz, J., & Mayr, S. (2008). Comparison of methods to quantify loss of hydraulic conductivity in Norway spruce. *Annals of Forest Science*, *65*, 502.

Hubbart, J. A. (2011). An inexpensive alternative solar radiation shield for ambient air temperature micro-sensors. *Journal of Natural & Environmental Sciences*, *2*, 9–14.

Hylander, K., Greiser, C., Christiansen, D. M., & Koelemeijer, I. A. (2022). Climate adaptation of biodiversity conservation in managed forest landscapes. *Conservation Biology*, *36*, e13847.

Intergovernmental Panel on Climate Change (IPCC). (2021). Climate change 2021: The physical science basis. In V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. J. Gomis, C. Huang, K. Leitzell, E. Lonnoy, J. B. R. Mattews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, & B. Zhou (Eds.), *Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University.

John, A., Michalak, J., Randels, C., & Lawler, J. (2026). Identifying climate-change refugia for species management and conservation in the Pacific northwest. *Conservation Science and Practice*, *8*(1), e70174.

Keppel, G., Anderson, S., Williams, C., Kleindorfer, S., & O'Connell, C. (2017). Microhabitats and canopy cover moderate high summer temperatures in a fragmented Mediterranean landscape. *PLoS One*, *12*, e0183106.

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. *Frontiers in Ecology and the Environment*, *13*, 106–112.

Keppel, G., Robinson, T. P., Wardell-Johnson, G. W., Yates, C. J., Van Niel, K. P., Byrne, M., & Schut, A. G. (2017). A low-altitude mountain range as an important refugium for two narrow endemics in the southwest Australian floristic region biodiversity hotspot. *Annals of Botany*, *119*, 289–300.

Keppel, G., Sarnow, U., Biffin, E., Peters, S., Fitzgerald, D., Boutsalis, E., Waycott, M., & Guerin, G. R. (2023). Population decline in a *Pleistocene refugium*: Stepwise, drought-related dieback of a south Australian eucalypt. *Science of the Total Environment*, *876*, 162697.

Keppel, G., Stralberg, D., Morelli, T. L., & Bátori, Z. (2024). Managing climate-change refugia to prevent extinctions. *Trends in Ecology & Evolution*, *39*, 800–808.

Keppel, G., Van Niel, K. P., Wardell-Johnson, G. W., Yates, C. J., Byrne, M., Mucina, L., Schut, A. G. T., Hopper, S. D., & Franklin, S. E. (2012). Refugia: Identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography*, *21*, 393–404.

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. *Functional Ecology*, *33*, 1035–1049.

Lloret, F., Escudero, A., Iriondo, J. M., Martínez-Vilalta, J., & Valladares, F. (2012). Extreme climatic events and vegetation: The role of stabilizing processes. *Global Change Biology*, *18*, 797–805.

Losso, A., Challis, A., Gauthey, A., Nolan, R. H., Hislop, S., Roff, A., Boer, M. M., Jiang, M., Medlyn, B. E., & Choat, B. (2022). Canopy dieback and recovery in Australian native forests following extreme drought. *Scientific Reports*, *12*, 21608.

Maclean, I. M. D., & Early, R. (2023). Macroclimate data overestimate range shifts of plants in response to climate change. *Nature Climate Change*, *13*, 484–490.

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. *Journal of Vegetation Science*, *27*, 493–503.

McGinn, K. A., Peery, M. Z., Zulla, C. J., Berigan, W. J., Wilkinson, Z. A., Barry, J. M., Keane, J. J., & Zuckerberg, B. (2023). A climate-vulnerable species uses cooler forest microclimates during heat waves. *Biological Conservation*, *283*, 110132.

Morelli, T. L., Mozelewski, T., Cavalieri, C. N., Caven, A. J., Dreiss, L. M., Hovel, R. A., Hua, M., Jennings, M. K., John, A., Kehm, G., Keppel, G., Langdon, S. F., Lawler, J. J., Lyon, L. M., Meigs, G. W., Mora-Gonzalez, M., Nadeau, C. P., Slowinska, S., Stolar, J., … Stralberg, D. (2026). Conserving climate-change refugia: Insights from research and practice. *Conservation Science and Practice*, *8*(1), e70160.

Morelli, T. L., Barrows, C. W., Ramirez, A. R., Cartwright, J. M., Ackerly, D. D., Eaves, T. D., Ebersole, J. L., Krawchuk, M. A., Letcher, B. H., Mahalovich, M. F., Meigs, G. W., Michalak, J. L., Millar, C. I., Quiñones, R. M., Stralberg, D., & Thorne, J. H. (2020). Climate-change refugia: Biodiversity in the slow lane. *Frontiers in Ecology and the Environment*, *18*, 228–234.

Morelli, T. L., Daly, C., Dobrowski, S. Z., Dulen, D. M., Ebersole, J. L., Jackson, S. T., Lundquist, J. D., Millar, C. I., Maher, S. P., Monahan, W. B., Nydick, K. R., Redmond, K. T., Sawyer, S. C., Stock, S., & Beissinger, S. R. (2016). Managing climate change refugia for climate adaptation. *PLoS One*, *11*, e0159909.

Nolan, R. H., Gauthey, A., Losso, A., Medlyn, B. E., Smith, R., Chhajed, S. S., Fuller, K., Song, M., Li, X., Beaumont, L. J., Boer, M. M., Wright, I. J., & Choat, B. (2021). Hydraulic failure and tree size linked with canopy die-back in eucalypt forest during extreme drought. *The New Phytologist*, *230*, 1354–1365.

Nolan, R. H., Tarin, T., Rumman, R., Cleverly, J., Fairweather, K. A., Zolfaghar, S., Santini, N. S., O'Grady, A. P., & Eamus, D. (2018). Contrasting ecophysiology of two widespread arid zone tree species with differing access to water resources. *Journal of Arid Environments*, *153*, 1–10.

O'Sullivan, O. S., Heskel, M. A., Reich, P. B., Tjoelker, M. G., Weerasinghe, L. K., Penillard, A., Zhu, L., Egerton, J. J., Bloomfield, K. J., & Creek, D. (2017). Thermal limits of leaf metabolism across biomes. *Global Change Biology*, *23*, 209–223.

Pausas, J. G., & Keeley, J. E. (2017). Epicormic resprouting in fire-prone ecosystems. *Trends in Plant Science*, *22*, 1008–1015.

Pausas, J. G., Pratt, R. B., Keeley, J. E., Jacobsen, A. L., Ramirez, A. R., Vilagrosa, A., Paula, S., Kaneakua-Pia, I. N., & Davis, S. D. (2016). Towards understanding resprouting at the global scale. *New Phytologist*, *209*, 945–954.

R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Redmond, M. D., Weisberg, P. J., Cobb, N. S., & Clifford, M. J. (2018). Woodland resilience to regional drought: Dominant controls on tree regeneration following overstorey mortality. *Journal of Ecology*, *106*, 625–639.

Rojas, I. M., Jennings, M., Conlisk, E., Syphard, A. D., Mikesell, J., Kinoshita, A. M., West, K., Stow, D., Storey, E., De Guzman, M. E., Foote, D., Warneke, A., Pairis, A., Ryan, S., Flint, L. E., Flint, A. L., & Lewison, R. (2022). A landscape-scale framework to identify refugia from multiple stressors. *Conservation Biology*, *36*, e13834.

Sánchez-Salguero, R., Camarero, J. J., Gutiérrez, E., Gonzalez Rouco, F., Gazol, A., Sangüesa-Barreda, G., Andreu-Hayles, L., Linares, J. C., & Seftigen, K. (2017). Assessing forest vulnerability to climate warming using a process-based model of tree growth: Bad prospects for rear-edges. *Global Change Biology*, *23*, 2705–2719.

Schrieke, D., & Livesley, S. (2017). *Optimising seedling survival in Stringybark forests*. https://fieldcapture.ala.org.au/document/download/2017-09/Optimising%20Seedling%20Survival%20in%20Stringybark%20Forests%20_FINAL_04042017.pdf

Schuurman, G. W., Cole, D. N., Cravens, A. E., Covington, S., Crausbay, S. D., Hoffman, C. H., Lawrence, D. J., Magness, D. R., Morton, J. M., Nelson, E. A., & O'Malley, R. (2021). Navigating ecological transformation: Resist–accept–direct as a path to a new resource management paradigm. *Bioscience*, *72*, 16–29.

Sperry, J., Donnelly, J., & Tyree, M. (1988). A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell & Environment*, *11*, 35–40.

Steane, D. A., Mclean, E. H., Potts, B. M., Prober, S. M., Stock, W. D., Stylianou, V. M., Vaillancourt, R. E., & Byrne, M. (2017). Evidence for adaptation and acclimation in a widespread eucalypt of semi-arid Australia. *Biological Journal of the Linnean Society*, *121*, 484–500.

Stoneman, G. (1994). Ecology and physiology of establishment of eucalypt seedlings from seed: A review. *Australian Forestry*, *57*, 11–29.

Stralberg, D., Lewis, D., Stolar, J., Kehm, G., Cosgrove, C., Morgan, D., Nelson, E., Kuntzemann, C., Raymundo, A., Sang, Z., Viliani, L., Jumean, Z., Meier, M., Enslow, C., Estevo, C., Fraser-Reid, E., Campbell, E., Grant, J., Howard, S., … Carroll, C. (2026). Integrating climate-change exposure and refugia into landscape planning: A practical guide. *Conservation Science and Practice*, *8*(1), e70171.

Vilà-Cabrera, A., Premoli, A. C., & Jump, A. S. (2019). Refining predictions of population decline at species' rear edges. *Global Change Biology*, *25*, 1549–1560.

Wheeler, J. K., Huggett, B. A., Tofte, A. N., Rockwell, F. E., & Holbrook, N. M. (2013). Cutting xylem under tension or supersaturated with gas can generate PLC and the appearance of rapid recovery from embolism. *Plant, Cell & Environment*, *36*, 1938–1949.

Zhao, P., Xu, C., Zhou, M., Zhang, B., Ge, P., Zeng, N., & Liu, H. (2018). Rapid regeneration offsets losses from warming-induced tree mortality in an aspen-dominated broad-leaved forest in northern China. *PLoS One*, *13*, e0195630.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Bentze, C., Guerin, G. R., Hurren, A., & Keppel, G. (2026). Using in situ microrefugia to safeguard stringybark eucalypts from hot droughts. *Conservation Science and Practice*, *8*(1), e70093. https://doi.org/10.1111/csp2.70093