Physiological strategies explain mortality differences amongst ecologically and culturally significant Australian desert plants following a hotter drought

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Lay summary: We linked morphological and physiological traits and their spatial and temporal variability in culturally important Australian desert plants to dieback severity from a recent extreme heatwave and drought event. A range of physiological strategies exist, with stress avoiding species generally surviving more than stress tolerating species.

Pitjantjatjara summary: To be created after submission and appropriate.

Abstract:

Climate change-induced drought and heatwave events (hotter droughts) are causing mass plant dieback events globally. Recently, Uluṟu-Kata Tjuṯa National Park (UKTNP) in central Australia saw a widespread plant dieback (mortality) event, resulting in negative impacts to the ecosystems and concern and a desire to understand more about the underlying causes of mass plant death from Aṉangu (Traditional Owners). We measured morphological and physiological traits that were hypothesised to drive physiological mechanisms underpinning the patterns of dieback observed at UKTNP in culturally important species chosen by Aṉangu. Maintenance of leaf relative water content (RWC) was the leaf trait that best predicted dieback severity, with all low dieback severity species exhibiting drought-avoidance strategies, where RWC was maintained between spring and summer. Most moderate and high dieback severity species exhibited drought-tolerance strategies, evidenced by large declines in seasonal RWC compensated by higher wood densities. However, two small shrub species with high dieback severity likely died due to failure of different physiological mechanisms - one of hydraulic failure and one of carbon starvation - highlighting the importance of considering species-specific trait combinations to understand drivers of mortality. Hotter drought events in central Australia are likely to impact not only plant communities, but Aṉangu culture.

Pitjantjatjara abstract: To be translated once finalised if appropriate.

Key words:

Climate change, plant physiology, drought, heatwave, arid, culturally important, leaf traits, Australia, Indigenous knowledge, dieback

Introduction:

The frequency of mass dieback (including mortality) in plant communities is increasing globally (Luna-Aranguré *et al.*, 2025). Dieback is a complex physiological process and can involve several contributing or interacting factors, making determining the causes of decline difficult in individual cases (Allen, 2009). However, drought and heatwaves are known to be one of the most widespread drivers of mass plant death. In water-limited environments, local extreme heat can combine with severe drought to cause rapid plant mortality (Choat *et al.*, 2018). Anthropogenic climate change is causing a greater frequency of more intense drought and heatwave events (i.e., hotter droughts), increasing the likelihood of more frequent and widespread dieback (Bauman *et al.*, 2022; Hartmann *et al.*, 2022; McDowell *et al.*, 2022).

Global data show that as aridity and temperature increase, plant traits (both across and within species) change, often in a concerted manner (Niinemets, 2001). Generally, leaf area decreases whilst leaf mass per area (LMA) and leaf dry matter content (LDMC) increase, reflecting global convergence on a more conservative leaf structure to minimise water loss and maintain leaf function under dry and hot conditions (Niinemets, 2001; Li and Prentice, 2024). Further, higher wood density and narrower xylem vessels act to maintain water transport and reduce the risk of embolism under drier soil conditions (McDowell *et al.*, 2008). However, a variety of strategies with different trait combinations allow plants to exist across a range of environments (Laughlin *et al.*, 2023).

Several strategies have been postulated to explain how species survive in hot and dry environments (e.g. Ackerly, 2004). These can be conceptualised as 'stress escape', stress avoidance' and 'stress tolerance'. A stress escape strategy dictates that plants complete their life cycle within the window of favourable conditions, as exemplified by desert ephemeral plants with exceptionally high CO_2 assimilation rates (Mooney *et al.*, 1976). Stress-avoiding plants have characteristics such as deep root systems (to access more abundant water sources), stem succulence to store water, and sunken stomata and curled leaves to decrease stomatal water losses (Jordan *et al.*, 2008; Fang and Xiong, 2015). Often, stress-avoiding species will have conservative water use and limit water losses, and therefore operate well above their hydraulic safety thresholds (Choat *et al.*, 2012). Stress-tolerating plants, in contrast, maintain growth while operating close to their hydraulic safety thresholds through stressful conditions via adaptations such as high wood density and small, thick leaves that reduce water loss while maintaining conductance and preventing extreme leaf temperatures (Choat *et al.*, 2012). By maintaining growth under stressful conditions, stress-tolerating species also have less conservative stomatal behaviour under low soil moisture, leading to more variable leaf relative water content (RWC) than species that cease water use under low soil moisture (Nolan *et al.*, 2017). During mild stress, stress-tolerating species are able to maintain function at a much broader range of conditions than stress-avoiding species (Choat *et al.*, 2018). However, under extreme conditions, stress-tolerating species have a greater likelihood of exceeding hydraulic safety thresholds than stress-avoiding species. Consequently, stress-tolerating species generally have higher mortality rates than stress-avoiding species in response to climate change-induced hotter droughts due to hydraulic failure (Brodribb *et al.*, 2020). However, if hotter drought is prolonged, stress-avoiding species may die of carbon starvation if internal C stores are exhausted (McDowell *et al.*, 2022). A greater understanding of the range of strategies observed amongst species in an ecosystem experiencing dieback is needed to improve our understanding of the mechanisms underlying dieback (Pivovaroff *et al.*, 2016), especially in extreme arid environments already undergoing mass dieback.

After a record-breaking drought and heatwave event in 2018-2019, Uluṟu-Kata Tjuṯa National Park (UKTNP) in the deserts of Australia's Northern Territory experienced a mass mortality, dieback event (Wright *et al.*, 2023). Annual rainfall for 2019 was the lowest recorded at only 27 mm (38-year average rainfall is 269 mm – Bureau of Meteorology, 2025) coinciding with several weeks in summer with temperatures above 45 °C. Aṉangu (Pitjantjatjara and Yankunytjatjara people, the Traditional Owners) expressed their concern and a desire to understand why plants are dying on Country (Country is a term used by Aboriginal peoples to describe the lands, seas, and waterways, including cultural and spiritual connection, belief, law, language, and identity). A mortality study on a range of culturally and ecologically important species at UKTNP revealed that: (i) some species had very high mortality (> 90 %), whereas some had very low mortality (0 %); (ii) there was generally greater survival in larger individuals; and (iii) there were density-dependent mortality relationships that differed between species (Wright *et al.*, 2023). A follow-up study investigating landscape-level patterns in dieback suggested that species-specific mortality patterns across UKTNP are associated with topographic trends across dune sequences, and some are linked to stand density and size of individuals (Godfree and Knerr, 2025). However, the drivers and physiological mechanisms underpinning dieback in these culturally important species within UKTNP remains unknown.

The ecocultural impacts of climate-induced mortality, particularly for First Nations peoples, are only recently garnering attention. Loss of stewardship following colonisation, in addition to altered ecosystem processes from changed fire practices, invasive species and climate change, lead to disproportionate impacts on Indigenous Peoples and their Country (Wickham *et al.*, 2022; Hankins, 2024). UKTNP is a site of immense importance for Aṉangu. Thus, rather than study the rare or threatened species that western conservation management may consider, our team of university researchers and Aṉangu selected a range of species that are ecologically important and also hold cultural value. Understanding why and where these species are dying will allow Aṉangu to have a more holistic approach to managing Country and is of critical importance to conserving natural and cultural values.

Working on naturally occurring individuals in a range of vegetation types, we assessed a suite of morphological and physiological parameters (herein referred to simply as traits) hypothesised to confer the ability to tolerate or avoid heat and water stress. Our objectives were to: i) determine the traits or combinations of traits associated with observed dieback and understand whether those traits vary spatially among broad habitat types or temporally between seasons within an individual; and ii) elucidate the stress tolerance or avoidance strategy that each species employs to help explain the observed patterns of mortality. We hypothesised that the type of water use strategy used by each species, inferred from relative water content and its seasonal change, would be the strongest predictor of mortality risk. Low dieback severity species were predicted to show a stress-avoiding water use strategy with low seasonal change in leaf hydration. High mortality species were predicted to exhibit larger seasonal declines in leaf hydration, characteristic of a stress-tolerating strategy. Overall, we predicted that species with stress-tolerating strategies would show greater leaf trait variability across habitats and seasons, while low dieback, stress-avoiding species would maintain more stable trait values across space and time.

Methods

Study area

Uluṟu-Kata Tjuṯa National Park is located in the central desert region of Australia's Northern Territory (Figure 1), 300 km south-west of Alice Springs. The climate is classified as Grassland hot (persistently dry) under the Köppen climate types (Peel *et al.*, 2007). It has a mean maximum temperature of 30.3 °C and a mean minimum temperature of 14.2 °C (Bureau of Meteorology, 2025). Mean annual rainfall for Yulara airport (20 km from UKTNP) is 269 mm and median rainfall is 222.5 mm, indicating that interannual rainfall variability is high. Summers (Nov-Mar) are hot and usually wetter, with temperatures regularly exceeding 40 °C. However, preliminary data from microclimate logging stations deployed across the park suggest regular summer surface air temperatures > 50 °C. Winters are cool and dry with daytime temperatures at 20 °C, with a slow gradual increase in daily temperatures until summer. A deep, red siliceous sand dune fields vegetation complex dominates the majority of UKTNP, intersected by creek lines and gravel outwash plains. Unlike many dune systems worldwide, the dune fields complex at UKTNP is vegetated and not subject to short-term and large-scale dune movement from aeolian processes (Keith, 2017; Morton, 2022).

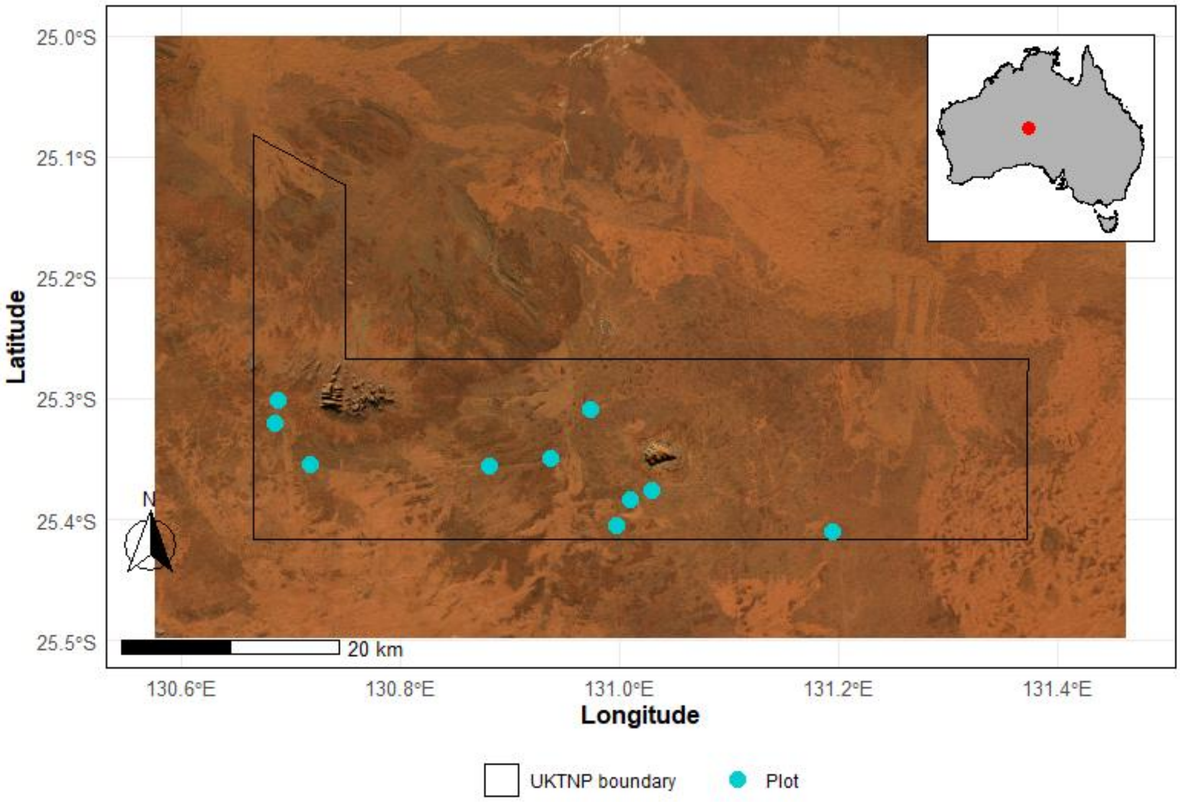

Figure 1 Location of Uluṟu-Kata Tjuṯa National Park in Australia’s Northern Territory (inset) and the location of the ten study plots.

Aṉangu have identified three main habitat types in the dune fields complex of UKTNP: tali (sand dune), pila (sand plain) and puṯi (woodland/scrubland) (Table 1). Soil moisture, nutrients, and particle size vary across the habitat types, associated with a catenary sequence from top of the tali, into the pila, with puṯi being the most low-lying point in the dune fields. Briefly, soil moisture and fractions of silt and clay increase from the top of tali, to pila, to puṯi (Table 1, Buckley, 1982. See Supplementary Material for further details of edaphic properties).

Table 1. Description of habitat types sampled.

Tali Sand dunes, including crest, upper and lower slopes – typically 5-10 m elevation. Low water availability, coarse sand. Range of perennial woody shrubs, diverse ephemeral herbs and spinifex grasses dominate.	 
Pila Sand plains. Inter-dune space between tali and puṯi. Medium-textured sand (3-5 % silt and clay, Buckley, 1982). Spinifex grass dominated with scattered small trees and ephemeral herbs.	 
Puṯi Woodland and scrubland; also known as swale. Lower lying parts of landscape. Moderate water availability and highest silt and clay proportions (> 5 %, Buckley, 1982).	 

Study species

We named this study Punu Tjuta – meaning many plants in Pitjantjatjara. Nine species were chosen with Anangu over many consultations and field trips on Country. The plants chosen reflected those that Anangu are concerned about, want to know more about, or hold cultural and ecological importance: mangata, kurkara, altarpa, tjanpi, wanari, ilykuwara, pukara, kaliny-kalinypa, kampurarpa (western scientific names in Table 2; Pitjantjatjara names used hereafter). The study species also represent the range of lifeforms and dominant plants present in the dune fields vegetation complex, ranging from spinifex grass of the pila (sand plain) and tali (sand dune) through to large trees on the puti (*Acacia* woodland).

The final species list had a range of overall mortality rates across UKTNP, with six of the nine species also assessed by Wright *et al.* (2023). Mortality rates varied across the species, with low rates for mangata (0 %) and kurkara (22 ± 7 %; means ± SE), moderate rates for wanari (42 ± 11 %) and tjanpi (53 ± 11 %), and high rates for kaliny-kalinypa (79 ± 9 %) and pukara (91 ± 5 %) (Table 2). Taking expert guidance from Anangu and other researchers at UKTNP (e.g. Wright *et al.*, 2023; Godfree and Knerr, 2025), we estimated dieback severity for the three remaining species; kampurarpa, ilykuwara and altarpa. Ilykuwara is an acacia and is similar in habit to two of the study species considered by Wright *et al.* (2023): *Acacia melleodora* had a mortality rate of 65 % and *Acacia maitlandii* 67 %. Furthermore, based on our observations and discussions, it seemed unlikely that ilykuwara had either very high or very low mortality, so we classified it with moderate dieback severity. Altarpa likely had low mortality due to the strong resprouting capacity, which concurs with our own observations at UKTNP. Kampurarpa, being a small ephemeral herb, would likely have had high dieback severity across UKTNP during the drought and heatwave event.

Some species are present in all three habitat types (e.g. tjanpi, altarpa), whereas others are restricted to a single habitat (e.g. ilykuwara). Given the differences in soil moisture, nutrients and particle size between habitat types (Buckley, 1982), and to further explain spatial variability in mortality identified by Wright *et al.* (2023), we designed a sampling regime to capture differences across the landscape in mortality rate both within and between species (Table 2).

Table 2. List of plant species surveyed at Uluru-Kata Tjuta National Park, ranked by mortality rate as quantified by Wright *et al.* (2023). For descriptions of habitats, see Table 1. Mortality class was determined from Wright *et al.* (2023) data and on-ground observations.

Species		**Family**	**Dieback severity ^**	**Description**	**Usage**
Pitjantjatjara name	Scientific name				
Mangata 	*Santalum acuminatum* (R.Br.) A.DC.	Santalaceae	Low (0 %)	Root hemiparasitic tree species with a broad geographic distribution, but locally endangered at UKTNP.	Highly sought after fruit – flesh. Kernal ground for mangka (hair conditioner). Tools from roots. [1]
Kurkara 	*Allocasuarina decaisneana* (F.Muell.) L.A.S.Johnson	Casuarinaceae	Low (22 %)	Large, slow growing, deep-rooted tree. Typically 10-16 m in height and found predominantly in pila (sand plain).	Seeds eaten. Lolly (white sugary exude) eaten from cones in warmer months. [1]
Altarpa 	*Eucalyptus gamophylla* F.Muell.	Myrtaceae	Low (estimate 10-20 %)	Mallee eucalypt species that forms a lignotuber and has strong resprouting capacity post disturbance (e.g. fire); patchy distribution, found in puti (woodland).	Habitat for unturngu (bush banana). [1]
Tjanpi 	*Triodia pungens* R.Br.	Poaceae	Moderate (53 %)	C_4 hummock grass. Widespread across arid Australia and found in many different landscape types, including puti, tali and especially pila.	Resin from leaves used to make kiti (wax for tools). [1, 3, 4]
Wanari	*Acacia aneura* F.Muell. ex Benth.	Fabaceae	Moderate (42 %)	Widespread small tree species that occurs across arid and semi-arid	Tools. Firewood. Branch ashes mixed with native tobacco.

Species		Family	Dieback severity ^	Description	Usage
Pitjantjatjara name	Scientific name				
				Australia, often in puti (woodland), specifically lower-lying interdune regions.	Culturally important tjala (honey ant) habitat. Tarulka (mulga apple). Bush banana – wintjulanypa. Bush lolly (sap) eaten. [1, 5, 6]
Ilykuwara 	*Acacia kempeana* F.Muell.	Fabaceae	Moderate (estimate 30-40 %)	Small spreading tree. Occurs across a range of habitats, but predominantly woodlands co-occurring with wanari on the puti.	Roots habitat for culturally important maku (witchetty grubs). [1, 7, 8]
Pukara 	*Aluta maisonneuvei* subsp. *maisonneuvei* (F.Muell.) Rye & Trudgen	Myrtaceae	High (91 %)	Small, woody shrub with highly reduced leaves that forms dense stands along dune systems from the crest to the lower slopes.	Nectar used to sweeten water (cordial). [1, 9]
Kaliny-kalinypa 	*Grevillea eriostachya* Lindl.	Proteaceae	High (79 %)	Woody shrub valued for its honey-like nectar that occurs across dune systems and sand plains.	Nectar eaten directly from flowers and mixed with water (cordial). [1, 7]
Kampurarpa 	*Solanum centrale* J.M.Black	Solanaceae	High (estimate 70-90 %)	Small ephemeral forb that increases greatly in abundance in areas recently burnt and following good rainfall.	Fruit eaten dried (brown) and fresh (yellow) - high in Vitamin C. [1, 7]

^ Percentage mortality from Wright *et al.* (2023).

[1] R. Okai (pers. comms.), [2] O'Connell *et al.* (1983), [3] Gamage *et al.* (2012), [4] Cane (1987), [5] Cleland and Tindale (1959), [6] Walsh (1990), [7] Latz (1995), [8] Kalotas (1983), [9] Ward *et al.* (2023).

Study design

Ten plots were selected from 30 survey plots established by CSIRO and Parks Australia in 2021 (Godfree and Knerr, 2025). Plots were chosen to (1) include all three habitat types, (2) maximise the number of target species, (3) capture the west-east extent of UKTNP, and (4) ensure access on-foot. Recently burnt areas (≤ 3 years) were excluded using fire scar maps from North Australia & Rangelands Fire Information (NAFI, 2025). Within each plot, sampling was stratified by habitat, with three-five individuals per species-habitat combination (except mangaṯa; see below), aiming for minimum 40 individuals per species (Table S1). Plot size varied from 1 to 30 ha to maintain similar replication across species despite uneven distributions. Mangaṯa, which has only nine known live individuals in UKTNP, was sampled independently. Two additional single-habitat plots were included to increase representation of species restricted to one habitat (e.g. wanaṟi, ilykuwara).

Sampling was conducted in spring (September) 2023 and summer (March) 2024 to capture mild versus extreme seasonal conditions. Volumetric soil moisture (0-5 cm depth) was measured at three locations within each plant's dripline using a FieldScout TDR 350 (Spectrum Technologies, USA) during both campaigns (except one plot in summer 2024 due to instrument failure).

Weather preceding spring 2023 sampling was mild (maximums <30 °C) with atypically high winter rainfall (June 2023; Figure S1a), suggesting low physiological stress despite dry surface soils (Figure S1b). In contrast, weather preceding summer 2024 featured prolonged heat (>40 °C) and low rainfall, followed by small rain events during sampling that raised surface soil moisture from 0.9 % to 3.1 %. Soil moisture was consistently lowest in tali (sand dune) compared with pila (sand plain) and puti (woodland) habitats (Figure S1b).

Plant and trait measurements

Only adult plants showing minimal signs of stress (e.g. necrosis, insect or pathogen damage, stem dieback) were sampled, with all individuals located > 50 m from roads to avoid hydrological edge effects. During the first campaign, plant height and stem diameter (woody species) or canopy dimensions (non-woody) were recorded. Each individual was assigned a 6-level relative health score (0.5–3, in 0.5 increments) based on visible symptoms such as leaf yellowing, necrosis, or defoliation. Leaves (including phyllodes and cladodes) were collected between 8 am and 11 am using secateurs or a pole pruner, sampling one plot per day. To standardise light exposure and leaf age, the newest fully expanded, north-facing adult leaves were selected. For each individual, 10-20 leaves were collected and stored in sealed bags within a cooler. For pukara, branchlets containing several hundred small, scale-like leaves were collected.

Samples were processed within 2-4 h of collection. Three leaves per individual were trimmed with a razor and weighed fresh, with leaf thickness measured using digital callipers (avoiding the midrib) and leaf area with the Easy Leaf Area app (Easlon & Bloom, 2014). Leaves were rehydrated overnight (12-16 h) before reweighing for rehydrated mass; preliminary trials showed six hours was insufficient for full rehydration in some species. For pukara, average fresh mass, area, and rehydrated mass were based on 30-100 leaves. Samples were pre-dried in the field (2 h) to prevent spoilage and oven-dried at 105 °C for 48 h at the Australian National University for dry mass determination.

All calculations were conducted on an average per leaf basis, whereby the cumulative weight (fresh, rehydrated or dry) and area were divided by the number of leaves per individual. Leaf mass per area (LMA, Table 3) was calculated by dividing mean leaf area by mean dry mass ($g\ m^{-2}$). Leaf dry matter content (LDMC, Table 3) was calculated as the ratio of dry mass to fresh mass. Leaf relative water content (RWC, Table 3) was calculated using the following formula:

RWC (%) = ((FM-DW) / (TM-DM)) x 100

where FM is fresh mass, DM is dry mass and TM is turgid mass (or rehydrated mass).

Between three and ten leaves per individual were placed in envelopes for carbon stable isotope and C:N ratio analysis (Table 3). A subset of individuals from each species were selected (10-15 per species, with 3-5 per habitat type). Samples were dried at 80 °C for 48 hours prior to being delivered to the Stable Isotope Laboratory at the Research School of Biology at the Australian National University for mass spectrometry and elemental analysis. Carbon stable isotope and C:N ratio analyses were only conducted for the spring 2023 sampling regime.

To standardise across a range of woody lifeforms (from shrubs to large trees), wood density (Table 3) was measured on stem segments 1–1.5 cm in diameter. For smaller shrub species, this represented more basal wood, while for larger trees, samples were from terminal branches. One individual per species per habitat was selected per plot. Using secateurs or pole pruners, a 10 cm-long segment was collected, sealed in a zip-lock bag, and stored in a cooler. Wood density was measured using the water displacement method (Sack et al. 2010). Each segment was trimmed to ~2.5 cm in length, with its fresh mass when submerged equalling its volume. Samples were then dried at 105 °C for 48 hours and reweighed. Wood density (g cm^{-3}) was calculated as dry mass divided by volume. Wood density was measured only during spring 2023 sampling.

Table 3. Plant traits measured for each individual. A description of the trait and its ecophysiological significance as well as the sampling frequency are given.

Trait	Description	Frequency of sampling
Morphological traits		
Leaf area (cm^2)	Total one-sided surface area of a leaf. Greater area reflects greater light interception for photosynthesis but increased potential water losses. [1]	Both seasons
Leaf mass per area (LMA, g m^{-2})	Dry mass divided by the one-sided area of a leaf. Higher LMA reflects greater structural investment. [2]	Both seasons
Leaf thickness (mm)	Distance between upper and lower leaf surfaces. Linked to specific adaptations such as photosynthetic capacity and efficiency, and temperature and water regulation. [3]	Both seasons
Leaf dry matter content (LDMC, ratio)	Ratio of leaf dry mass to leaf fresh mass. Higher values reflect greater investment into structural leaf components. [3]	Both seasons
Wood density (WD, g m^{-3})	Wood mass per volume. Higher WD indicates greater ability to tolerate higher water tensions. [4]	Spring 2023 only

Physiological traits		
Leaf relative water content (RWC, %)	Proportion of leaf water under field conditions relative to the fully-hydrated leaf. Indicator of water stress and water regulation strategy. [5]	Both seasons
Leaf carbon isotope fractionation ($\delta^{13}C$, ‰)	Ratio of the stable isotopes of C. Proxy for water use efficiency across the whole lifespan of a leaf. [6]	Spring 2023 only
Leaf carbon:nitrogen ratio (C:N)	Ratio of C to N in leaves. Reflects structural investment, growth capacity, and nitrogen use efficiency. [7]	Spring 2023 only

[1] Niinemets (2010), [2] Poorter *et al.* (2009), [3] John *et al.* (2017), [4] Chave *et al.* (2009), [5] Bartlett *et al.* (2012), [6] Seibt *et al.* (2008), [7] Reich (2014).

Data analysis

Broad trait patterns

All data analyses were conducted using RStudio (Posit team, 2025; R version 4.3.1). We used Bayesian multinomial logistic regression (using brms package (Bürkner, 2017) in R) to identify which leaf traits (RWC, LDMC, LMA, thickness and area) best predicted dieback severity. Separate models were fit for spring and summer with habitat treated as a random intercept to test whether trait-dieback relationships differed between non-stressful and stressful conditions (see Supplementary Methods for full details).

Using log-transformed data (or arcsine transformed for RWC and LDMC, as these were percentages), principal component analysis (PCA) was conducted, comparing the coordination of traits between seasons. Vector plots were produced for the five leaf traits measured across both seasons using the *FactoMineR* package (Lê *et al.*, 2008) in R. The seasonal change in coordination across the five traits was calculated from the vectors as degrees.

Species-level trait patterns

To examine species-level shifts in leaf traits, we calculated trait differences (Δ trait) by subtracting summer from spring values. Species were also grouped by dieback severity class (three species per class) to explore broader trait shifts among groups. Pairwise differences among species (linear models) and dieback classes (linear mixed-effects) were tested using the *emmeans* package in R (Lenth, 2023). For species-level comparisons, linear models were used with trait as the response and species as the predictor. For dieback class comparisons, linear mixed-effects models were used with dieback class as the predictor and species as a random effect. Tukey HSD was applied to estimate pairwise differences, with p-values adjusted for family-wise error. Model residuals were assessed using the *ggResidpanel* package (Goode and Rey, 2019), and cube-root transformations were applied to traits where assumptions were violated due to negative values. For traits only measured in spring (e.g. $\delta^{13}C$, C:N ratio, wood density), a similar approach was applied using spring data only.

To assess the influence of species identity, habitat type, season, and their three-way interaction on trait variation, we fit linear mixed-effects models using the lmer function from the *lme4* package in R (Bates *et al.*, 2003). We conducted analysis of deviance (Type III Wald chi-square tests) on each mixed-effects model. For a full description of the model structure for all linear and linear mixed-effects models, see the Supplementary Material.

Results

Extent of seasonal change varied among traits and dieback severity classes

Relative water content (RWC), or leaf hydration, was the best and most consistent predictor of dieback severity class for the leaf traits measured across both seasons (Table 4). In spring when conditions were relatively more benign, leaves of low dieback species were typified by maintaining relatively high RWC, while being structurally dense (higher LMA) and having on average, thinner leaves than the other dieback categories. Moderate and high dieback species generally had lower RWC and thicker leaves, with high LMA best predicting high dieback over low and moderate dieback species (Table 4). In summer, after extended periods of hot, dry weather, many of the trait differences among dieback classes had shifted and RWC was the only trait that continued to differentiate dieback classes. In summer, the RWC of low dieback species was similar to that of moderate dieback species, whereas high dieback species had significantly lower RWC. Leaf thickness and LMA in summer were not significantly different between low and high dieback classes, indicating that species-specific changes in those traits within each mortality class may overshadow broader dieback class trends. Overall, LDMC was not a good predictor of dieback class, with no significant trends in either season (Table 4). Differences in leaf area were species-specific, and predictions harder to generalise across dieback classes. However, on average, the moderate dieback species had smaller leaf areas, but this did not shift between seasons (Table 4).

When we assessed coordination among the five leaf traits, the change between seasons was particularly clear for RWC (Figure S2). In spring, RWC was positively correlated with LMA and LDMC (Figure S2a), indicating that leaf hydration was positively coordinated with leaf structure. However, in summer, RWC became decoupled from changes in LDMC and LMA, with the vector changing by 84 ° (Figure S2b). Therefore, differences in RWC in summer were independent of leaf structural traits. Coordination among all other traits changed much less markedly across seasons in overall vector angle and magnitude and therefore remained similarly coordinated in both seasons.

Table 4. Model predictions of leaf trait levels for each dieback severity class across both spring and summer. Bayesian multinomial logistic regression was used to estimate the log-odds of all five traits predicting each dieback class. The relationship between trait value estimates between dieback classes is shown by the order column. Significant (95% confidence interval of log-odds does not include zero) differences in predicted leaf trait levels between dieback classes are shown by > or < depending on the direction, with = representing a non-significant difference. A change in order of dieback classes between spring and summer is shown in bold. Separate models were created for each season, with habitat as a random effect. See Table S2 for the full summary of results.

	Order	
Trait	Spring	Summer
RWC	Low > Mod = High	Low **=** Mod **>** High
LDMC	Low = Mod = High	Low = Mod = High
LMA	Low = Mod > High	Low **<** Mod > High
Thickness	Low < Mod = High	Low **>** Mod **<** High
Area	Low > Mod < High	Low > Mod < High

The differences in traits among seasons can be illustrated in more detail by directly analysing the seasonal changes. Generally, species in moderate and high dieback severity classes exhibited greater seasonal change in RWC and increases in LDMC (Figure 2), indicating that low dieback severity species maintained leaf hydration between seasons, whereas moderate and high dieback species did not. Kaliny-kalinypa was the only high dieback species that did not have reductions in RWC in summer. At the species level, seasonal differences in LDMC were significant, with low dieback species either maintaining or even decreasing in dry matter content (i.e. increasing in water content) between spring and summer. Seasonal change in leaf thickness did not differentiate among either species or dieback severity classes (Figure 2). On the other hand, low dieback severity species tended to have reductions in LMA, likely due to increases in or maintenance of leaf area between seasons, relative to moderate and high dieback species which tended to have reduced leaf area (Figure 2). Altarpa, a low dieback species, had large seasonal differences in leaf area. Generally, kurkaṟa exhibited small seasonal differences in all traits.

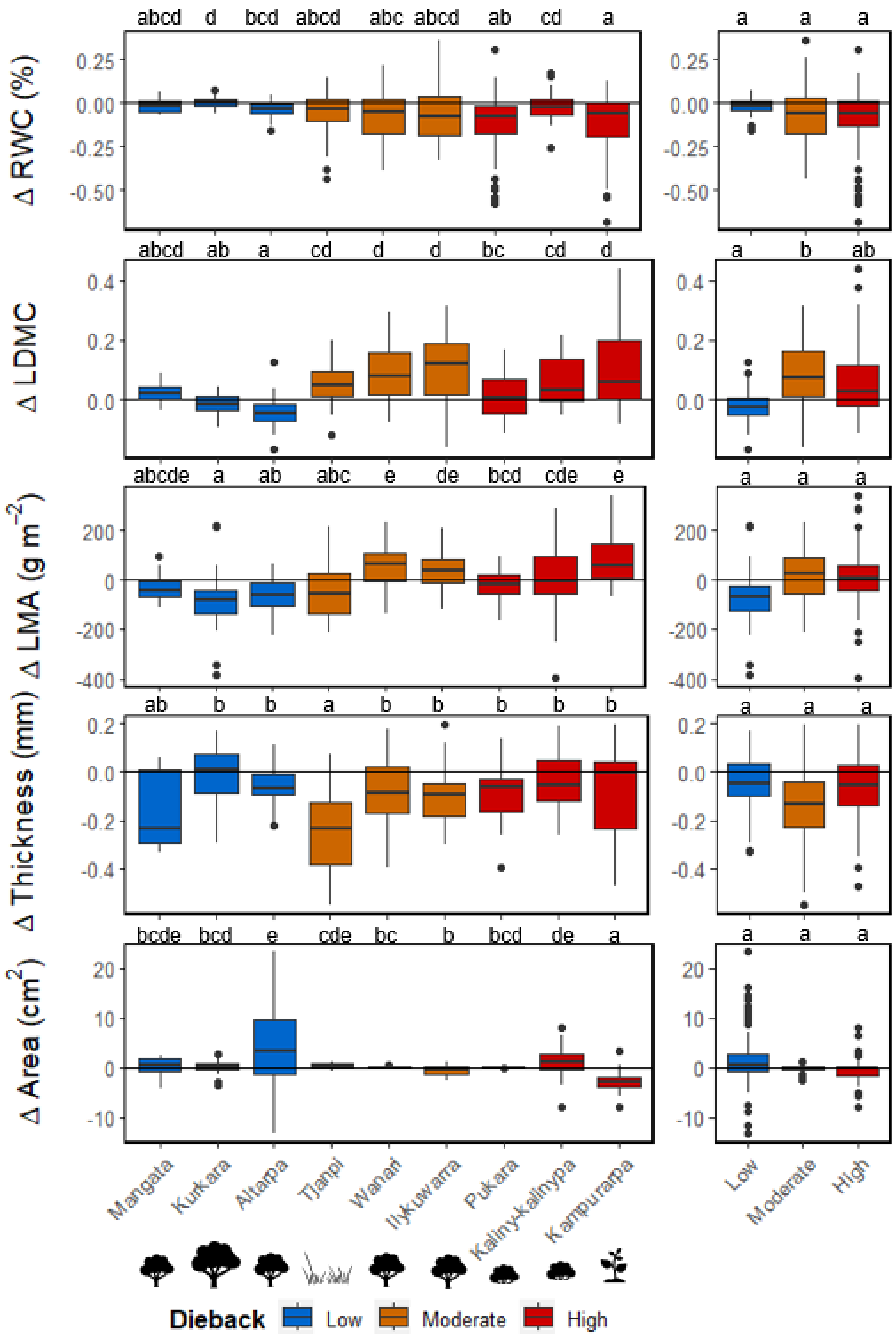

Figure 2. Seasonal differences in leaf traits among species and mortality classes. Summer measurements were subtracted from spring measurements for each individual. If a value was positive (i.e. above zero), the trait value increased between spring and summer (and vice versa). Species data were aggregated across species by mortality class for the side panels. Box and whisker plots show the median, 25th and 75th percentiles bound by the box, with the whiskers displaying the minimum and maximum values, plus outliers by points. Letters above each plot indicate significant differences at $p < 0.05$ from Tukey HSD pairwise comparisons. Pictorials under species names indicate life form (small tree, large tree, hummock grass, shrub, forb).

Wood density generally increases with dieback severity, but not water use efficiency or C:N ratio

Three of the traits, $\delta^{13}C$, C:N ratio and wood density were measured only in spring because they are indicative of integrated patterns and not likely to exhibit seasonal plasticity. Of the C_3 species, kaliny-kalinypa had the most conservative stomatal behaviour, with a $\delta^{13}C$ value of -24.7 ‰ (± 0.3), although not significantly different from kurkaṟa (-25.8 ± 0.2 ‰) and ilykuwara (-26.1 ± 0.4 ‰) (Figure 3a). Kampuraṟpa, an ephemeral forb, had the least conservative stomatal behaviour ($\delta^{13}C$ = -28.9 ‰ ± 0.2) and the lowest C:N ratio (16.1 ± 1.9), as expected for a fast-growing, non-woody species in the desert. The C_4 species, tjanpi, had a $\delta^{13}C$ ratio of -14.8 ‰ (± 0.1, Figure 3a), reflecting its photosynthetic pathway and water use efficiency. C:N ratio reflected life history in other ways, with the acacias (strong N-fixing species, ilykuwara and wanaṟi) and the root hemiparasite, mangaṯa, having lower C:N ratio values, indicating higher N concentrations in leaves (Figure 3b). Wood density generally increased with increasing dieback severity, with the exception of kaliny-kalinypa, which had comparable wood density to both low and moderate dieback species (Figure 3c). Pukaṟa, with the highest mortality rate, had the highest wood density at 0.81 g cm^{-3} (± 0.01), although not significantly different from ilykuwara.

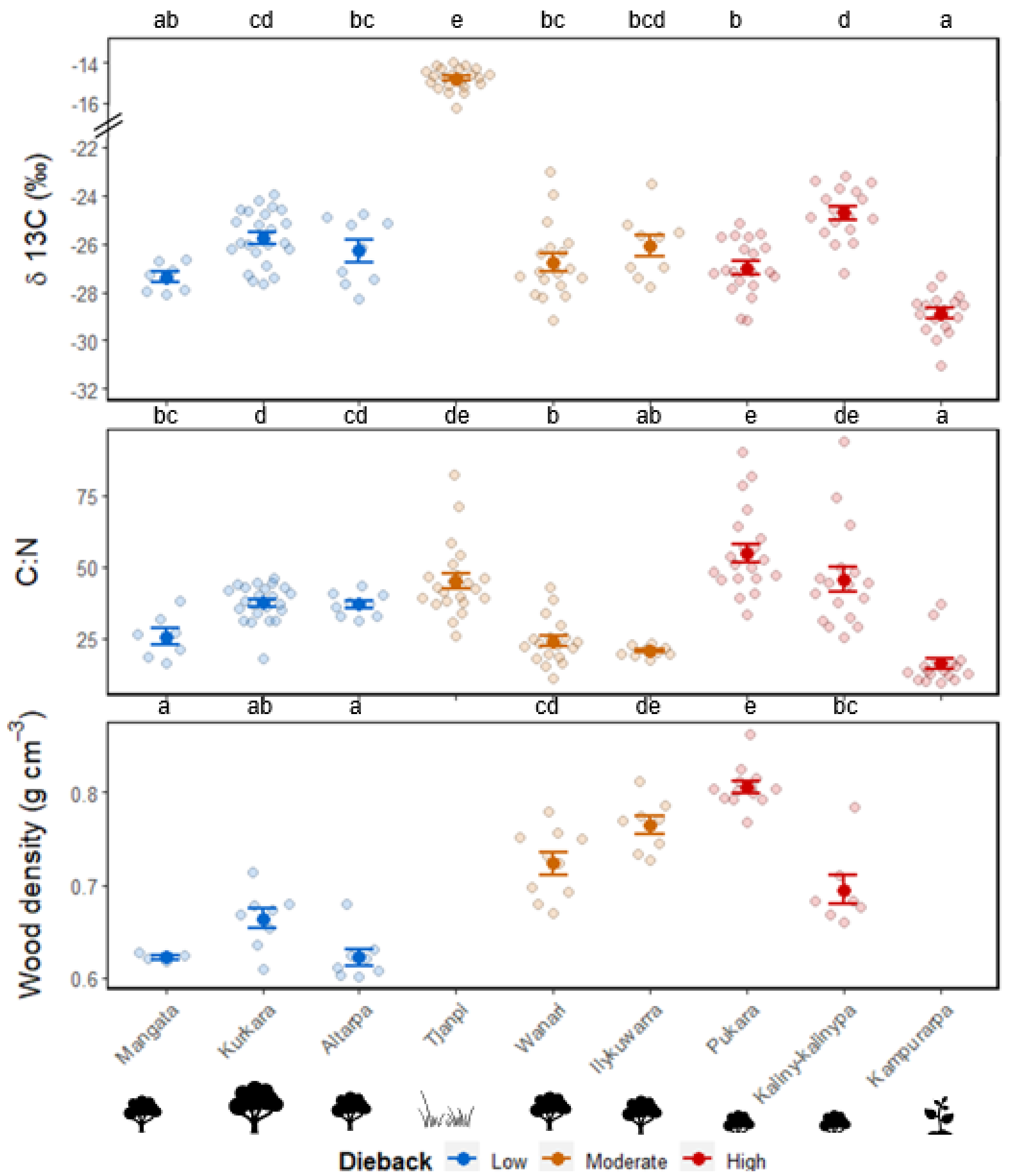

Figure 3. Leaf carbon stable isotope fractionation (a), leaf carbon:nitrogen (C:N) ratio (b), and wood density (c) values among species and mortality classes. Means ± standard error shown with background points representing each measurement. Letters above each plot indicate significant differences at $p < 0.05$. Measurements are from spring only.

For species showing seasonal shifts in trait values, there was significant variation among habitats

Seasonal change in leaf traits differed among habitats for some species, resulting in significant three-way interactions (Chisq = 28.2, p = 0.002, Table S3, Figures S3-6). Of these, RWC was particularly informative (Figure 4). Low dieback severity species maintained high RWC between seasons and showed no differences in seasonal change of RWC between habitats (Figure 4a-c). However, mangaṯa maintained RWC at a lower value of 67.6 % across both seasons (note that we have limited capacity to assess habitat differences for mangata due to a low sample size). Whilst overall reductions in RWC for tjanpi were low, as expected for a C_4 spinifex grass, those reductions were greatest in the pila (sand plain) habitat, at 13 % (Figure 4d). The woody moderate dieback species had reductions in RWC in summer, with 13 % for wanaṟi (Figure 4e) and 7 % for ilykuwara (Figure 4f), indicating sustained stomatal conductance during mild stress. Seasonal reductions in RWC for pukaṟa, the species with the highest dieback, were the largest of any species, but only in pila, with an average reduction of 34 % (88.3 – 54.7 %), compared to 6% on tali and 3% on puṯi (Figure 4g). Kaliny-kalinypa, which also had high dieback, had comparatively low mean reductions in RWC of 3 %, but slightly greater reductions in pila at 5.2 % (Figure 4h). Kampuraṟpa showed no habitat-dependent seasonal differences in RWC, despite RWC dropping by 10 % in summer (Figure 4i).

Seasonal differences in LDMC showed trends similar to those for RWC across species and habitats, although there was not a significant three-way interaction (Table S3). The LDMC of a species was dependent on season and habitat, but not the interaction between them, agreeing with previous results that traits associated with leaf hydration, RWC and LDMC, became decoupled and vary in different ways in summer (i.e. Figure S3).

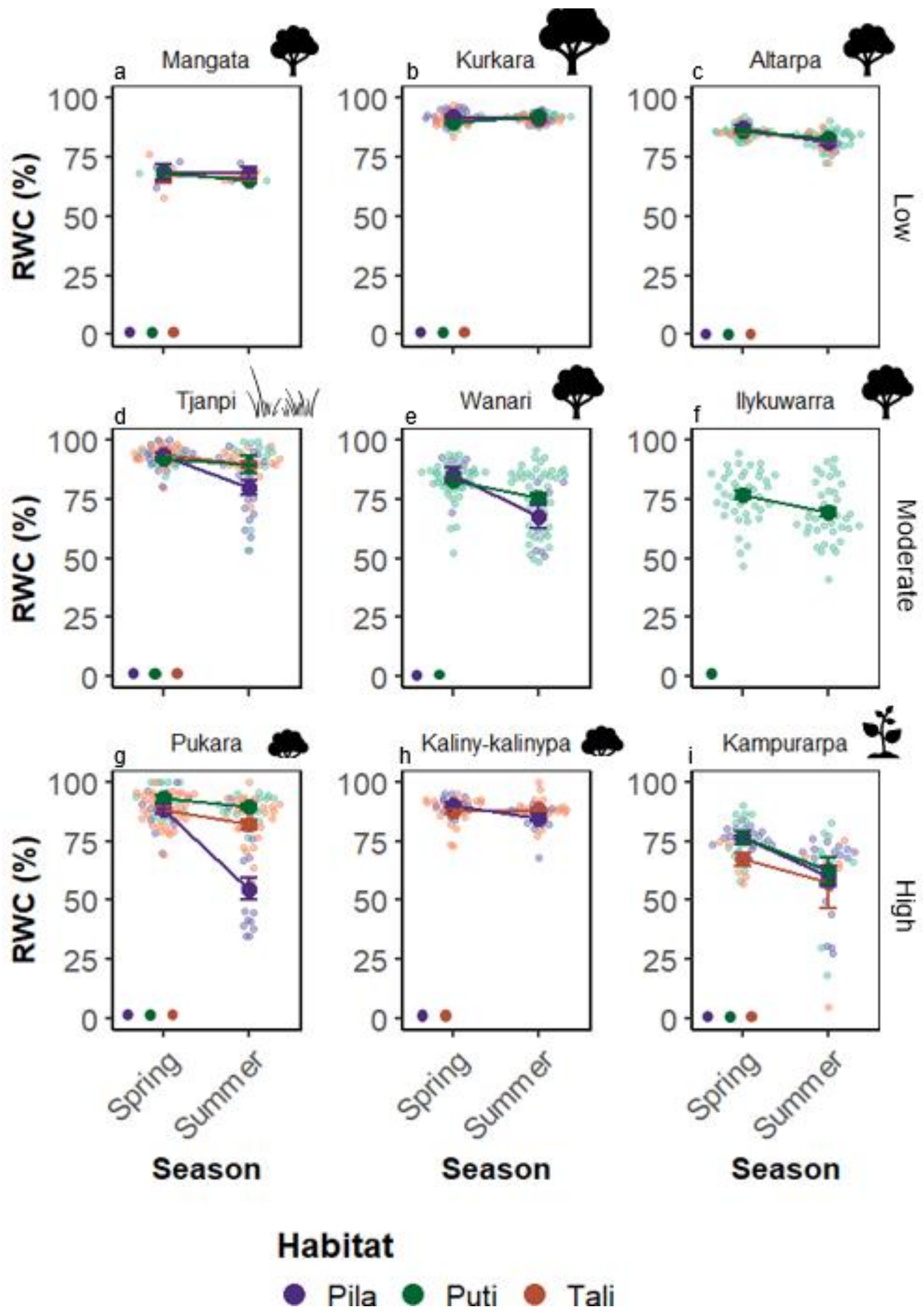

Figure 4. Relative water content (%) differences among habitats and between seasons for all species. Means (± standard error) are shown with lines connecting habitat means between each season. Species are organised by rows based on mortality class from low (a-c), moderate (d-f), to high (g-i). The circles in the bottom corner of each panel represent the habitats in which a species was measured.

Given the importance of RWC in distinguishing dieback (Table 4), and the apparent decoupling of this trait from structural leaf traits (Figure S2), we further explored how changes in the relationship between RWC and LDMC differed with species, season and dieback category. The relationship between these two traits varied notably across species and seasons (Figure 5), highlighting contrasting water-use strategies. A negative relationship suggests that as leaf density increases, hydration is reduced - particularly when RWC spans a broad range of values. A steeper (more negative) slope under stress (summer) indicates greater water loss for a given leaf density, implying that species are maintaining stomatal conductance despite stressful conditions. All species with moderate to high dieback severity showed strong negative relationships between RWC and LDMC in summer (Figure 5), and all except the ephemeral forb, kampurarpa, exhibited significantly steeper slopes from spring to summer (Figure 4, Table S4). In contrast, low dieback severity species showed positive or neutral relationship between RWC and LDMCs, indicating stable hydration at a given leaf density regardless of seasonal stress.

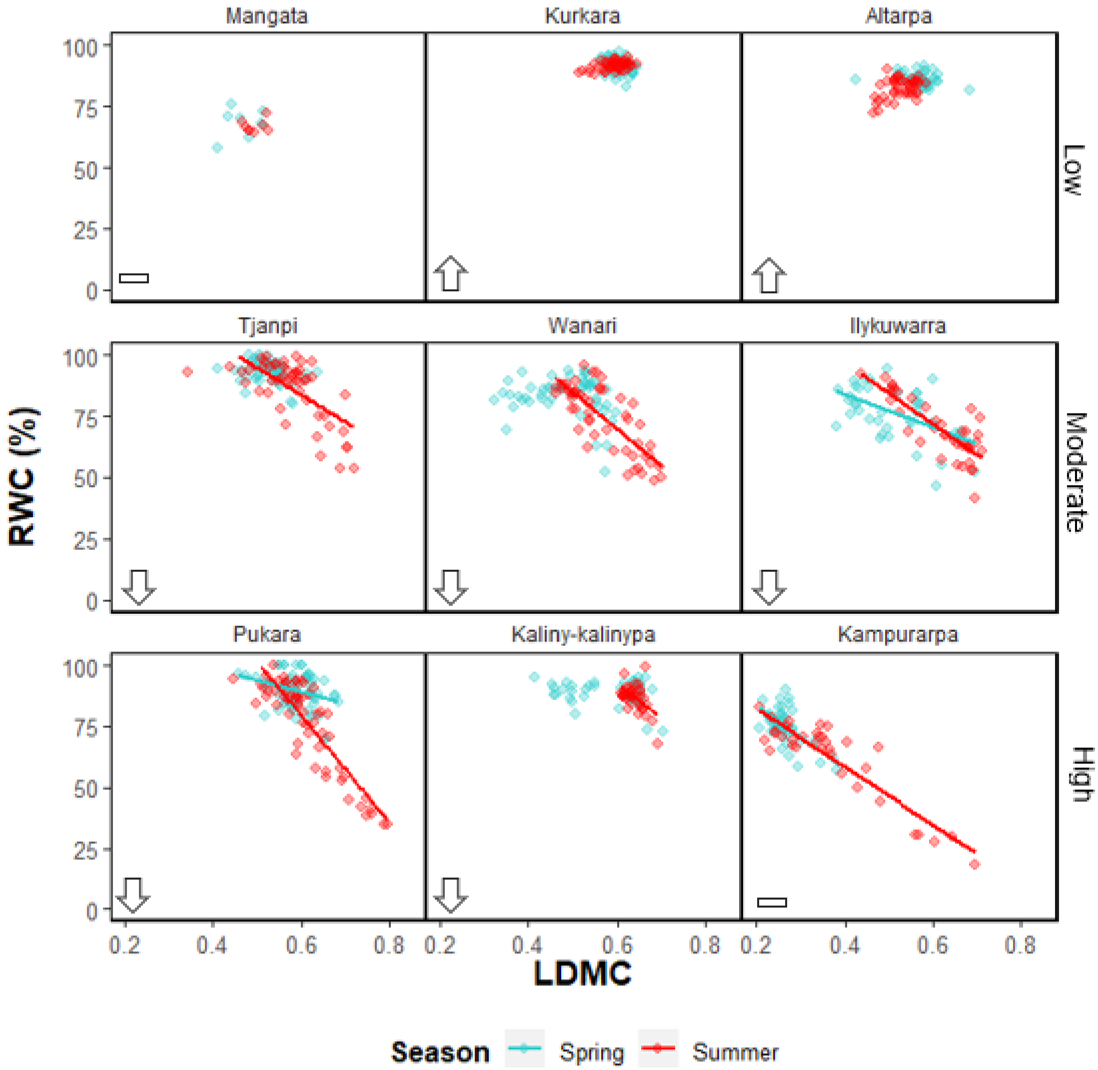

Figure 5. Relationship between leaf dry matter content (LDMC) and relative water content (RWC) between seasons for all species. Linear models were fit for each species and season combination with significant slopes (from zero, $p < 0.05$) marked with a solid line and non-significant slopes left blank. If there was a significant difference in slope between spring and summer, the direction of the change in slope is indicated by the arrow in the bottom corner of each sub-plot (see Table S4 for a summary of linear models comparing differences in slopes between seasons for each species). Each point represents data from a single individual.

Discussion

We hypothesised that differences in physiological strategies, inferred by a suite of traits, would explain observed differences in drought-induced dieback among culturally important Australian desert plant species. Overall, we found that species that had high mortality in a recent hotter drought event exhibited large reductions in relative water content (RWC), or leaf hydration, between spring and summer, suggesting a drought-tolerating strategy. Broad coordination in leaf traits across all species suggests that decoupling of RWC from LDMC occurred in summer compared to spring, further indicating that many species sacrifice leaf hydration to maintain growth and are likely drought tolerators (Fang and Xiong, 2015), especially those in the moderate and high dieback severity classes. Here we examine whether it is better to avoid or tolerate droughts in the Australian desert and consider the cultural and ecological significance of these differing drought strategies in the context of increasingly frequent hotter droughts.

Is it better to avoid or tolerate hotter droughts in the Australian desert?

As expected at a local level, there are a range of ecophysiological strategies present that confer different advantages in dry and hot environments (Laughlin *et al.*, 2023). In our study, the species with low dieback severity (mangaṯa, kurkaṟa and altarpa) all exhibited drought-avoiding strategies. Broadly, these species exhibited stable leaf RWC across seasons, suggesting conservative stomatal behaviour (Jin *et al.*, 2023). In addition, these species had low wood densities, which despite being linked to higher vulnerability to embolism (Choat *et al.*, 2018), have lower mortality risk during extreme drought associated with conservative stomatal behaviour and operating within hydraulic safety margins (Brodribb *et al.*, 2020). The moderate and high dieback severity species, especially wanar̲i, ilykuwara and pukar̲a, generally exhibited a stress tolerating strategy, typified by large reductions in RWC in summer and higher wood densities. Therefore, these species are likely operating closer to their hydraulic safety thresholds during mild stress (i.e. seasonal drought) and are more easily pushed to hydraulic failure, despite a greater resistance to embolism (Brodribb *et al.*, 2020). Below, we explore in more detail the species-specific strategies within each dieback severity class.

Low dieback severity species

Mangat̲a is a root hemiparasite, and therefore with a healthy host can maintain function (Nge *et al.*, 2019), potentially during extreme drought or heatwave conditions. Its requirement to maintain water flow from its host is suggested via consistently low, but seasonally stable RWC values and low wood density (Loveys *et al.*, 2001). Mangat̲a is a culturally important and locally endangered species, with its future resilience tied to the health of its nearby hosts, the latter anecdotally observed to be mainly kurkar̲a in our study. Kurkar̲a is an exceptionally deep-rooted species (Morton *et al.*, 2011), with adults that can access deeper soil water sources likely less influenced by surface-level soil moisture stress. In our study, kurkar̲a exhibited relatively conservative stomatal behaviour, evident by the seasonally stable and high RWC and moderate mean $\delta^{13}C$ value of -25.8 ‰. The water-use efficient cladode morphology of kurkar̲a, with stomata in furrows to decrease water loss and drooping architecture to increase convective cooling and reduce light interception (Curtis *et al.*, 2012), all aid in maintaining this species within its safe physiological thresholds. Here we focused on adult kurkar̲a; we note that what dieback did occur in this species was observed to be biased towards younger individuals (Wright *et al.*, 2023), which may reflect the susceptibility of younger individuals to extremely low surface soil moisture. However, Godfree and Knerr (2025) found that spatially explicit dieback in kurkar̲a occurred, with patches of death in larger individuals. Further investigations into hydraulic and thermal vulnerability of kurkar̲a across its distinct life stages will allow a holistic understanding of what is driving dieback in such a culturally and ecologically important species.

Altarpa exhibits conservative stomatal behaviour and maintains high RWC during summer. During prolonged and extreme drought, the large lignotuber carbon reserves could offset reduced carbon assimilation and effectively avoid drought whilst maintaining function. Field observations showed that new leaf flush was present between spring and summer, resulting in large seasonal differences in leaf area and overall reductions in LMA among individuals. Therefore, timing of rainfall is important for the onset of new growth, which will determine leaf morphology in this species. Conversely, the lower LMA of spring leaves in this species could reflect a strategy to facilitate higher photosynthetic capacity (Han *et al.*, 2008) during short-term pulses of rainfall during the optimal growth period. With increasing interannual rainfall variability in central Australia with climate change, there will be greater and more frequent drought periods alongside more intense flash flooding rainfall (CSIRO, 2024). Therefore, if altarpa is able to withstand extreme drought through its conservative stomatal behaviour and large carbon reserves, having lower LMA may be an advantage for this species to take advantage of larger rainfall events.

Moderate dieback severity

Ilykuwara and wanar̲i are good examples of stress-tolerating species. Typically, these species have high wood densities and high LMA and LDMC, or structural components to withstand the sustained growth and greater water tensions during periods of mild stress (McDowell *et al.*, 2008). Additionally, RWC decreased in summer, implying that both species are sacrificing leaf hydration to sustain growth. Wanar̲i has extremely high stem resistance to embolism (P_{50} = -11.3 MPa, Peters *et al.*, 2021). Clearly, the hotter drought in 2018-2019 in central Australia was extreme enough to push a large proportion of individuals in this drought tolerant species beyond its safety margins. Interestingly, although wanar̲i was classed as a moderate dieback species on average at the landscape scale, dieback in this species was spatially variable (Wright *et al.*, 2023; Godfree and Knerr, 2025), suggesting that factors such as stand density and topographic position may be more important than hydraulic safety alone in this species. In agreement with spatially explicit dieback, we did observe habitat differences in physiology, with wanaṟi in pila (sand plain) showing greater reductions in leaf RWC in summer compared to individuals in puṯi. It is unlikely, though, that the low level of trait variation we observed among habitats and across the landscape were a large contributor to the marked spatial variation in dieback severity for wanaṟi. As wanaṟi is known to be a strong competitor for shallow soil water (Nano and Clarke, 2010), a greater understanding of how geology and topography influence soil water content may better explain patterns of mortality across the landscape (Trugman *et al.*, 2021; Callahan *et al.*, 2022), which is of active interest for other researchers at UKTNP (e.g. Godfree and Knerr, 2025). In contrast to wanaṟi and ilykuwara, tjanpi (or spinifex) is a quintessential drought-avoider. It is a C_4 hummock grass with high water use efficiency and maintenance of high RWC via curled leaves with sunken stomata to reduce stomatal conductance (Xian, 2021). At UKTNP, intraspecific competition appeared to be the downfall for tjanpi, with larger individuals in areas of greater tjanpi density having significantly higher mortality (Wright *et al.*, 2023; Godfree and Knerr, 2025). Our study showed tjanpi had large reductions in leaf RWC in summer, but only in pila, which may reflect a tendency for larger individuals in greater densities to occur in the vast sand plains where tjanpi dominates.

High dieback severity

Pukaṟa, a small myrtaceous shrub, was the species worst affected by the 2018–2019 heatwave and drought, with a mortality rate over 90% (Wright *et al.*, 2023). In fire-prone Californian shrublands, species with the lowest vulnerability to embolism (i.e. highest wood density, most negative P_{50}) experienced the highest mortality during drought (Paddock *et al.*, 2013). This pattern is mirrored by pukaṟa, which had both the highest dieback and highest wood density. Paddock *et al.* (2013) proposed that post-fire recruitment during mild conditions helped explain subsequent dieback.

Pukar̲a is an obligate seeder with mass recruitment following fire (Wright *et al.*, 2019), and the last mass recruitment may have occurred under less extreme conditions, potentially predisposing these stands to mortality during severe drought. Further, pukar̲a had spatially explicit patterns of dieback from the hotter drought, seemingly linked to topographic position along tali (sand dune) slopes (Wright *et al.*, 2023; Godfree and Knerr, 2025). For the individuals that survived, we measured large habitat-specific differences in maintenance of leaf RWC across seasons. To elucidate the mechanisms causing spatially-explicit mass mortality in pukar̲a, a thorough investigation into topographic variability in microclimate at UKTNP is required, especially wind speed, vapour pressure deficit, and soil moisture, combined with experimental testing of the physiological impacts of heat and drought stress pukar̲a hydraulic stress and thermal loads.

Kaliny-kalinypa also experienced widespread dieback across UKTNP. It is likely that a drought avoidance strategy in this species led to mortality from carbon starvation, rather than hydraulic failure associated with drought tolerance. Maintenance of high leaf hydration and $\delta^{13}C$ values indicate conservative stomatal behaviour, and along with low wood density (i.e. higher stem vulnerability to embolism), these traits suggest this species ceases growth and avoids desiccation during mild stress (Choat *et al.*, 2018). Furthermore, kaliny-kalinypa resprouts after fire, but Wright *et al.* (2023) found that it did not resprout after drought death, indicating that the belowground carbon reserves were likely depleted. Interestingly, the two small-statured shrub species with high mortality at UKTNP have seemingly opposing strategies to water use, with kaliny-kalinypa ceasing water loss at the cost to growth, and pukar̲a sacrificing leaf hydration to maintain growth. These opposing strategies and causes of mortality in co-occurring small shrub species highlights the range of strategies employed to overcome water stress and thermal extremes experienced in an arid ecosystem. For both kaliny-kalinypa and pukar̲a, we suggest burning areas of pila (sand plain) near tali (fire sensitive dunes) during cool winter time and establishing long-term monitoring plots, aimed at understanding the impact of abiotic conditions post-fire and post-germination on the fitness of individuals to hotter droughts.

Unlike all other species, kampurarpa employs a stress-escape strategy. Being a desert herb, it has a facultative perennial habit, whereby, depending on conditions the year following germination it can either persist and reproduce another season, or abort and rely on the next generation of germinants from seed (Van Buren *et al.*, 2021). Therefore, widespread mortality of kampurarpa is expected during extreme dry and hot periods. Perhaps of more importance to kampurarpa are the impacts of climate change on reproductive phenology and germination related to greater interannual rainfall variability (Milner *et al.*, 2023) and altered fire regimes (Ahmed *et al.*, 2006). Understanding the interactions between timing of rainfall, fire frequency and intensity, and increasing growing season temperatures, in combination with the ever-increasing abundance of the grassy weed buffel grass (*Cenchrus ciliaris*) which aids to further transform fire regimes in central Australia (Ryan-Colton *et al.*, 2024), will be an important topic of research at UKTNP and central Australia more broadly.

Impacts of dieback on Country and culture

Climate change is already having profound impacts on Anangu Country. The mass dieback that followed the drought and heatwave event in 2018-2019 will have large, ongoing, and uncertain consequences for vegetation as the climate continues to become hotter and drier. Drastic shifts in community composition and declines in biomass will continue to occur. For example, pukara naturally suppresses fire along dune systems and acts as a natural firebreak (Wright *et al.*, 2019). However, with its recent mass dieback and field observations of small tussock grasses taking pukara's place, the dune fields vegetation complex in central Australia may undergo significant restructuring, with replacement of fire-retardant species with fire-promoting species along dune systems. Instability of dune system vegetation may also have impacts on rare and threatened fauna such as tjakuṟa (great desert skink, *Liopholis kintorei*) and itjaritjari (marsupial mole, *Notoryctes typhlops*) which rely on the dune systems and pukaṟa for habitat (Bennison *et al.*, 2014; Ridley and Schlesinger, 2023). Another potential shift is in areas of puṯi (acacia woodland), which are important to Aṉangu for many reasons, including being an important habitat for tjala (honey ants) and maku (witchetty grubs). With mass death of wanaṟi, the dominant species in puṯi habitat, we may see an encroachment of tjanpi (spinifex) and a retraction of woody puṯi species (Nano and Clarke, 2008). Furthermore, wanaṟi is a very important species for Aṉangu used for ceremony, tools, and food, as well as many important plants and animals growing on or within (R. Okai, pers. comms.). Buffel grass is a strong competitor and has been observed to persist and dominate understories beneath large kurkaṟa (desert oaks), which may decrease the competitive ability of important and large kurkaṟa individuals (R. Okai, T. Guest pers. comms.). With spatial patterns and underlying causes still unresolved (Wright *et al.*, 2023; Godfree and Knerr, 2025), predicting the locations and extent of community shifts will be difficult without further research.

Despite now knowing more about the patterns of and mechanisms underpinning dieback at UKTNP, there may be limited effective management options. Managing fire across the landscape via active cultural burning promotes ecosystem heterogeneity and, if supported to continue, will likely help reduce the impacts of mass plant dieback, and even mitigate future dieback, particularly for tjanpi in the sand plains. An ongoing research priority is to explore whether there are any areas that, because of features such as topography, ground water and microclimatic conditions, confer some resilience to drought and heatwaves – such areas, if they exist, might be a priority for management. Also, Aṉangu would like to increase their capacity at the local community nursery at Muṯitjulu for growing culturally important species to maintain cultural connection, bank seed and re-plant important areas. However, with rapid and increasing anthropogenic forcing of hotter droughts, there seem to be few effective solutions to the climate change conundrum in the Australian desert.

Conclusions and key questions remaining

Large-scale plant mortality associated with climate change is already occurring at UKTNP. Seasonal declines in leaf RWC, a proxy for stomatal behaviour and water use strategy, was the trait that best predicted high dieback severity across all species. Generally, species with greater dieback severity demonstrated water stress-tolerating strategies, where desiccation is risked at the cost of sustained growth during stress. All low dieback severity species had drought-avoiding strategies, although each species achieved avoidance in different ways (hemiparisitism, large carbon reserves, or deep roots accessing deep water sources). We highlighted that species-specific strategies are important to consider at a local level, given that several stress tolerance or avoidance strategies resulted in moderate or high dieback severity in a range of species. Therefore, the spatial variation in dieback at UKTNP (as per Wright *et al.*, 2023; Godfree and Knerr, 2025) was also reflected in leaf traits in these species, with clear habitat-level differences, especially for the highest dieback severity species – pukar̲a. Ultimately, while managing Country at UKTNP is mitigating detrimental impacts, the long-term impacts to An̲angu, flora, and fauna are likely to be extensive without strong measures to halt and reverse climate change. Worryingly, extreme and long drought is not a new phenomenon in Australia's landscapes (e.g. the Federation Drought 1895-1903, see Godfree, 2025). A return of the extreme droughts of the past under the elevated contemporary temperatures and more frequent heatwaves, could harbour devastating consequences for Australia's desert ecosystems. We hope that this study, and associated research in the region, provides a foundation for further investigation of resilience and vulnerability of plant species and communities to extreme events and supports potentially identification of focal areas for conservation management.

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Author Contributions

Jay Nicholson: Conceptualisation, Investigation, Data curation, Formal analysis, Visualisation, Writing – original draft; Rita Okai: Conceptualisation, Traditional knowledge holder, Investigation, Writing – review & editing; Mala Rangers: Conceptualisation, Traditional knowledge holder, Investigation, Writing – review & editing; Andy Leigh: Conceptualisation, Investigation, Writing – review & editing; Danielle Way: Conceptualisation, Writing – review & editing; Nicholas Macgregor: Conceptualisation, Writing – review & editing, Funding acquisition; Rebekah Robertson: Conceptualisation, Investigation, Writing – review & editing; Samuel Merson: Conceptualisation, Writing – review & editing; Tracey Guest: Conceptualisation, Writing – review & editing, Supervision, Resources; Adrienne Nicotra: Conceptualisation, Investigation, Writing – review & editing, Supervision.

Conflicts of Interest

The authors have no conflicts of interest to declare.

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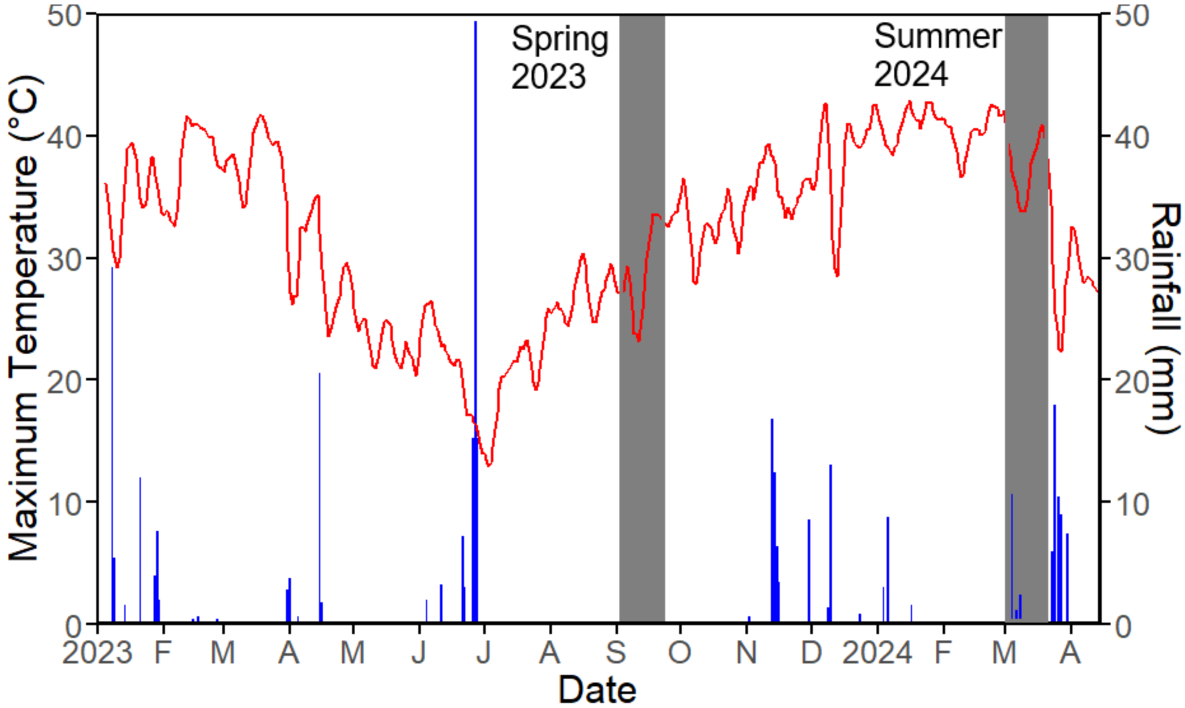
Supplementary material

Additional information for study sites.

For dune systems in central Australia, including those at UKTNP, Buckley (1982) found that soil moisture consistently increased from dune crest (top of tali) to swale (middle of puṯi). Represented as a percentage of water by weight in shallow soils (top 20 cm), on average crests had 0.6 % water content, mid-slopes 0.8 %, low-slopes 1.8 %, and swales 2.5 % (Buckley, 1982). Water content in deeper soil (1 m) followed similar trends, but was on average twice as high, especially in the low-slopes and in the swale. Fine soil fraction proportions also increase from crest to swale with very little silt and clay on dune crests, increasing to 3 % silt and clay on lower slopes and 5 % or more in the sandplain and swales (Buckley 1982). Nitrogen and carbon (mg kg-1) showed similar trends with both increasing between 3- to 10-fold from crests to swales (C from 500 to 2000 mg kg-1 and N from 50 to 200 mg kg-1, Buckley 1982). However, phosphorus showed no significant catenary pattern (20-30 mg kg-1 across sequence).



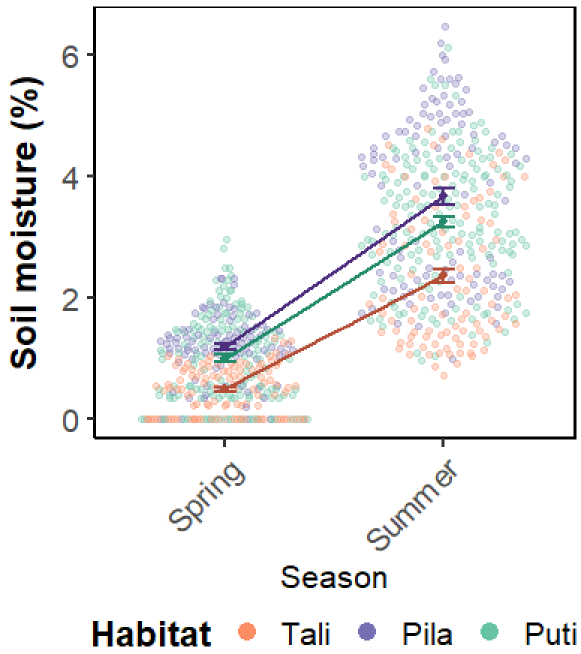


Figure S1a. Daily maximum temperature and rainfall total at Yulara Airport (NT) from January 2023 to April 2024. Maximum temperature is shown in red as a smoothed 5-day average. Daily rainfall total shown in blue. Sampling periods are shown in grey and were the first 3 weeks of September 2023 and the first 3 weeks of March 2024. Data accessed from https://reg.bom.gov.au/climate/data/. **Figure S1b**. Seasonal change in soil water content (%) as measured by a time-domain reflectometry (TDR) meter at the base of individual study plants in the top 5 cm for each habitat. Filled circles show the mean for each habitat (± standard error). The solid lines connect each habitat mean between seasons.

Table S1. Number of individuals sampled for each species, separated by habitat type.

Species	Pila	Puṯi	Tali	Total
Altarpa	5	25	15	**45**
Ilykuwara	0	40	0	**40**
Kaliny-kalinypa	15	0	24	**39**
Kampuṟarpa	22	14	7	**43**
Kurkaṟa	24	10	14	**48**
Mangaṯa	-	-	-	**8**
Pukaṟa	17	10	37	**64**
Tjanpi	18	12	26	**56**
Wanaṟi	8	44	0	**52**
Total	**112**	**161**	**122**	**395**

Supplementary information for Methods (Data analysis) - *Broad trait patterns*

Bayesian multinomial logistic regression models were fitted using the *brms* package (Bürkner, 2017) in R to investigate which leaf traits best predict dieback severity in both seasons. Dieback was modelled as a categorical response variable with species-level data aggregated into three dieback levels: low, moderate, and high, with high dieback set as the reference category. Five leaf traits measured across both seasons – relative water content (RWC), leaf dry matter content (LDMC), leaf mass per area (LMA), leaf thickness, and leaf area – were used as predictor variables. All traits were scaled and centred (mean = 0, divided by standard deviation) prior to analysis. To account for potential variation among habitat types, habitat was included as a group-level effect (random intercept).

Separate models were run for spring and summer to assess whether particular traits were more predictive of dieback severity under non-stressful (spring) versus stressful (summer) conditions. Models were fitted using four Markov Chain Monte Carlo (MCMC) chains with 4,000 iterations each (including 2,000 warm-up iterations). Convergence was evaluated using trace plots and the potential scale reduction factor ($\hat{R}$), with all models showing good convergence. Posterior predictive checks confirmed adequate model fit. Trait effects were considered significant when the 95 % confidence interval for the estimated log-odds did not include zero. Full model results are provided in Table S2.

Species-level trait patterns

For species-level comparisons, linear models were used with trait as the response and species as the predictor. For dieback class comparisons, linear mixed-effects models were used with dieback class as the predictor and species as a random effect. Tukey HSD was applied to estimate pairwise differences, with p-values adjusted for family-wise error. Model residuals were assessed using the *ggResidpanel* package (Goode and Rey, 2019), and cube-root transformations were applied to traits where assumptions were violated due to negative values. For traits only measured in spring (e.g. $\delta^{13}C$, C:N ratio, wood density), a similar approach was applied using spring data only.

To assess the influence of species identity, habitat type, season, and their three-way interaction on trait variation, we fit linear mixed-effects models using the *lmer* function in the *lme4* package (Bates *et al.*, 2003). Trait values were log-transformed where necessary to improve model fit based on residual inspection. Random effects included individual ID (to account for intraspecific variation), plot ID (for spatial effects), and plant health rating (qualitative health estimates). Random terms explaining negligible variance were removed based on singularity checks.

Table S2. Summary table of Bayesian multinomial logistic regression predicting mortality class from leaf traits. Separate models were run for each season of measurement to determine if certain traits are better at predicting mortality class during stressful (summer) and non-stressful (spring) conditions. For structure of models, see the methods section. Low, Mod[erate], High are mortality classes. Trait levels between mortality classes are determined to be significantly different if the 95% confidence interval does not intercept zero (emboldened). Random effect standard deviations reflect the variability in dieback probability attributable to habitat, with non-zero SDs (based on confidence interval not overlapping zero) suggest habitat influences the intercepts across dieback categories. All other estimates represent the log-odds of an individual plant being assigned to the Low or Moderate dieback class, relative to the High class. Rhat ($\hat{R}$) indicates model parameters converged successfully with all values < 1.01.

Parameter	Estimate	Error	95% CI	Rhat
Spring (a)				
Random Effect (habitat)				
Low (intercept SD)	1.99	1.228	**0.669, 5.169**	1
Mod (intercept SD)	2.097	1.148	**0.790, 5.144**	1
Fixed Effects				
Low (intercept)	-1.754	1.174	-3.970, 0.731	1.001
Mod (intercept)	-0.752	1.156	-3.133, 1.564	1.001
RWC (Low-High)	2.16	0.543	**1.173, 3.281**	1
RWC (Mod-High)	-0.143	0.236	-0.608, 0.321	1
LDMC (Low-High)	0.833	0.489	-0.119, 1.816	1
LDMC (Mod-High)	-0.587	0.247	**-1.079, -0.120**	1.001
LMA (Low-High)	2.315	0.433	**1.520, 3.214**	1.001
LMA (Mod-High)	1.043	0.322	**0.409, 1.677**	1.001
Thickness (Low-High)	-1.478	0.377	**-2.239, -0.776**	1
Thickness (Mod-High)	-0.015	0.284	-0.575, 0.538	1
Leaf area (Low-High)	1.555	0.318	**0.966, 2.212**	1
Leaf area (Mod-High)	-2.094	0.521	**-3.175, -1.119**	1.001
Summer (b)				
Random Effect (habitat)				
Low (intercept SD)	1.574	1.046	**0.449, 4.280**	1
Mod (intercept SD)	1.907	1.087	**0.691, 4.774**	1
Fixed Effects				
Low (intercept)	-1.044	0.996	-2.864, 1.171	1.002
Mod (intercept)	-0.547	1.032	-2.686, 1.562	1.001
RWC (Low-High)	2.45	0.473	**1.594, 3.454**	1
RWC (Mod-High)	0.456	0.146	**0.176, 0.745**	1.001
LDMC (Low-High)	-0.252	0.377	-1.008, 0.492	1.001
LDMC (Mod-High)	-0.009	0.222	-0.444, 0.430	1
LMA (Low-High)	0.541	0.377	-0.197, 1.302	1
LMA (Mod-High)	1.078	0.317	**0.484, 1.730**	1
Thickness (Low-High)	-0.164	0.344	-0.855, 0.490	1
Thickness (Mod-High)	-1.142	0.307	**-1.762, -0.571**	1
Leaf area (Low-High)	1.553	0.262	**1.070, 2.098**	1
Leaf area (Mod-High)	-1.411	0.376	**-2.181, -0.706**	1

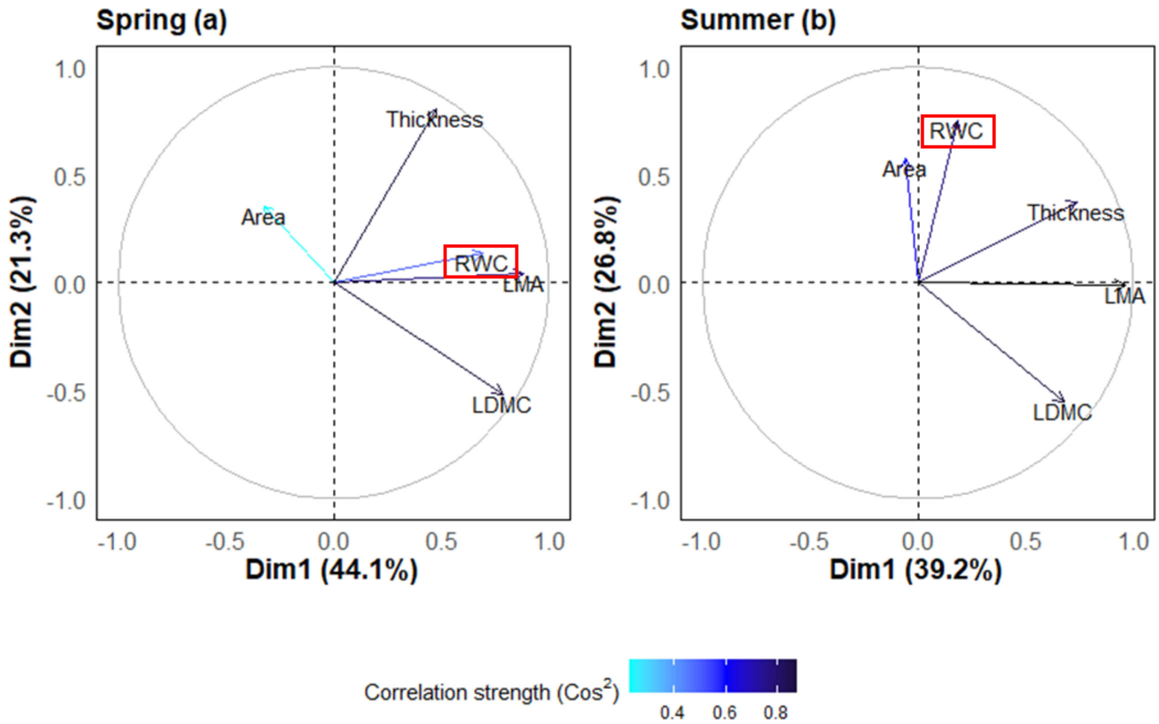


Figure S2. Principal component analysis (PCA) correlation vectors for five leaf traits measured in spring (a) and summer (b). The scale shows cosine squared (cos^2) values, with higher values indicating better quality of representation for the principal components. Trait codes follow Table 3. RWC is highlighted with a red box to indicate the shift between seasons. Other trait trajectories are largely unchanged.

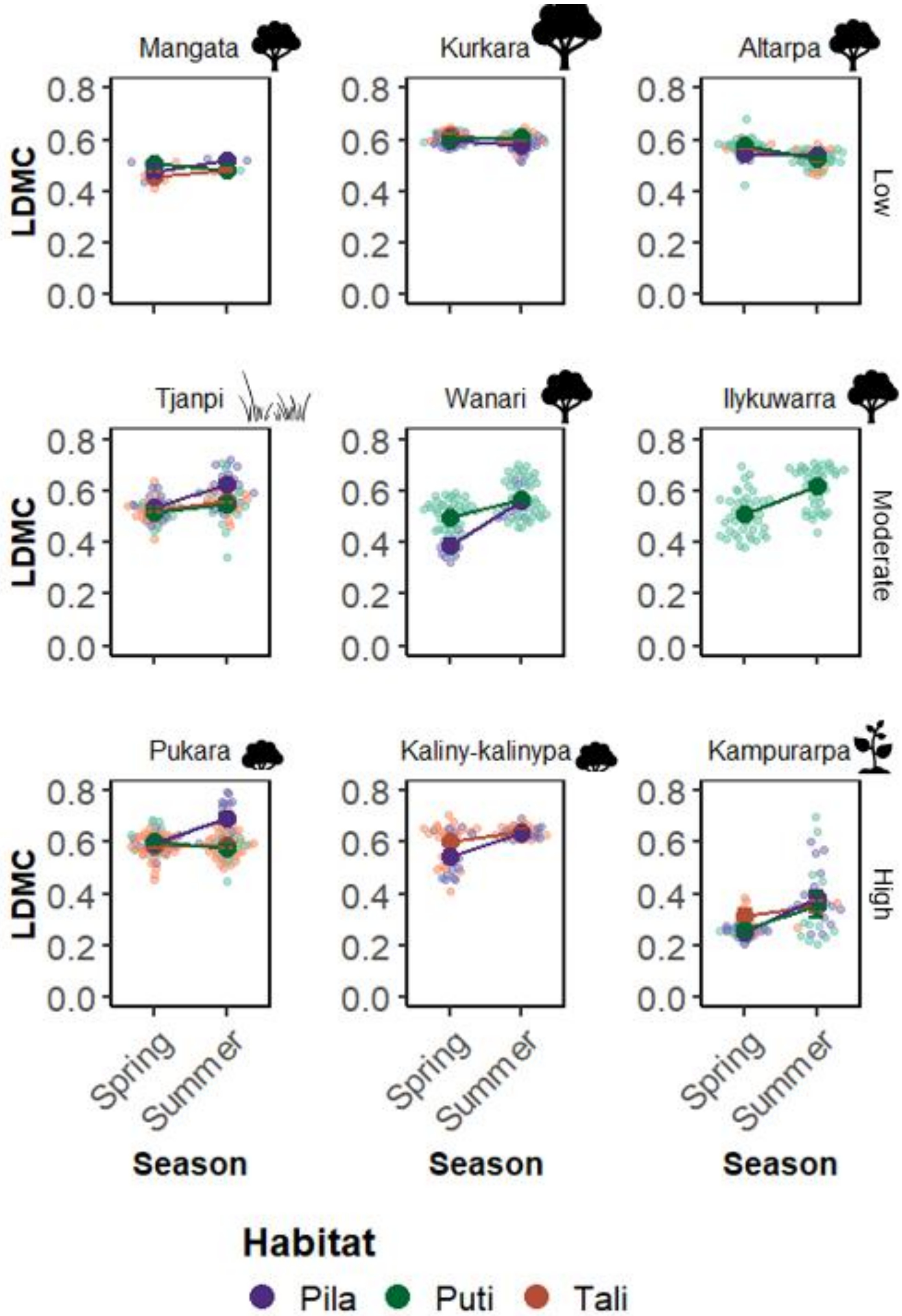


Figure S3. Leaf dry matter content (LDMC) differences among habitats and between seasons for all species. Means (± standard error) are shown with lines connecting habitat means between each season. Species are organised by rows based on dieback severity class from low-high.

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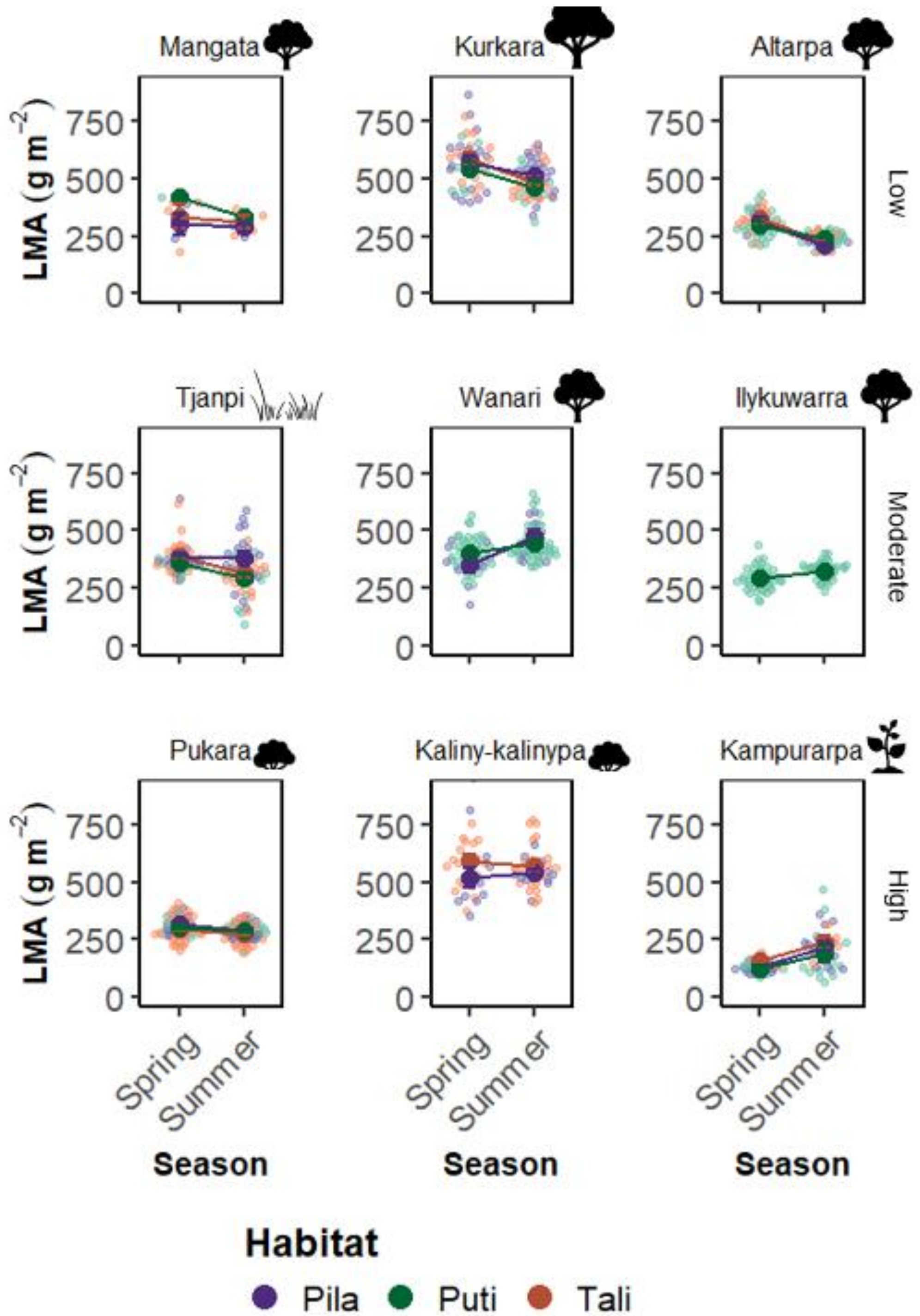

893 **Figure S4.** Leaf mass per area (LMA, g m^{-2}) differences among habitats and between seasons for all
894 species. Means (± standard error) are shown with lines connecting habitat means between each
895 season. Species are organised by rows based on dieback severity class from low-high.

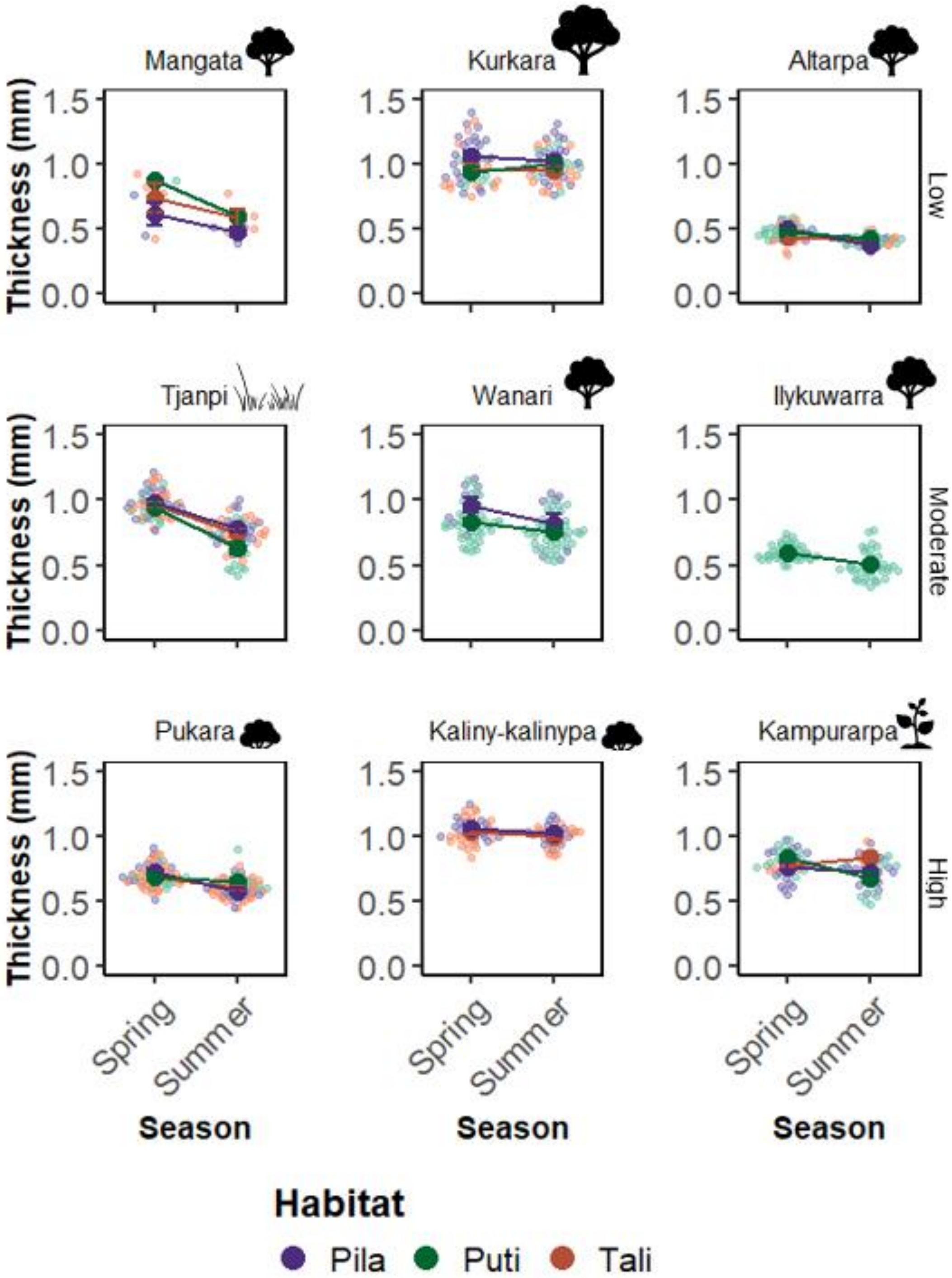

Figure S5. Leaf thickness (mm) differences among habitats and between seasons for all species. Means (± standard error) are shown with lines connecting habitat means between each season. Species are organised by rows based on dieback severity class from low-high.

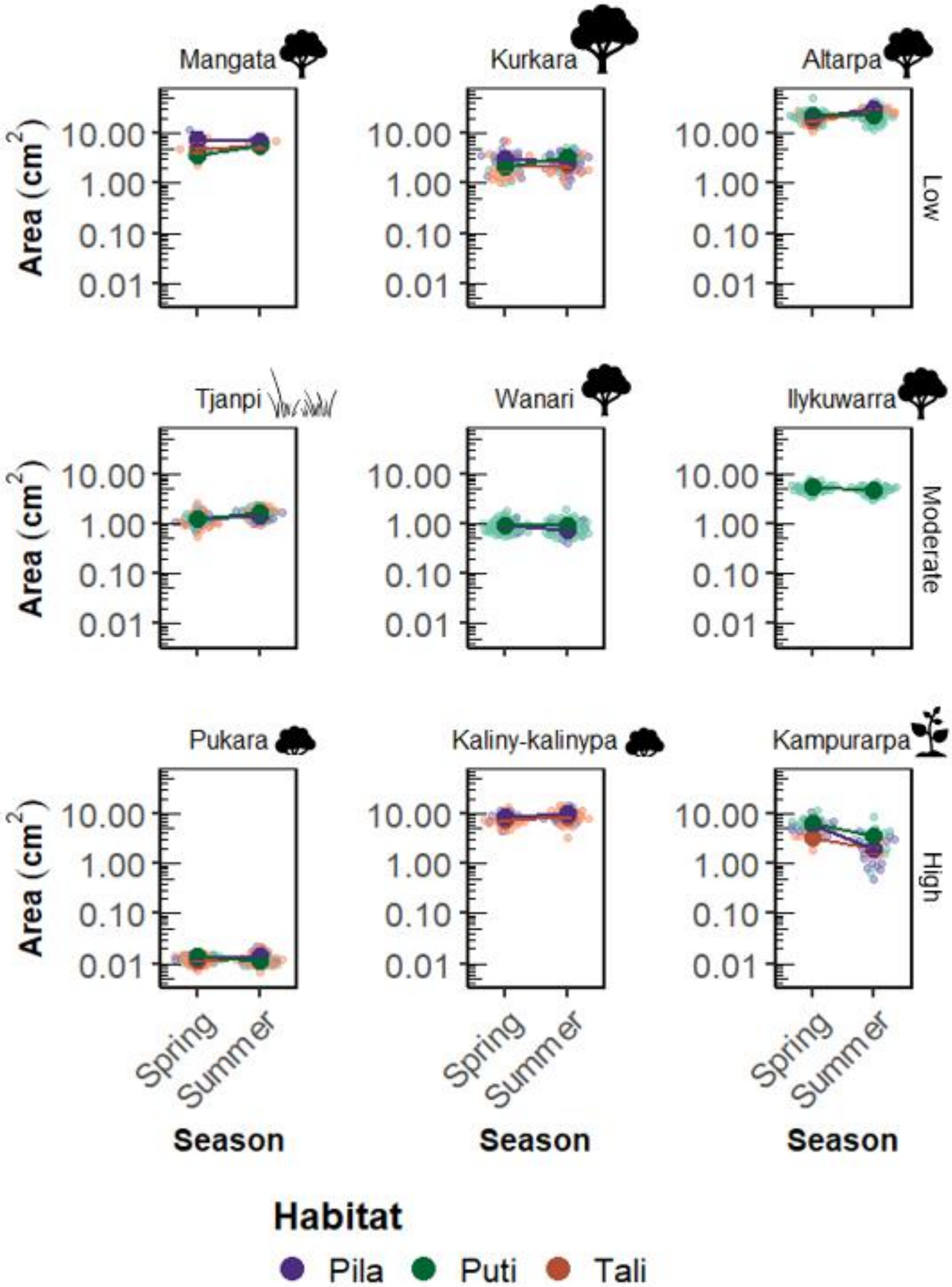

Figure S6. Leaf area (cm^2) differences among habitats and between seasons for all species. Means (± standard error) are shown with lines connecting habitat means between each season. Species are organised by rows based on dieback severity class from low-high.

Table S3. Summary of analysis of deviance (e.g. ANOVA comparing goodness of fit, not sum of squares) applying Type III Wald chi-square tests on each mixed effects model below. Intercept is the reference level for all models (species = Altarpa, season = spring, habitat = pila), with significant intercepts for all models indicating that the reference group is not zero on average for all traits.

Trait	Effect	Chisq	Df	p	Variance
RWC	Intercept	242.6	1	**< 0.001**	
Fixed	Species	213.8	7	**< 0.001**	
	Habitat	0	2	0.977	
	Season	2.3	1	0.126	
	Species:Habitat	64.5	10	**< 0.001**	
	Species:Season	71.4	7	**< 0.001**	
	Habitat:Season	1	2	0.621	
	Species:Habitat:Season	28.2	10	**0.002**	
Random	Plot				12.28
	Health				52.81
	Residual				64.77
LDMC	Intercept	252.4	1	**< 0.001**	
Fixed	Species	363	7	**< 0.001**	
	Habitat	0.2	2	0.905	
	Season	0	1	0.935	
	Species:Habitat	25.1	10	**0.005**	
	Species:Season	144.6	7	**< 0.001**	
	Habitat:Season	2.6	2	0.279	
	Species:Habitat:Season	10.9	10	0.368	
Random	Plot				< 0.001
	Health				0.004
	Residual				0.003
LMA	Intercept	2328.1	1	**< 0.001**	
Fixed	Species	399.4	7	**< 0.001**	
	Habitat	2.9	2	0.238	
	Season	10.7	1	**0.001**	
	Species:Habitat	36.8	10	**< 0.001**	
	Species:Season	103.1	7	**< 0.001**	
	Habitat:Season	3.6	2	0.169	
	Species:Habitat:Season	22.7	10	**0.012**	
Random	Plot				0.002
	Health				0.021
	Individual ID				0.005
	Residual				0.034
Thickness	Intercept	246.9	1	**< 0.001**	
Fixed	Species	371.1	7	**< 0.001**	
	Habitat	5	2	0.082	
	Season	15.1	1	**< 0.001**	
	Species:Habitat	52.3	10	**< 0.001**	
	Species:Season	38.1	7	**< 0.001**	
	Habitat:Season	6.8	2	**0.034**	

Trait	Effect	Chisq	Df	p	Variance
	Species:Habitat:Season	43.1	10	**< 0.001**	
Random	Plot				< 0.001
	Individual ID				0.005
	Residual				0.014
Area	Intercept	198.1	1	**< 0.001**	
Fixed	Species	4481.4	7	**< 0.001**	
	Habitat	5	2	0.084	
	Season	3.2	1	0.074	
	Species:Habitat	47.3	10	**< 0.001**	
	Species:Season	138.9	7	**< 0.001**	
	Habitat:Season	10.9	2	**0.004**	
	Species:Habitat:Season	44.5	10	**< 0.001**	
Random	Plot				0.005
	Health				0.15
	Individual ID				0.043
	Residual				0.052

Table S4. Summary of linear models comparing the relationship between LDMC and RWC for each species between seasons. If the estimate is > 0, there is a more positive relationship between LDMC and RWC in spring compared to summer. If the estimate is < 0, there is a more negative relationship between LDMC and RWC in spring compared to summer.

Species	Mortality	Estimate	SE	p
Mangaṯa	Low	-6.9	91.9	0.942
Kurkaṟa	Low	72	19.7	< 0.001
Altarpa	Low	73.5	20.2	< 0.001
Tjanpi	Moderate	-82	28.1	0.004
Wanaṟi	Moderate	-132	22.8	< 0.001
Ilykuwara	Moderate	-58.4	24.7	0.02
Pukaṟa	High	-172.4	26	< 0.001
Kaliny-kalinypa	High	-119.6	40.3	0.004
Kampuṟarpa	High	8.2	29.5	0.782