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Morphological and heat-tolerance traits are associated with progression and impact of, but not vulnerability to, tree decline

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ABSTRACT

Warming and drying climate trends have been linked to tree-dieback phenomena worldwide with broad-reaching impacts on ecosystem services. Studying tree decline is unavoidably a retrospective exercise in which a challenge lies in determining whether trait values contribute to, or are consequences of, decline. Here we used sub-alpine snow gum (*Eucalyptus pauciflora* ssp. *niphophila*) to test whether plant traits explain vulnerability of individual trees to decline, assess how progression of dieback symptoms affect traits and physiological tolerance, and ask whether those responses could exacerbate decline. Snow gum woodlands are in widespread decline reflecting the compounding effects of climate warming and drought, and infestation by the wood-boring cerambycid, *Phoracantha mastersi*. While the impact of drought on tree mortality is well documented, we considered the potential role of heat stress, given exposure of high-elevation forests to increasing temperature. We measured changes in leaf and stem morphology, and stomatal anatomy across orthogonal dieback severity and elevation gradients. Trees showing severe dieback exhibited trait values indicating water stress, while less severely- and un-affected trees did not differ. This suggests observed differences are responses to stress caused by the impacts of wood-borer infestation and provide no evidence of underlying differences in vulnerability. We also modelled the viability of photosynthetic machinery in leaves under current and future climate scenarios; models indicated that leaves on severely-affected trees were likely to accumulate lethal damage to photosystems within a growing season. Even under the current thermal regime, dieback affected trees have lower capacity to tolerate compounded extreme events, contributing to a feedback cycle of decline.

1. Introduction

Recent warming and drying trends have been linked to increases in tree and stand mortality across forested biomes globally (Adams et al., 2009; Allen et al., 2010; Andrus et al., 2024; Hammond et al., 2022; Hartmann et al., 2022). Forest dieback can significantly alter biodiversity and ecosystem services and has been associated with declines in co-occurring species, changes to water catchments and streamflow, and reduced carbon sequestration (Boyd et al., 2013; Camarero et al., 2015; Martin et al., 2015; Mitchell et al., 2014). Dieback events are complex, typically reflecting a combination of abiotic stressors and altered biotic interactions that together bring about tree decline (Jurskis, 2005; Manion, 1991; Mueller-Dombois, 1988).

Variation in plant traits along environmental gradients may correlate with dieback susceptibility and assist in explaining spatial patterns in dieback distribution. Specifically, trait variation may increase or decrease tolerance of climatic stressors, and/or contribute to vulnerability to insects or pathogens. For example, traits that facilitate high rates of plant-water use and contribute to drought stress may increase vulnerability of individual trees to mortality in response to reduced water availability (Choat et al., 2018; McDowell et al., 2008). There is also the possibility, however, for variation to occur in plant traits, not associated with trait-related vulnerability, as a consequence of dieback. Given that trees are long lived organisms and dieback research is most often conducted in the field and after onset of a dieback event, disentangling trait-based consequences from causes is made more complex by spatial variation in traits associated with environmental gradients. Where dieback phenomena exhibit temperature or water-stress

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dependence, it is important to identify trait variation relationships with dieback severity independently of those associated with abiotic factors such as elevation. For example, morphological traits such as leaf area, leaf mass per unit area (LMA), and Huber value (ratio of stem cross-sectional area to distal leaf area) generally exhibit a conservative response to water stress whether induced by abiotic (e.g. drought) or biotic (e.g. stem girdling borers) drivers. These responses include smaller leaf area, higher Huber values, higher LMA and reduced stomatal size and density, which limit water loss (Carter and White, 2009; Hosseini et al., 2019; Lin et al., 2021; Niinemets, 2001; Poorter et al., 2009; Wright et al., 2017). In many cases these same conservative leaf traits are also associated with higher elevation where cooler temperatures limit leaf expansion and favour thicker, more frost resistant leaves.

Given the likely connection between altered thermal regimes and dieback, thermal tolerance of leaves and photosynthetic machinery may also be an important contributor to tree-level decline; the stress imposed by dieback may alternatively trigger increases in thermal tolerance or lead to declines therein. Water limitation can be instigated by drought, heat or by impacts of wood-boring insects. Water limitation has been shown to result in increased heat tolerance due to acclimation to limited evaporative cooling and associated higher leaf temperatures (Cook et al., 2021; Havaux, 1992; Valladares and Pearcy, 1997). Alternatively, functionality may decline under water limitation as the activation of multiple stress-response pathways limit resources available for photosynthetic function (Ben Rejeb et al., 2014; Zhu et al., 2021). The duration of exposure to heat also affects photosystem function, whereby the temperature that the leaf tissue can functionally tolerate decreases as duration of heat exposure increases, i.e., with increased heat load (Cook et al., 2024; Faber et al., 2024; Neuner and Buchner, 2023). Thus, it is unclear whether, or to what point, biotic stressors associated with dieback would enhance or diminish photosystem heat stress tolerance and further affect trees' vulnerability to warming environmental conditions. To date, the relative impact of thermal stress as a direct driver of decline has received little attention (Allen et al., 2010; Anderegg et al., 2015; Camarero et al., 2015; Choat et al., 2018; Meir et al., 2015).

Sub-alpine and montane ecosystems are particularly vulnerable to climate change-induced dieback as rates of warming at high elevations exceed the global average (Gobiet et al., 2014; IPCC et al., 2022). In addition to directly affecting plant function, reduced thermal constraints on insects and pathogenic organisms at high elevations, as temperatures rise, can increase the susceptibility of high-altitude forests to biotic infestations (Adams et al., 2009; Jaime et al., 2024; Mitton and Ferrenberg, 2012; Raffa et al., 2008). A similar phenomenon may also underlie dieback in sub-alpine stands of snow gum (*Eucalyptus pauciflora* ssp. *niphophila* (Maiden & Blakely) L.A.S. Johnson & Blaxell) in south-east Australia, associated with infestations by the bark- and wood-boring cerambycid *Phoracantha mastersi* (Pascoe) (Brookhouse et al., 2024). Decline of snow gum is negatively associated with elevation, a trend that may reflect the increased vulnerability of high-elevation stands in response to warmer temperatures, and/or, akin to northern-hemisphere dieback events, a direct effect on reproductive and behavioural characteristics of the mediating insect taxon (Brookhouse et al., 2024; Bryant et al., 2024).

We used subalpine snow gum (*Eucalyptus pauciflora* ssp. *niphophila*) as a case study to test whether plant traits explain vulnerability of individual trees to decline, assess how progression of dieback symptoms affect traits and physiological tolerance, and ask whether those responses could exacerbate decline. Although trait-based relations with elevation and severity of snow-gum dieback have been previously described (Bryant et al., 2024), no attempt has yet been made to disentangle drivers from consequences at the plant nor landscape scale. In this study, we aim to address global knowledge gaps around forest decline. First, using an orthogonal study design, we sought to disentangle the impacts of plant-traits from elevation as an abiotic driver of dieback. We postulate that if trait values are associated with vulnerability to dieback, then values in trees affected by *P. mastersi*—even those in the earliest stages of dieback—will differ from those in unaffected trees. Alternatively, if a product of the onset and progression of dieback, a trend in trait values will be evident with increasing infestation severity. Second, we aimed to test a feedback cycle between dieback severity and declining physiological tolerance, specifically that of photosynthetic heat tolerance. In addition, we applied dynamic models of heat load to explore the influence of exposure duration on leaf heat tolerance and its implications for viability of leaf photosynthetic machinery under current and future climate scenarios (i.e., thermal load sensitivity (Arnold et al., 2025)). We examined whether water limitation would improve or reduce heat tolerance and predicted that in severely affected individuals, heat tolerance would be reduced such that heat load models would highlight a positive feedback cycle where accumulated leaf damage reduces carbon assimilation capacity. Thus, we predict that heat load exacerbates tree decline in snow gum and other dieback events elsewhere.

2. Materials and methods

2.1. Study species and field site

This study was conducted in sub-alpine woodlands in the Snowy River valley between 1680 and 1890 m asl in Kosciuszko National Park (KNP; Fig. 1, see also supplemental information, S1), New South Wales, Australia. Consistent with forest composition throughout KNP above 1600 m asl, stands within the study area are comprised entirely of sparsely spaced, multi-stemmed *E. pauciflora* ssp. *niphophila* with a shrub or grassy understory.

Snow gum dieback was first reported in the late twentieth century as localised patch-scale decline (Banks, 1982, 1989; Shields, 1993), but is now widespread throughout the Australian Alps. Dieback affected trees show canopy decline, variation in the extent of which can be mapped using remote sensing (Charerntantanakul et al., 2025). In addition affected trees show tissue damage distinctive of the native wood-boring beetle *Phoracantha mastersi.* Other species of the genus *Phoracantha* have been documented to cause significant damage in *Eucalyptus* plantations in Australia and overseas. Studies of these species note that the survival of the wood-boring larvae is aided by dry conditions, allowing larvae to reach cambial tissue more successfully (Da Conceição Caldeira et al., 2001; Hanks et al., 1991, 1999; Seaton et al., 2015). Larvae of *P. mastersi* feed circumferentially on cambial tissue of snow gum, consuming both the outer xylem and inner phloem tissue, effectively ring-barking the stem (Brookhouse et al., 2024). The presence and frequency of *P. mastersi* infestations is inversely correlated with elevation above 1600 m asl, the lower elevational limit of *E. pauciflora* ssp. *niphophila* (Brookhouse et al., 2024; Bryant et al., 2024). This elevational pattern raises two possibilities that require further exploration. First, thermal limitation of *P. mastersi* behaviour may suppress infestation rates at high elevation, consistent with outbreaks of insects in alpine and montane forests elsewhere (Bentz et al., 2010; Jaime et al., 2024). Second, temperature-mediated variation in plant traits may promote vulnerability to infestations at lower elevation.

To disentangle the role of elevation in dieback we established a network of temporary plots on elevational transects positioned along a naturally occurring dieback gradient between the Guthega ski resort and Spencers Creek snow-depth monitoring station (36°24'31"S 148°21'28"E, Fig. 1). Prior field surveys indicated that *P. mastersi* infestations declined in severity with increasing distance from Guthega ski resort as well as with increasing elevation (Brookhouse et al., 2024). This association between wood-borer associated decline and disturbance e.g. a stand edges where historical grazing or ski-resort infrastructure occur has been documented previously for snow gums (Shields, 1993; Smith and Smith, 1987). Sixteen elevational transects were established to span the full range of forest cover within the study area, ranging from 1680 m to 1890 m asl. Variable-radius plots were established at six fixed elevations (1680, 1710, 1760, 1810, 1860 and 1890 m asl), using a basal

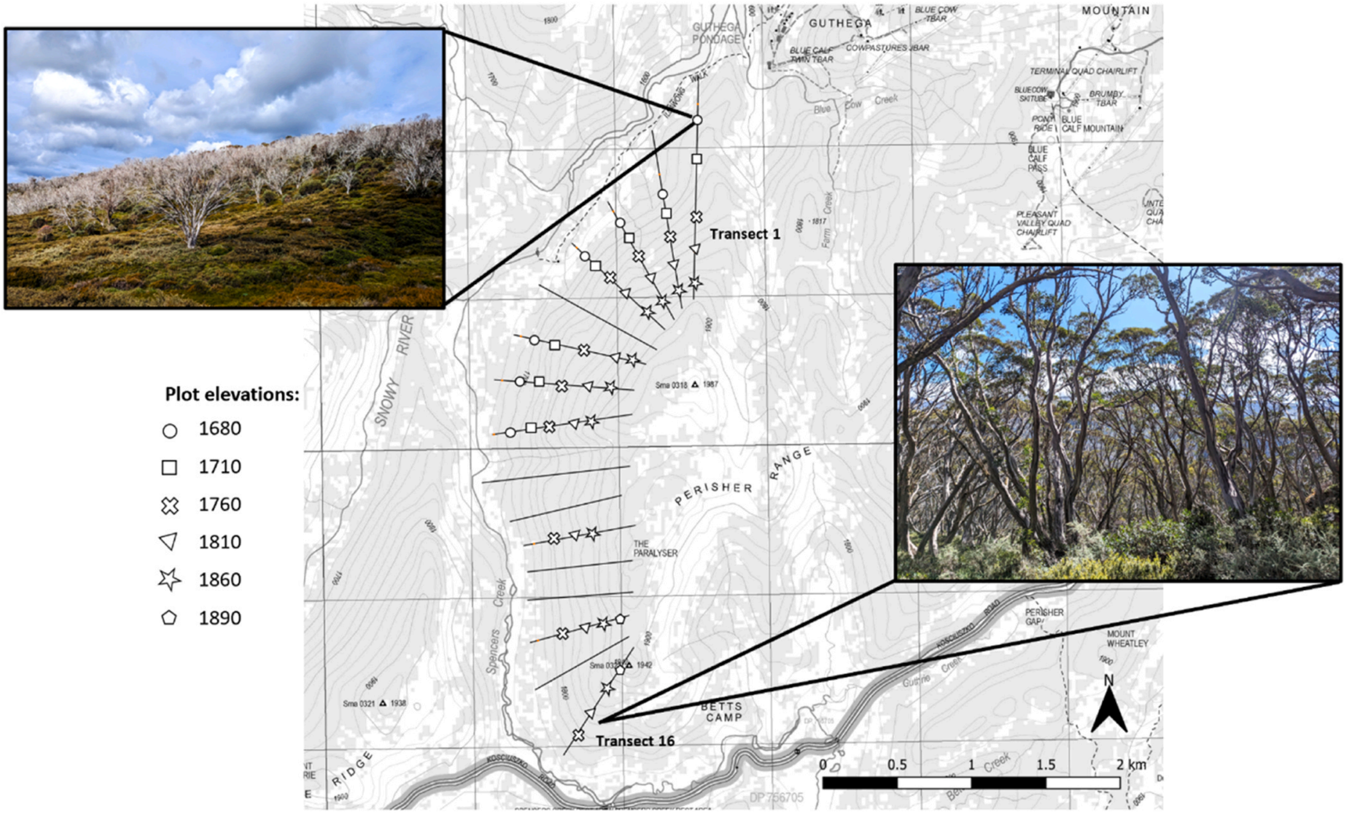

Fig. 1. Location of 46 study plots, along 10 transects on slopes of The Paralyser, Kosciuszko National Park, NSW, Australia. Inset images show comparison of dieback severity at transect #1 (severe dieback) to transect #16 (largely unaffected by dieback). Study plots range in elevation from 1680 m asl to 1890 m asl.

area factor of 2. Consistent with Brookhouse et al. (2024), canopy health and level of wood-borer damage, were used to classify the severity of dieback of each tree as either none, low, moderate or severe (see S1a-c, and Figures S1 and S2 for more detail).

2.2. Effects of dieback severity and elevation on leaf morphology and stomatal anatomy

In each of 46 plots from a subset of ten of the original transects, three representative trees with live canopy were selected for sampling. Collection took place during the austral summer-autumn (February-April) of 2023. For leaf-trait measurements, small branches growing in full sun were retrieved from the upper canopy of the tree using an arborist's throwline. Branches were wrapped in damp paper towel and stored in zip-lock bags in the field to prevent loss of leaf water then measured at the field laboratory within ~8 h of collection.

Because the spread of dieback in the study area was quite recent, symptoms of dieback may have begun in the previous 12 months. To test for progression of dieback symptoms, leaves from both the current and previous growing season were sampled. For each tree, three healthy leaves that expanded during the current growing season (2022/2023) (hereafter referred to as 'young leaves') and three healthy leaves that expanded during the preceding growing season (2021/2022; hereafter 'old leaves') were randomly sampled from collected branches for leaf trait measurements. The distinction between young and old leaves was made visually based on location on the branch and leaf and petiole colour (see S1d, Figure S3). Leaf area, leaf mass per unit area (LMA) were measured for each leaf, stomatal size, stomatal density and stomatal pore index (Lin et al., 2021; Sack et al., 2003) were measured on one leaf per leaf age class per tree and Huber values for one branch per tree (see supplemental information S1e-f).

Given hydraulic damage caused by woodborers, we predicted that dieback affected trees would show conservative leaf traits, generally associated with water stress (including smaller leaf areas, stomatal size, stomatal density and Huber values). We further anticipated that the most recent cohort of leaves would show stronger signals of dieback than the previous cohort.

2.3. Photosystem heat tolerance

Leaves for photosystem heat tolerance assays were sampled from *E. pauciflora* ssp. *niphophila* trees at a single site (36°24'35.9"S 148°24'52.2"E, 1780 m asl), independent of the transect network used for leaf-trait sampling. This site, which falls in the mid-elevational range of dieback-affected trees, was selected because it contained a range of dieback severity. Leaf samples were collected from eight trees within each of three dieback-severity classes representing none, moderate, and severe symptoms classified as described above.

We measured both an instantaneous point metric and a cumulative measure of photosystem heat tolerance. As a point metric, we measured the critical thermal threshold (T_{crit}) at which basal chlorophyll fluorescence (F_0) begins to rise rapidly, indicative of the temperature at which stress within the photosystem occurs (Arnold et al., 2021; Schreiber and Berry, 1977). Because T_{crit} does not account for the influence of duration on thermal stress, we also considered thermal load sensitivity (TLS), using maximum quantum yield of PSII (F_V/F_M) response to steady-state heat assay/challenge. This TLS analysis offered insight into the effect of exposure duration in determining the impact of temperature stress on plant physiological processes (Arnold et al., 2025; Cook et al., 2024; Faber et al., 2024; Neuner and Buchner, 2023). Here we characterised the critical temperature at which plants reached irreparable F_V/F_M values, less than 0.3 ($T_{0.3}$, (Curtis et al., 2014)) as a function of duration. For detailed methods see supplemental information (S2).

2.4. Simulating thermal load sensitivity effects under field thermal regimes

Finally, as a simulated demonstration of the impact of accumulating heat load to which the leaves were exposed in the 2022–23 summer, we modelled realistic local field leaf temperatures using the microclimate and ectotherm models of 'NicheMapR' R package (Kearney and Leigh, 2024; Kearney and Porter, 2017, 2020). We simulated microclimate at 2 m above ground level using the *micro_era5* function (Kearney et al., 2020; Klinges et al., 2022), which extracts climatic and topographic variables from the ERA5 dataset (Hersbach et al., 2020) at the study location from which TLS leaves were sampled (36°24'35.9"S 148°24'52.2"E, 1780 m asl). Leaves were specified to be an ellipsoid shape (length = 66.7 mm, width = 18.4 mm and thickness = 0.63 mm) with tissue density $= 1\ \mathrm{g\ cm^{-3}}$. Previous field measurements of *E. pauciflora* ssp. *niphophila* were used to parameterise leaf shape and other functional traits required for the modelling: leaf wet weight = 0.53 g (mean summer wet weight) and solar absorptivity of the leaf = 0.93. Plausible values of mean leaf diffusive conductance $= 0.30\ \mathrm{mol\ m^{-2}\ s^{-1}}$, and maximum leaf diffusive conductance $= 0.35\ \mathrm{mol\ m^{-2}\ s^{-1}}$ were derived from relevant elevation populations of *E. pauciflora* from Körner and Cochrane (1985). Leaf temperature models (derived using leaf mode in the *ectotherm* function) were then run for two stomatal states: open during appropriate diurnal conditions or always closed, representing functional and water-stressed leaves, respectively. Using the TLS parameter estimates (CT_{max}' and z) from none, moderate, and severe dieback severity classes measured in this study, we fit 'thermal tolerance landscape' models (Rezende et al., 2014, 2020). These models estimate the leaf survival probability (%) at each day, based on the temperatures that the leaves reach across time (heat load), and their capacity to tolerate heat load before accumulating damage to PSII. We then fit an + 4°C increase in temperature over the same time course to assess the extent to which heat load would lead to compounded leaf damage under a high climate-warming scenario (SSP3, (IPCC et al., 2022)), for open and closed stomata states, and different dieback-severity classes.

2.5. Data analysis

All statistical analyses were performed using R Statistical Software, v4.2.3 (R Core Team, 2021). For transect-based data (leaf morphology and stomatal traits), the 'nlme' R package (Pinheiro et al., 2023) was used to fit linear mixed-effects regression (LMER) models. These models assessed the change in leaf traits associated with dieback severity (none, low, moderate, severe), elevation and leaf age (young, old) as fixed effects. The identity of each sample tree was included as a random factor where multiple measurements were taken from a single tree. All models also included a spatial correlation structure (derived from the geographic position of each sample tree) to account for potential spatial autocorrelation in dieback severity. The R package 'nlme' offers five different spatial correlation structures and the corrected Akaike Information Criterion (AICc) was used to determine the most suitable structure (see supplemental information S3). The inclusion of this spatial correlation term consistently improved model fit compared to models without (Table 1). The AICc was also used to determine if interaction terms improved model fit. For all traits except LMA final models did not include interactions (see supplemental information S3). To analyse heat tolerance data, we fit similar LMER models, but without elevation and spatial autocorrelation terms as these data were collected at a single site. Dieback severity and leaf age were fixed effects while tree and sampling day were random variables.

Table 1

Effects of dieback, elevation and leaf age on leaf morphology and stomata anatomy of *Eucalyptus pauciflora* ssp. *niphophila*: results from linear mixed effects regression models. Note that Huber value was measured at the branch level so there is no effect of leaf age for this trait. Intercept corresponds to old leaves from unaffected trees.

	Leaf area (cm^2) n = 748*			**LMA (g/m^2) n = 748**			**Huber value (cm^2/m^2) n = 114**			**Stomata length (μm) n = 233**			**Stomata density (no. stomata/mm^2) n = 233**			**Stomatal pore index n = 233**		
	Est.	***(se)***	***P*-value**	**Est.**	***(se)***	***P*-value**	**Est.**	***(se)***	***P*-value**	**Est.**	***(se)***	***P*-value**	**Est.**	***(se)***	***P*-value**	**Est.**	***(se)***	***P*-value**
Intercept	2.181	0.547	< 0.001	397.46	70.049	< 0.001	18.551	9.436	0.052	44.451	10.216	< 0.001	4.142	0.509	< 0.001	2.055	0.653	0.002
Elevation	9.5e-5	3.0e-4	0.752	-0.024	0.038	0.538	-0.007	0.005	0.183	-0.008	0.006	0.148	4.79e-4	2.82e-4	0.091	2.7e-4	3.60e-4	0.453
Dieback (low)	-0.037	0.040	0.358	-9.134	5.733	0.114	-0.592	0.655	0.368	0.411	0.625	0.511	-0.047	0.026	0.066	-0.008	0.0411	0.846
Dieback (mod)	-0.047	0.060	0.431	-6.981	8.534	0.415	-0.334	0.945	0.724	**-2.762**	**0.927**	**0.003**	0.035	0.038	0.352	-0.102	0.0597	0.090
Dieback (severe)	**-0.198**	**0.056**	**0.001**	-9.680	7.841	0.219	**2.772**	**0.929**	**0.004**	**-2.024**	**0.937**	**0.032**	0.037	0.038	0.326	-0.025	0.0610	0.686
Leaf age (young)	**-0.235**	**0.018**	**< 0.001**	**-99.33**	**3.152**	**< 0.001**	-	-	-	-0.427	0.307	0.165	**0.035**	**0.016**	**0.034**	0.007	0.0231	0.772
Db(low):L(young)	-	-	-	**18.174**	**4.964**	**< 0.001**	-	-	-	-	-	-	-	-	-	-	-	-
Db(mod):L(young)	-	-	-	8.165	7.454	0.273	-	-	-	-	-	-	-	-	-	-	-	-
Db(sev):L(young)	-	-	-	**14.885**	**6.297**	**0.028**	-	-	-	-	-	-	-	-	-	-	-	-
Spatial correlation structure	***AICc with CorStruc:*** −33.61 ***AICc without:*** 23.87			***AICc with CorStruc:*** 7059.7 ***AICc without:*** 7088.1			***AICc with CorStruc:*** 570.10 ***AICc without:*** 565.83			***AICc with CorStruc:*** 1230.9 ***AICc without:*** 1264.7			***AICc with CorStruc:*** −211.31 ***AICc without:*** −190.64			***AICc with CorStruc:*** −18.17 ***AICc without:*** −1.92		
Random effect of Tree ID	***Marginal R^2:*** 0.214 ***Conditional R^2:*** 0.414			***Marginal R^2:*** 0.674 ***Conditional R^2:*** 0.739			-			-			-			-		

[*] Sample size n = 748 corresponds to 128 trees × 2 leaf ages × 3 leaf replicates, see S1f for full account of sample size.

3. Results

3.1. Effects of elevation and dieback severity on leaf and stem traits

Contrary to our expectations, leaf morphological traits did not vary significantly with elevation. Further, while trait variation between dieback-severity classes broadly aligned with our predictions (Table 1), that variation largely only distinguished leaves from trees with the highest severity rating from those with no, low or moderate dieback severity. Thus, our results do not indicate any inherent differences in leaf traits that might predispose these trees to dieback.

Across all dieback severities, old leaves (formed during 2021/22) were larger than young leaves (formed during 2022/23) (Fig. 2A, Table 1). Trees with severe dieback had smaller leaves than those from less severely affected, being significantly smaller than unaffected trees across both leaf age cohorts (Fig. 2A, Table 1). Average leaf area for trees in low and moderate dieback categories did not differ from that of unaffected trees (Table 1). In addition to smaller leaves, severely affected trees also had significantly less leaf area per given stem area than unaffected stems so that Huber values were on average 60 % greater in severely affected trees (Fig. 2C, Table 1).

There was no change in LMA with increasing dieback severity (Fig. 2B); however, young leaves had lower LMA than old leaves (Fig. 2B). The model indicated a significant interaction between dieback severity and leaf age because the extent of difference in LMA between young and old leaves varied among dieback severity classes.

We did not detect any decrease in stomatal size or density with elevation, however, as predicted, moderately and severely dieback-affected trees had significantly smaller stomata than those without evidence of dieback (Fig. 2D, Table 1). Young leaves had significantly higher stomatal density than old leaves (Table 1) but there was no change in stomatal density with increasing dieback severity (Fig. 2E). While the average stomatal pore index (SPI) of moderate and severely dieback-affected trees was slightly lower than that of unaffected trees, the difference was not statistically significant (Fig. 2F, Table 1).

3.2. Photosystem heat tolerance

The maximum quantum yield of PSII (F_V/F_M) measured prior to temperature ramping was significantly lower in trees with severe dieback than unaffected trees, indicating reduced photosystem health associated with advanced *P. mastersi* infestation (Fig. 3A, Table 2). The upper critical temperature at which stress is incurred within PSII, T_{crit}, was also significantly lower in severely affected than unaffected trees (Fig. 3B, Table 2). There was a decline of ~1°C in T_{crit} with each increasing level of dieback severity (Fig. 3B) and trees with higher initial F_V/F_M generally had a higher T_{crit} (see Figure S5). There was no effect of leaf age on initial F_V/F_M or T_{crit} values (Table 2).

The thermal load sensitivity experiment demonstrated that increased duration of exposure significantly reduced the temperature at which plants reached an F_V/F_M value less than 0.3 ($T_{0.3}$) (Fig. 3C, Table 2). Trees with severe dieback also had significantly lower values for critical temperature at 1 min (CT_{max}'), than unaffected individuals (Fig. 3D, Table 2). The slope (thermal sensitivity parameter, z) was also significantly lower in severely dieback affected trees than unaffected trees (Fig. 3D, Table 2). For comparisons of CT_{max}' to T_{crit} see S2d and Figure S5.

Modelled probability of leaf survival based on simulated leaf temperatures indicates that even at current temperatures and with the benefit of evaporative cooling through open stomata, leaves from severely dieback affected trees had dramatically reduced probability of survival. If the model simulated trees that were water-stressed and had closed stomata, the probability of leaf survival was even lower (Fig. 4A, B). When a future climate warming scenario with an increase of 4°C is added to this simulation, the model indicates that leaves of these severely affected trees would accumulate lethal heat loads about halfway through the growing season under severe water stress or after two months with the benefit of evaporative cooling (Fig. 4C).

4. Discussion

As global climate change places more tree species at risk of dieback, it is important to identify the drivers of dieback phenomena, and the physiology associated with decline or recovery of affected trees. This endeavour is complicated by challenges in distinguishing the causes from consequences of decline and often does not incorporate feedback loops associated with trait and physiological tolerance changes in response to decline. In this study, we used snow gum (*E. pauciflora* spp. *niphophila*) as a case study to assess whether leaf traits relate to tree level vulnerability to the unfolding dieback event and explore how dieback-driven changes in functional traits may hasten tree decline. While we found significant changes in leaf traits in severely dieback affected trees (smaller leaves, higher stem to leaf area ratios, smaller stomata lengths and lower photosystem heat tolerance), the isolation of these changes to only the most severely affected individuals implies that these leaf traits likely do not contribute to initiation of woodborer infestation. Our findings also suggest that increased water stress, as evidenced by conservative leaf and branch traits in dieback affected snow gums, is accompanied by reduced vigour and physiological heat tolerance. Together with our models of accumulated damage from heat load, our case study illustrates how these changes likely compound the direct hydraulic effects of woodborer damage through a positive feedback cycle, limiting carbon assimilation and growth, and hastening insect-mediated decline.

4.1. Elevation effects on dieback driven by insect, not leaf traits

Our study was designed to enable separation of abiotic (elevation) effects and insect mediated effects. Accounting for spatial variation, we found no changes in leaf and branch morphology or stomatal anatomy along the abiotic elevation gradient, nor was there any interactive effect between elevation and dieback on leaf traits. Although *E. pauciflora* ssp. *niphophila* trees growing at the lower edge of their elevational range, were more frequently infested by *P. mastersi* than those at higher elevation sites. The absence of an elevational effect on leaf traits suggests that the observed landscape patterning in snow-gum dieback is more likely driven by biological and/or behavioural attributes of the insect, *P. mastersi,* rather than leaf traits of the affected trees. In the study of leaf, bark and hydraulic traits in *E. pauciflora* ssp. *niphophila* and closely related *E. pauciflora* ssp. *pauciflora* which occurs at lower elevations, Bryant et al. (2024) found that LMA and Huber values both increase with elevation and bark thickness of branches declines, but these were considered over two subspecies (*niphophila* and *pauciflora*) and a wider elevation range which likely explains why similar changes in LMA and Huber values were not seen in the present study. Further examination of leaf and bark traits across the wider species distribution, and of the ecology of *P. mastersi*, are warranted to better understand patterns of its infestation and predict future impacts on the two subspecies distributions.

4.2. Increasing dieback severity and water limitation in snow gums

Significant changes in leaf morphology were evident in trees with the most severe dieback symptoms, but not those with moderate dieback, indicating that the trait changes are responses to, rather than drivers of, vulnerability. Severely affected trees had smaller individual leaf areas and higher Huber values. This altered morphology is consistent with changes due to water stress; a likely consequence of damage to the xylem caused by *P. mastersi* larvae. Limited water availability is often associated with a reduction in leaf area, and thus less surface area through which water loss can occur (Leigh et al., 2017; Shao et al., 2008), but smaller leaf area can also reflect the effects of low turgor on leaf

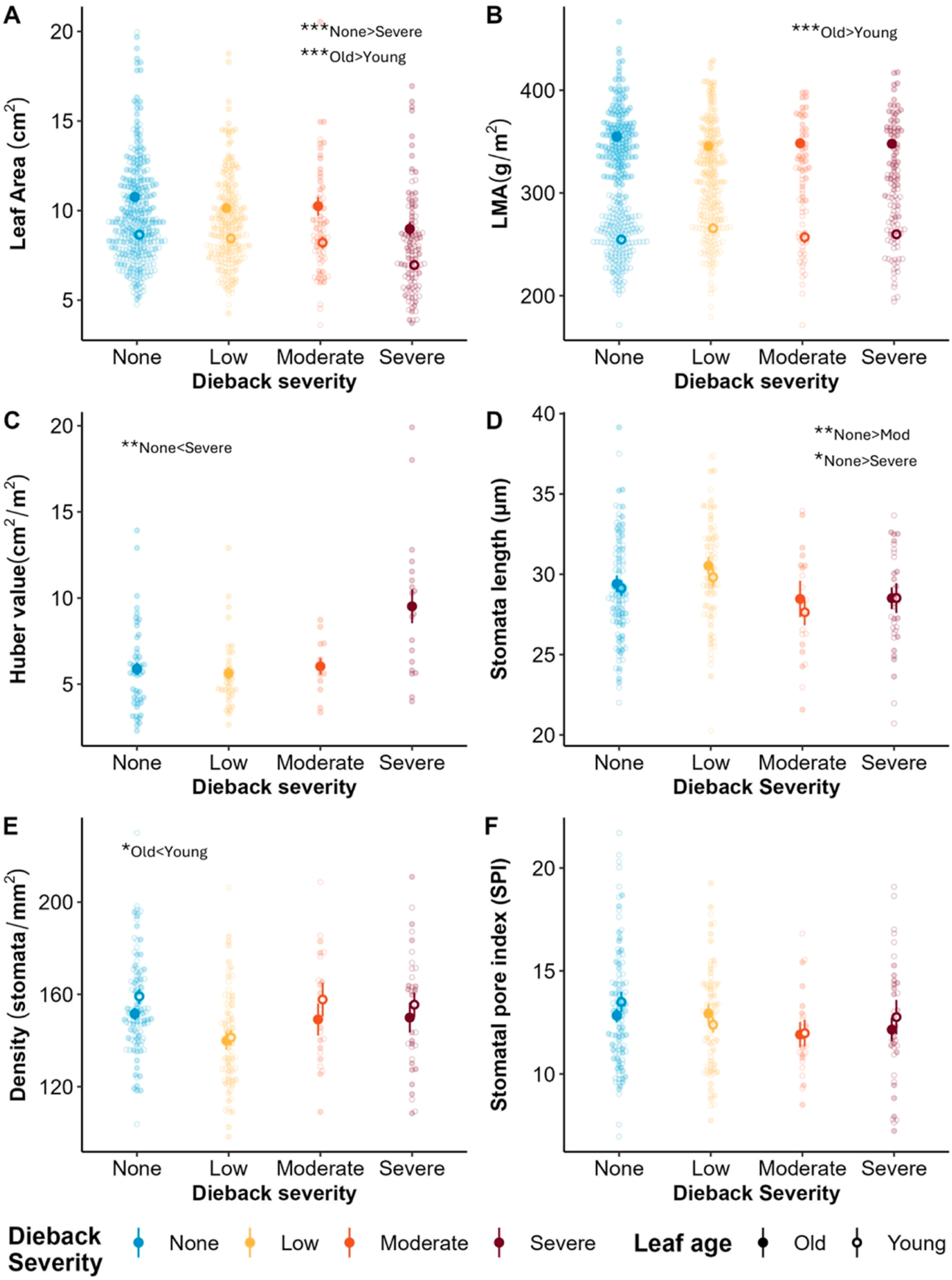

Fig. 2. The response of morphological and stomatal traits to increasing dieback severity in *Eucalyptus pauciflora* ssp. *niphophila*. (A) individual leaf area (cm^2), (B) leaf mass per area (LMA, g m^{-2}) and (C) Huber value (ratio of stem cross-sectional area (cm^2) to distal leaf area (m^2)), (D) stomatal length (μm), (E) stomatal density (no. stomata mm^{-2}) and (F) stomatal pore index (SPI, dimensionless), a proxy for maximum conductance potential considering both stomatal density and stomatal length. Huber value was measured on a branch level so there is no effect of leaf age. Closed circles indicate 'old' leaves i.e. those that expanded in the 2021/2022 growing season, while open circles indicate 'young' leaves i.e. those that expanded in the 2022/2023 growing season. Error bars reflect standard error about the mean. Asterisks indicate statistical significance of results (*=$P < 0.05$, **=$P < 0.01$, ***=$P < 0.001$). See Table 1 for full statistical analysis.

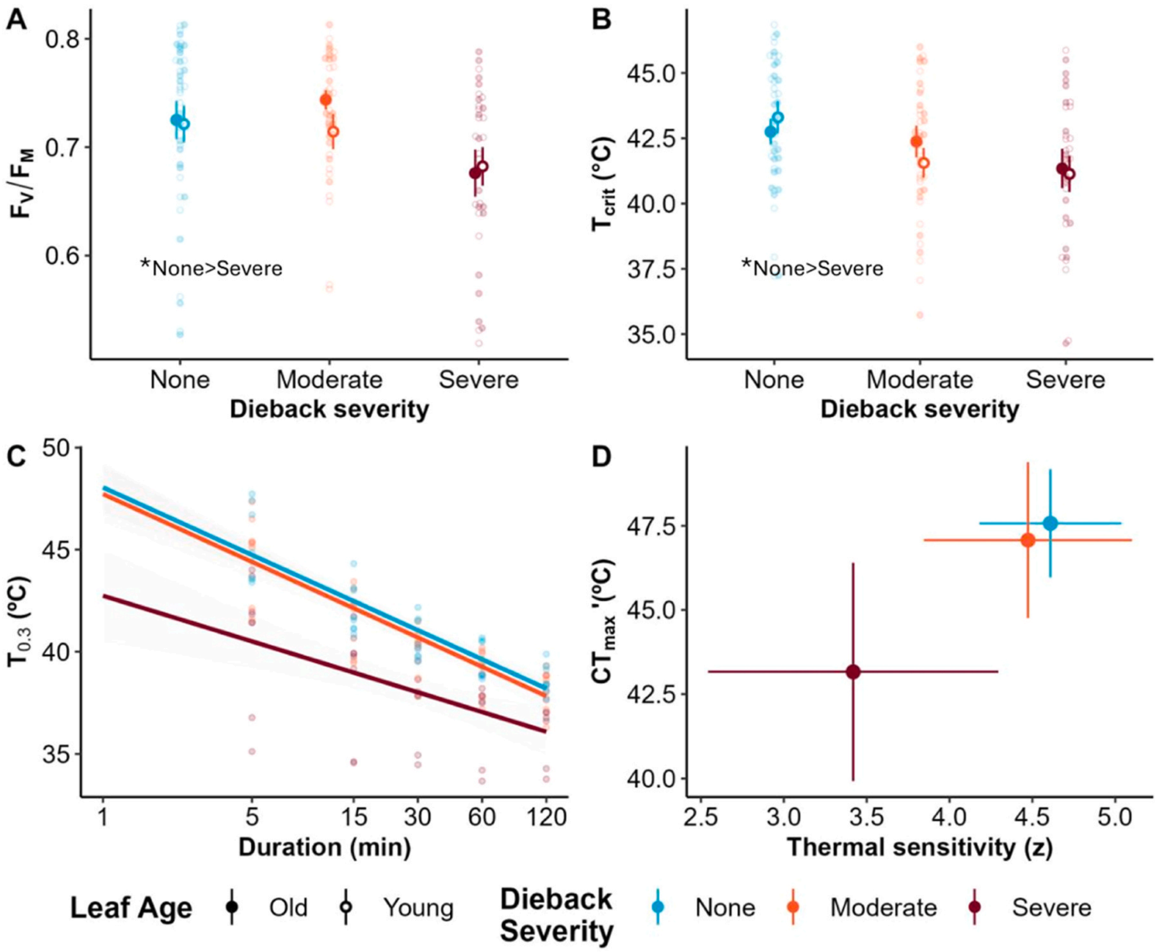

Fig. 3. Changes in photosystem heat tolerance with increasing dieback severity in *Eucalyptus pauciflora* ssp. *niphophila*. (A) Pre-assay F_V/F_M (maximum quantum yield of PSII); (B) T_{crit} (°C) (i.e. the upper temperature at which stress is incurred within PSII); (C) $T_{0.3}$(°C) for any given duration (i.e. the temperature at which $F_V/F_M = 0.3$, indicative of irreversible damage to PSII, shaded error bars reflect 95 % confidence interval; (D) Comparison of slope (thermal sensitivity, *z*) and intercept (CT_{max}'; heat tolerance ($T_{0.3}$ in °C) at 1 min duration) from plot (C), error bars reflect standard deviation about the mean. Asterisks indicate statistical significance of results (*=P < 0.05, **=P < 0.01, ***=P < 0.001). See Table 2 for full statistical analysis.

Table 2
Effects of dieback and leaf age on photosystem heat tolerance measures in *Eucalyptus pauciflora* ssp. *niphophila*: results from linear mixed effects regression models. Intercept corresponds to old leaves from unaffected trees. Heat tolerance data included 3 classes of dieback severity (none, moderate, and severe).

	Initial F_V/F_M n = 112			**T_{crit} (°C)** n = 112			**$T_{0.3}$ (°C)** n = 24			**Sensitivity parameter (*z*)** n = 24			**Heat tolerance at 1 min (CT_{max}'; °C)** n = 24		
	Est.	***(se)***	***P*-value**	**Est.**	***(se)***	***P*-value**	**Est.**	***(se)***	***P*-value**	**Est.**	***(se)***	***P*-value**	**Est.**	***(se)***	***P*-value**
Intercept	0.725	0.029	0.010	43.011	0.802	0.001	42.875	0.696	< 0.001	4.609	0.305	0.002	47.575	1.129	< 0.001
Dieback (mod)	0.015	0.015	0.327	-0.788	0.639	0.235	-0.240	0.730	0.746	-0.135	0.316	0.674	-0.500	1.171	0.674
Dieback (severe)	**-0.038**	**0.016**	**0.018**	**-1.668**	**0.661**	**0.023**	**-2.767**	**0.730**	**0.001**	**-1.19**	**0.316**	**0.001**	**-4.412**	**1.171**	**0.001**
Leaf age (young)	-0.008	0.013	0.509	-0.093	0.483	0.847	-	-	-	-	-	-	-	-	-
Duration	-	-	-	-	-	-	**-0.042**	**0.003**	**< 0.001**	-	-	-	-	-	-
Random effects of Tree ID and sampling day	***Marginal R^2*:** 0.077 ***Conditional R^2*:** 0.295			***Marginal R^2*:** 0.058 ***Conditional R^2*:** 0.191			***Marginal R^2*:** 0.522 ***Conditional R^2*:** 0.763			***Marginal R^2*:** 0.378 ***Conditional R^2*:** 0.489			***Marginal R^2*:** 0.379 ***Conditional R^2*:** 0.489		

expansion (Coussement et al., 2021). Similarly, the observed increases in Huber values are the result of either reduced leaf production (number and/or size) or increased senescence, both of which would improve water status as they contribute to maintaining favourable water potential gradients and limit the risk of xylem cavitation in severely dieback affected trees (Carter and White, 2009). These results support the conclusion that the observed morphological changes are part of the trees' response to late-stage dieback and woodborer damage to xylem rather than an intrinsic leaf trait of vulnerable trees.

Stomatal traits also changed in response to increasing dieback severity, consistent with water limitation. Trees with moderate and severe dieback had significantly smaller stomata than unaffected trees.

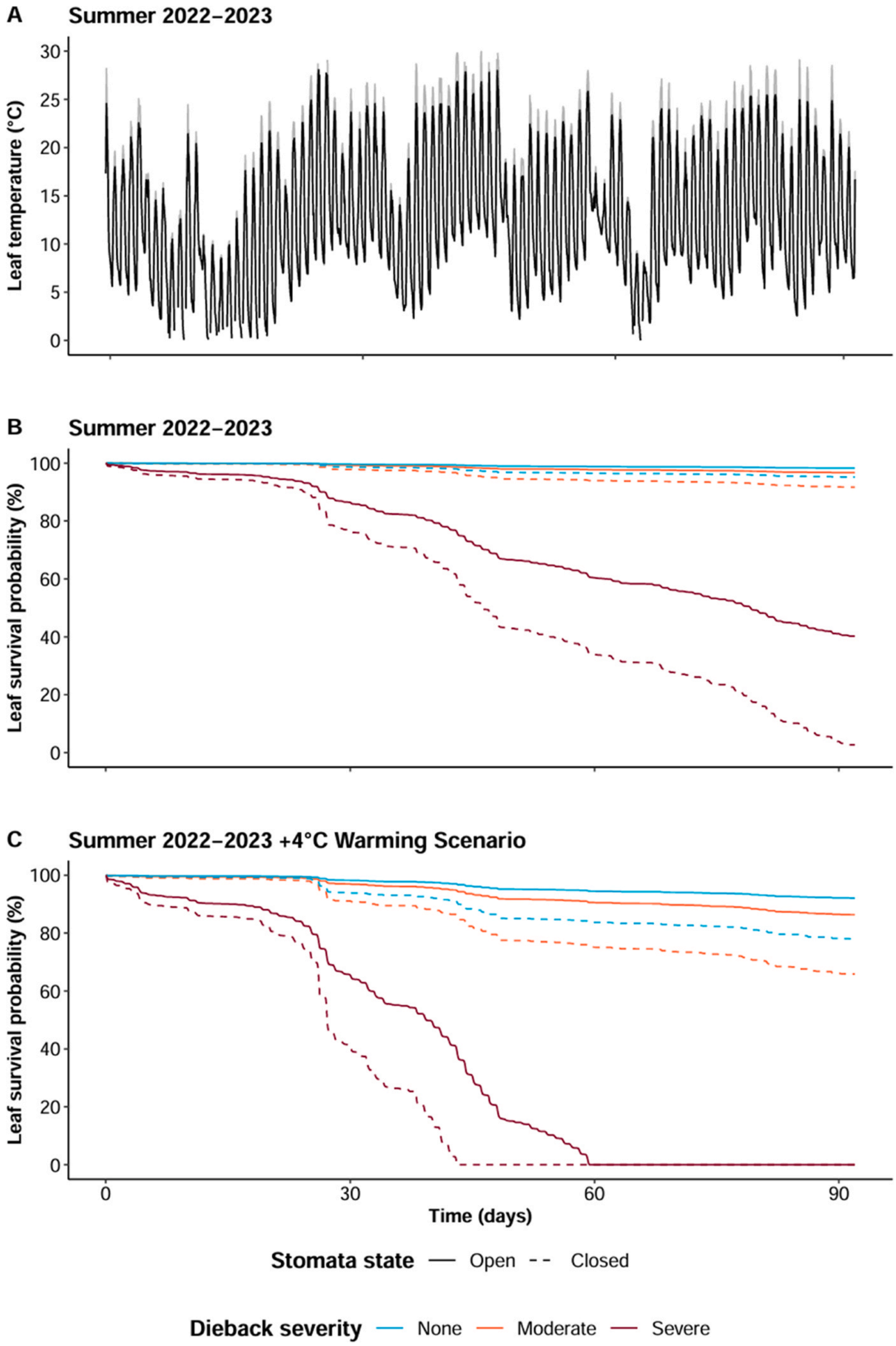

Fig. 4. Modelled leaf temperatures and leaf survival probabilities across summer 2022–2023. Time (days) refers to days after 30 November 2022, the beginning of the summer growing season. (A) Modelled leaf temperature for a standard *Eucalyptus pauciflora* ssp. *niphophila* leaf during the summer 2022–2023 growing season. Black lines indicate modelled leaf temperatures with open stomata, while light grey indicates leaf temperature with closed stomata. (B) Declining leaf survival probability modelled based on cumulative heat load and TLS curve parameters for leaves of increasing dieback severity in the presence or absence of evaporative cooling (stomata open or closed). (C) Leaf survival probability as per B but with a simulated + 4°C increase in temperatures across the entire season.

Trees in the moderate dieback category showed evidence of early canopy decline and visible *P. mastersi* feeding galleries or puckering bark, suggesting that some xylem disruption had already occurred and the tree was likely operating with reduced canopy water supply. Smaller stomata in moderately and severely affected trees may therefore have arisen as a consequence of this water limitation as greater water limitation is generally associated with reduced stomatal size and density, reducing overall pore area and water loss (Bertolino et al., 2019; Driesen et al., 2023; Henry et al., 2019; Hetherington and Woodward, 2003; Zhao et al., 2015). Smaller stomata can also open and close more rapidly than larger stomata offering greater physiological stomatal control that may be advantageous in unfavourable conditions (Drake et al., 2013; Hetherington and Woodward, 2003; Raven, 2014). Despite having smaller stomata, dieback-affected trees showed no change in stomatal pore index, a proxy for maximum potential conductance per unit area that integrates both stomata density and length (Sack et al., 2003). Thus the change in stomata length was offset by small increases in stomatal density (Haworth et al., 2023). As trees with severe dieback had smaller stomata, smaller leaves and higher Huber values, the overall effect would be lower water demand and greater stomatal control, but at the cost of reduced potential carbon gain.

Future consideration of the interplay between stomatal thermal dynamics and microclimatic conditions on thermoregulation, in conjunction with assays of carbon isotopes and non-structural carbohydrates in underground storage organs and stems of snow gums and other dieback affected species would assist in identifying the extent to which carbon assimilation and growth are limited by stomatal closure or carbon starvation (Farquhar et al., 2003). The approaches used here, in conjunction with consideration of dendrochronological series may assist to identify wood and bark trait variation and reveal other changes in growth preceding dieback as well as the relationship between growth changes and climatic factors such as annual temperatures and precipitation (Brookhouse and Bi, 2009).

4.3. *Dieback reduces physiological tolerance of heat*

In addition to morphological changes associated with *P. mastersi* infestation, we found a significant reduction in the photosystem heat tolerance of leaves from severely dieback-affected trees. This lowered tolerance threshold was consistent across both instantaneous and heat load tolerance measurements. While some studies find that mild to moderate water limitation can trigger increased heat tolerance (Cook et al., 2021; Havaux, 1992; Valladares and Pearcy, 1997), our results suggest that once the combination of heat and dieback induced (i.e. water limitation) stresses is severe enough, it triggers activation of multiple stress response pathways that limit the resources available for photosystem function (Zhu et al., 2021).

Interestingly, this finding suggests dieback may create stress that exceeds the acclimatory potential of thermal tolerance. Prior studies indicating an acclimatory effect of water limitation considered temperate and desert species and attribute increased tolerance to acclimation of leaves to higher leaf temperatures. For example, Cook et al. (2021) found that leaves of drought-affected individuals reach higher, more stressful temperatures potentially due to stomatal closure and limited capacity for transpirational leaf cooling, but these leaves also had higher heat tolerance. We found no evidence of increased heat tolerance in dieback affected trees. This could mean that these sub-alpine trees are not subject to conditions in which water limitation leads to substantially higher leaf temperatures, although our models suggest that stomatal closure can increase leaf temperatures by 2–3°C (Fig. 4A). However, we suspect that the stress caused by woodborer damage may be significantly greater than stress faced by trees in the aforementioned drought studies; for example, the shrubs measured by Cook et al. (2021) were water limited for four weeks prior to heat tolerance measurement but were otherwise healthy. Trees with severe dieback showed evidence of significant woodborer damage (feeding galleries) that has likely been limiting canopy water and nutrient supply, leading to reductions carbon assimilation for an entire growing season (or longer), leaving these trees in a precarious position with few resources to cope with additional stresses. Microsite variation, in canopy cover and aspect for example, are also likely to explain variation in thermal load and water limitation that would influence damage accumulation. Further study to assess the generality of these results for other broadleaf, evergreen, temperate forests is needed as we know little about the physiological consequences of dieback in those systems.

This study is one of few to apply an emerging measure of thermal tolerance, thermal load sensitivity (TLS), to plants to assess the interactive effects of time and intensity of heat (Arnold et al., 2025). Results from our TLS assays generally aligned with T_{crit} results but provide more nuanced insight. We found that duration of heat exposure (heat load) affected the occurrence of heat stress, with the thermal sensitivity of all dieback categories increased by extended exposure durations. While photosystem heat tolerance of all dieback categories declined with increasing duration, severely affected trees had a significantly lower critical temperature (CT_{max}') than unaffected trees, indicating a reduced tolerance for high temperatures. In these severely affected trees, exposure to 40°C (leaf temperature) for as little as 15 min could lead to significant damage to PSII (Fig. 3C). Even in the relatively mild conditions of the Kosciuszko region, leaf temperatures can regularly exceed air temperatures by 10°C or more (Salisbury and Spomer, 1964). Moreover, even at moderate temperatures the Calvin cycle can be impaired, and chloroplast heat shock proteins upregulated (Wahid et al., 2007), indicating that the potential for accumulation of heat-induced damage in our trees with severe dieback is not trivial.

The dynamic models of heat load further indicate that even under relatively mild conditions, such as those experienced during the 2022/2023 growing season, leaves of severely dieback affected snow gums were likely to have reduced survival probability, particularly if they do not have the benefit of transpirational cooling. It is worth noting that the 2022/2023 summer season was mild compared to average current summer temperatures. These models therefore also present a stark illustration of how a hotter summer would impact and exacerbate dieback effects, leading to greater leaf mortality and reduced potential for the trees to grow or recover from insect infestation. This result may be a harbinger of the feedback associated with insect mediated decline in forest stands elsewhere in the world.

5. Conclusions

Around the world forest ecosystems are exhibiting dieback events that are likely to herald widespread species turnover. These changes are particularly impactful in systems like the Australian sub-alpine, where the forest canopy is largely monospecific. Broadleaf evergreen mixed forests dominate the southern hemisphere and the tropics more broadly, but little is known about the dynamics of forest decline in these systems. Decline or loss of dominant canopy species will alter the ecological, hydrological and cultural values of the landscape, and in some cases – including snow gums – stands to impact state and national water-supply and power-generation networks. Using snow gums as a case study this project has illustrated an approach to separate biotic and abiotic drivers of dieback and to detect the extent to which variation among traits along a dieback severity gradient are drivers versus consequences of decline. This study considered elevation as a potential abiotic driver of dieback, but the general approach may be adapted to account for other abiotic influences. For snow gum, leaf trait variation is not associated with variation in vulnerability to dieback within the affected subspecies, though previous studies indicate that bark traits may explain variation among subspecies. The present study also demonstrates how changes in traits in response to water stress likely form part of a positive feedback loop that hastens tree decline by reducing both capacity for photosynthetic assimilation and physiological tolerance of heat. Our results indicate that the impact of heat load associated damage on long lived leaves of evergreen species is a critical knowledge gap to address for anticipating and managing global forest decline.

CRediT authorship contribution statement

Danzey Lisa: Writing – review & editing, Visualization, Methodology, Investigation, Formal analysis. **Harris Rosalie:** Writing – review & editing, Visualization, Methodology, Investigation, Formal analysis. **Cook Alicia:** Writing – review & editing, Visualization, Methodology, Investigation, Formal analysis. **Arnold Pieter:** Writing – review & editing, Visualization, Validation, Methodology, Investigation, Formal analysis. **Brookhouse Matthew:** Writing – review & editing, Visualization, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Aitken Sabina:** Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Andy Leigh:** Writing – review & editing, Visualization, Methodology, Investigation, Formal analysis. **Nicotra Adrienne:** Writing – review & editing, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123523.

Data Availability

Data will be archived on Dryad after acceptance of the paper.

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