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RESEARCH ARTICLE

Mortality rates of desert vegetation during high-intensity drought at Uluṟu-Kata Tjuṯa National Park, Central Australia

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Abstract

Precipitation variability and heatwaves are expected to intensify over much of inland Australia under most projected climate change scenarios. This will undoubtedly have impacts on the biota of Australian dryland systems. However, accurate modelling of these impacts is presently impeded by a lack of empirical research on drought/heatwave effects on native arid flora and fauna. During the 2018–2021 Australian drought, many parts of the continent's inland experienced their hottest, driest period on record. Here, we present the results of a field survey in 2021 involving indigenous rangers, scientists and national parks staff who assessed plant dieback during this drought at Uluṟu-Kata Tjuṯa National Park (UKTNP), central Australia. Spatially randomized quadrat sampling of eight common and culturally important plants indicated the following plant death rates across UKTNP (in order of drought susceptibility): desert myrtle (*Aluta maisonneuvei* subsp. *maisonneuvei*) (91%), yellow flame grevillea (*Grevillea eriostachya*) (79%), Maitland's wattle (*Acacia maitlandii*) (67%), waxy wattle (*A. melleodora*) (65%), soft spinifex grass (*Triodia pungens*) (53%), mulga (*A. aneura*) (42%), desert oak (*Allocasuarina decaisneana*) (22%) and quandong (*Santalum acuminatum*) (0%). The sampling also detected that seedling recruitment was absent or minimal for all plants except soft spinifex, while a generalized linear mixed model (GLMM) indicated two-way interactions among species, plant size and stand density as important predictors of drought survival of adult plants. A substantial loss of biodiversity has occurred at UKTNP during the recent drought, with likely drivers of widespread plant mortality being extreme multi-year rainfall deficit (2019 recorded the lowest-ever annual rainfall at UKTNP [27 mm]) and record high summer temperatures (December 2019 recorded the highest-ever temperature [47.1°C]). Our findings indicate that widespread plant death and extensive vegetation restructuring will occur across arid Australia if the severity and frequency of droughts increase under climate change.

KEYWORDS
arid, drought survival, population dynamics, recruitment, seedling survival, stem cavitation, tree dieback

INTRODUCTION

High-intensity droughts and severe regional heatwaves are expected to increase in frequency and magnitude under anthropogenic climate change (ACC) (Crouchet et al., 2019; Dai, 2011; IPBES, 2019; Vicente-Serrano et al., 2020). This will undoubtedly have consequences for the biota of many marine and terrestrial ecosystems, although impacts are expected to vary globally depending on latitude (Ndehedehe et al., 2021), altitude (Yuan et al., 2021) and what actions are, or are not, taken now to mitigate climate change (Garnaut, 2012; IPCC, 2021; Naumann et al., 2021). Some key impacts of climate change on vegetation are expected to include extensive tree and shrub death during extreme droughts (Crouchet et al., 2019; Olano et al., 2017), directional shifts between grass and woody plant dominance in certain systems (Fensham et al., 2005), impacts on carbon cycling and nutrient sequestration (Arca et al., 2021) and increased risk of uncontrollable wildfires (Gannon & Steinberg, 2021; Kemter et al., 2021; Pausas & Keeley, 2021). Additionally, at the level of the Earth system, increasing drought severity and concomitant vegetation dieback may amplify global temperature rises by weakening the ability of vegetation reservoirs to act as carbon sinks (Anderegg et al., 2016; Fekete et al., 2017; Fensham et al., 2009).

In Australia, climate change assessments by the Commonwealth Scientific and Industrial Research Organization (CSIRO) indicate that rainfall variability, temperature maximums, and the number of annual dry days across the continent will increase as ACC proceeds (CSIRO, 2008a, 2020). Droughts are forecast to increase in frequency and severity in southern parts of the continent, while inter-annual rainfall variability in arid and semi-arid regions is expected to become exaggerated (CSIRO, 2020; Garnaut, 2012; Horton et al., 2010). In addition, temperatures are predicted to increase across the continent, with arid inland regions expected to experience greater temperature increases than coastal areas. Under a 'no-mitigation' climate change scenario, annual average temperatures in most arid areas are expected to increase from 1990 levels by c. 2.5–4°C by 2070 and by 5°C by 2100 (CSIRO, 2008b). Under the best possible 'low-emissions' scenario, which is considered highly unlikely to occur, continental-scale warming of approximately 2°C is expected by 2050 (CSIRO, 2020; IPCC, 2021).

Between 2018 and 2021, Uluṟu-Kata Tjuṯa National Park (UKTNP) in south-west central Australia experienced its most intense dry period on record (Australian Government Bureau of Meteorology, 2022a). Long-term weather data from Tempe Downs, Curtin Springs and Yulara weather stations (located c. 173, 40 and 5 km distance from the UKTNP boundary, respectively) indicate that the only drought conditions of comparable intensity since 1886 occurred between the late 1950s and mid-1960s (Figure 1). This earlier drought period, which lasted for nearly a decade, was of longer duration than the current drought. However, even in its driest year, 1961, when only 67 mm fell, this earlier drought received more than double the rainfall of the driest year of the present drought (which was 2019, when 27 mm fell) (Figures 1, 2). In addition to severe annual rainfall deficits during the current drought, extreme heatwave conditions have occurred. Yulara weather station recorded its highest and fourth highest temperatures on record in the summers of 2019 (47.1°C) and 2018 (46.1°C) respectively (Figures 2, 3a) (Australian Government Bureau of Meteorology, 2022b). Moreover, its three highest-ever annual mean maximum temperatures were recorded in consecutive years between 2018 and 2020 (Figure 3b).

Given that the rainfall deficits and high-temperature conditions of the 2018–2021 drought are of unprecedented extremity, the impacts of this drought on biological systems are likely to be at least as severe as – or

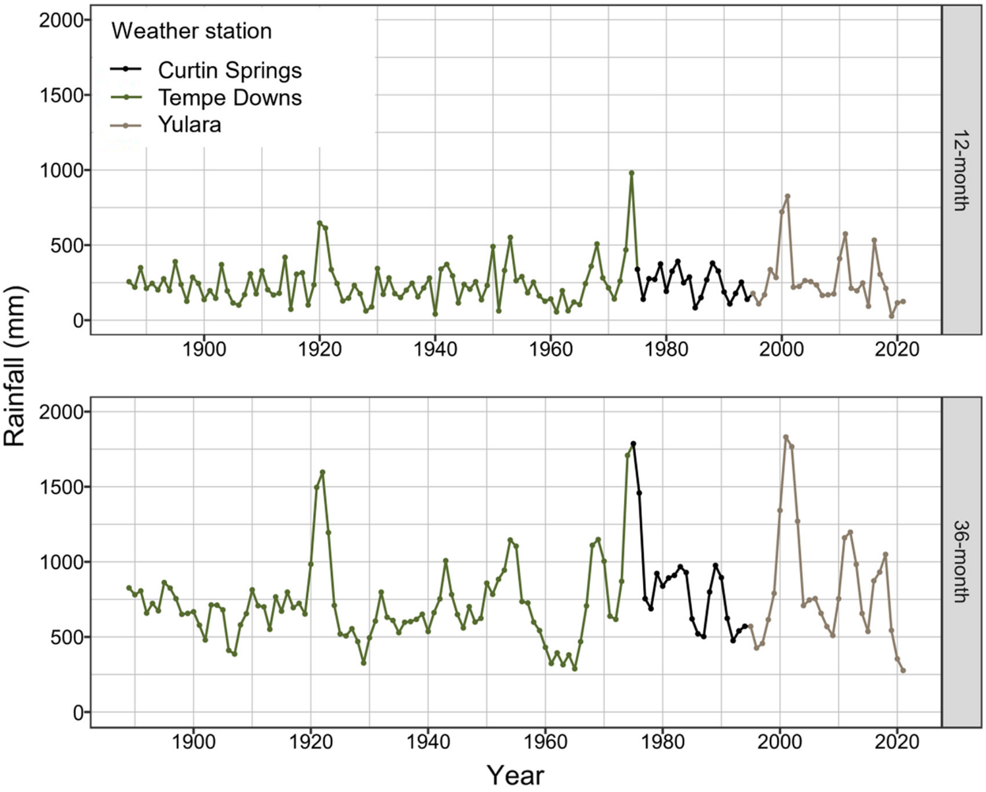

FIGURE 1 Twelve- and 36-month cumulative rainfall from Tempe Downs (data from 1888–1974), Curtin Springs (data from 1975–1994) and Yulara (data for 1995–2020) weather stations in the south-west Northern Territory.

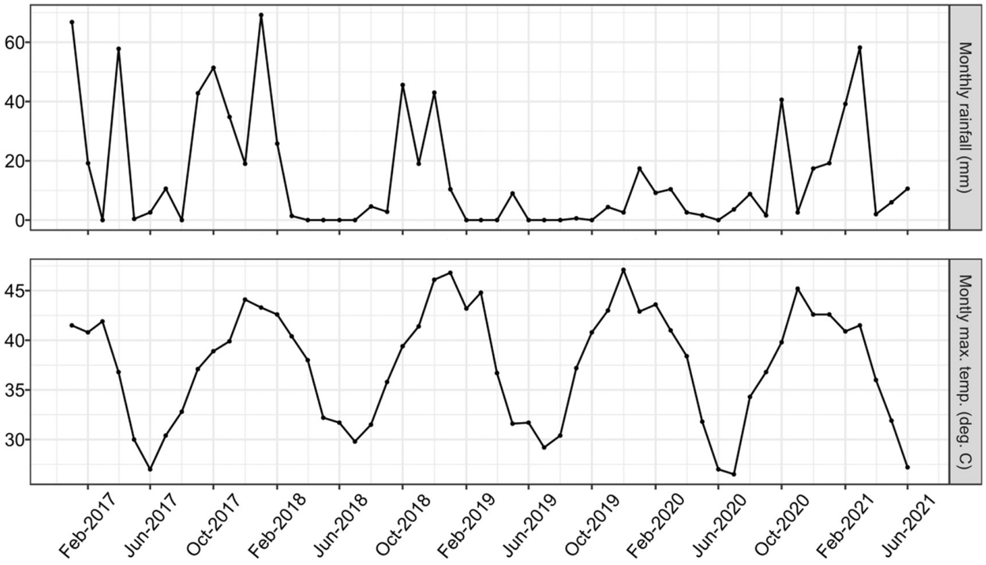

FIGURE 2 Monthly rainfall (mm) and monthly maximum temperatures (°C) from Yulara weather station from Jan 2017 to June 2021.

more severe than – the impacts of previously reported droughts. Extensive drought-related tree, shrub and spinifex (*Triodia* R.Br. spp.) grass death are already evident in UKTNP (Figure 4a–d), raising serious concerns among park managers, scientists and the traditional owners of Uluṟu-Kata Tjuṯa, the Pitjantjatjara and Yankunytjatjara people. Additionally, as

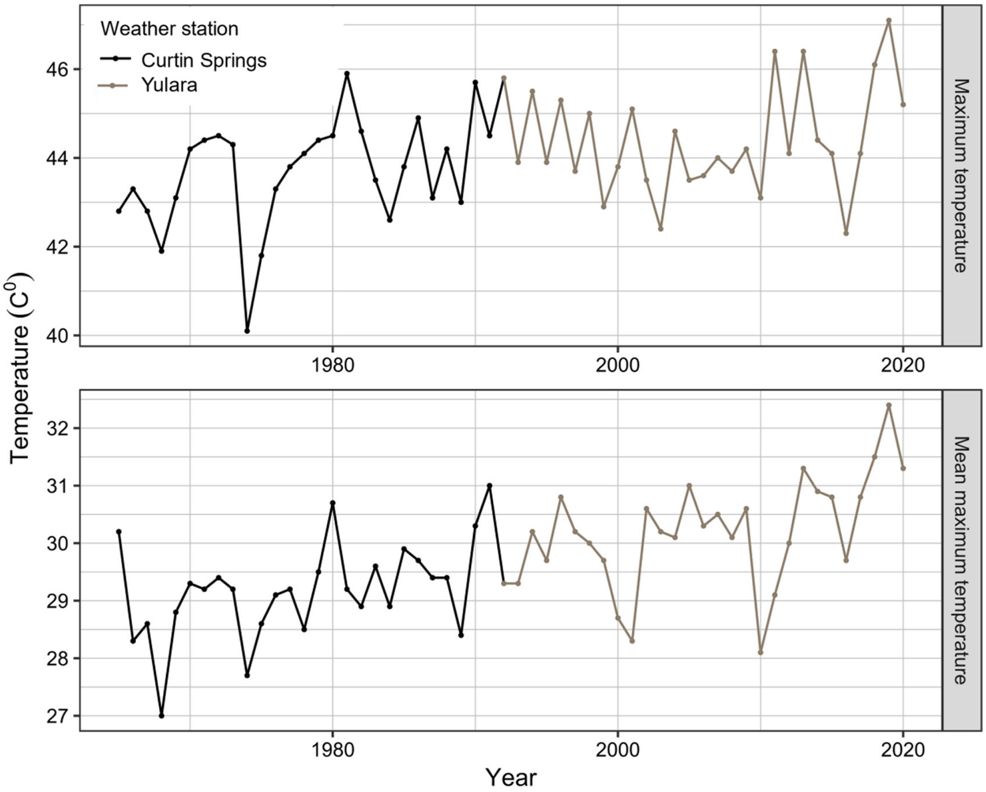

FIGURE 3 Maximum annual temperature and mean maximum monthly temperature for the UKTNP study area (1965–2020). Data from 1965 to 1991 were obtained from Curtin Springs weather station. Data from 1992 to 2020 were obtained from the Yulara weather station.

drought-breaking rains have not yet occurred in the UKTNP region, it is possible that much higher rates of vegetation mortality than those already experienced will occur before the drought ends.

Monitoring to obtain drought-related vegetation mortality data from the 2018–2021 drought is crucial because high-severity droughts happen infrequently, and empirical estimates of drought impacts on arid zone vegetation are largely non-existent. This study improves our understanding of how high-intensity drought and heatwave conditions impact Australian arid zone vegetation by addressing the following questions:

1. What mortality rates have been experienced by the arid zone flora at UKTNP during the 2018–2021 drought and are these rates variable between species?
2. Within a species, does drought mortality relate to plant size? (This is expected, as larger plants with better-developed root systems should experience higher survival than smaller individuals with smaller/shallower root systems.)
3. Within a species, does drought mortality relate to stand density? (This is expected, as greater competition for soil moisture in denser stands should result in higher mortality rates than in less densely packed stands.)
4. Has seedling recruitment occurred after good, but not drought-breaking, rainfall (c. 130 mm) at UKTNP during the early part of 2021?

By addressing these questions, this research will provide an important overview of the impacts of the present drought on the floristic biodiversity of UKTNP. This information is important to inform long-term management of UKTNP habitats under a changing climate. Assessing these impacts will be relevant for other land managers across a large portion of the Australian arid

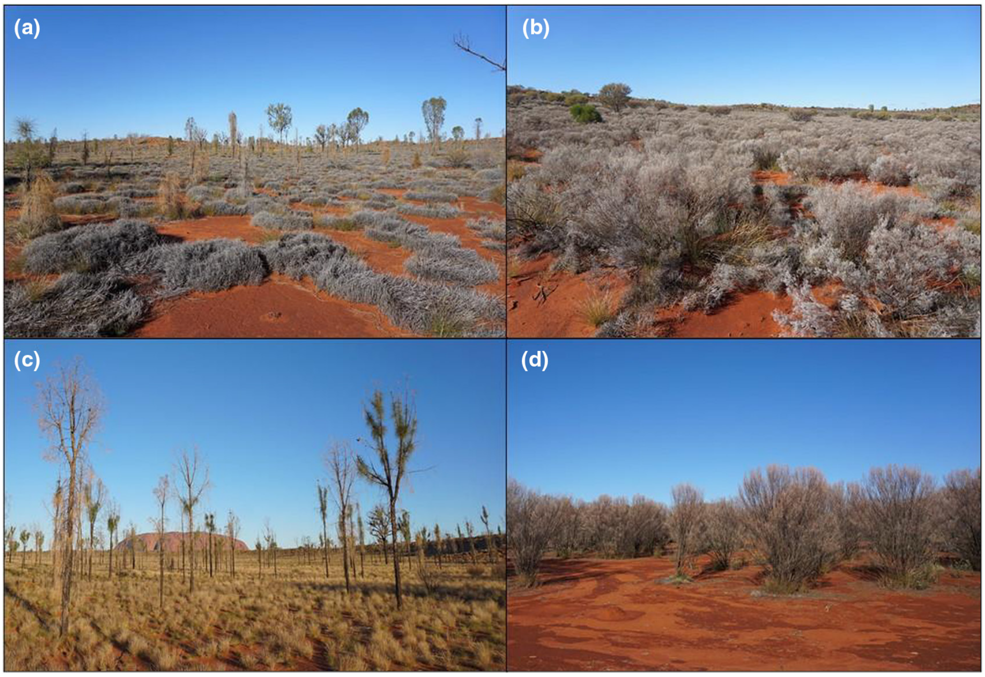

FIGURE 4 Context of the Uluru-Kata Tjuta National Park study area (clockwise from top-left): (a) drought-killed soft spinifex grasses (*Triodia pungens*) on sand plain in northern UKTNP; (b) stand of drought-killed desert myrtle (*Aluta maisonneuvei* subsp. *maisonneuvei*) on inter-dune area in central UKNTP; (c); drought affected desert oaks (*Allocasuarina decaisneana*) on sand plain north of Uluru and (d) drought-killed mulga (*Acacia aneura*) shrubs on red earth plain north of Uluru.

zone, as 2019 was also the lowest rainfall year on record for most of South Australia, the southern Northern Territory and the eastern portion of inland Western Australia (Figure S1). Finally, by sharing traditional ecological knowledge about drought impacts on plants, our Pitjantjatjara and Yankunytjatjara co-authors provided indigenous perspectives on the climate change impacts we observed on vegetation and ecological processes. This information can collectively inform long-term monitoring of vegetation communities in the park.

METHODS

Study area

Uluṟu-Kata Tjuṯa National Park is c. 1181 km^2 in area and is located c. 330 km south-west of Alice Springs in Australia's Northern Territory. Land systems within the park consist of dune fields, creek lines, gravelly plains and the sandstone-conglomerate mountain formations of Uluṟu-Kata Tjuṯa. Mean annual precipitation in the park is highly variable between years and averages 268.1 mm (Yulara weather station, Australian Government Bureau of Meteorology, 2022a). The climate of the region corresponds to the 'grassland hot (persistently dry)' climate type of the Köppen classification. Soils of the dune systems that occupy most of UKTNP comprise deep, red siliceous sands that are extremely infertile and have little organic layer development. Vegetation in the dune fields is almost always dominated by one or more species of the following three spinifex grass species: *Triodia pungens* R.Br., *T. basedowii* E. Pritz and *T. schinzii* (Henrard) Lazarides. These grasses are typically intermixed with a sparse tree/shrub layer comprising species of the genera *Acacia* Mill., *Allocasuarina* L.A.S. Johnson, *Eremophila* R. Br., *Eucalyptus* L. Hér., *Grevillea* Knight, *Hakea* Schrad. & J.C. Wendl. or *Senna* Mill.

Study species

Field surveys incorporating a spatially randomized quadrat sampling design were conducted to assess drought-induced mortality rates of the following eight common and culturally important plant species: mulga (*Acacia aneura* F.Muell.ex Benth., Pitjantjatjara/Yankuntjatjara name: wanaṟi), desert oak (*Allocasuarina decaisneana* L.A.S. Johnson, Pitjantjatjara/Yankuntjatjara name: kurkaṟa), desert myrtle (*Aluta maisonneuvei* subsp. *maisonneuvei* (F.Muell.) Rye & Trudgen, Pitjantjatjara/Yankuntjatjara name: pukara), soft spinifex (*Triodia pungens*, Pitjantjatjara/Yankuntjatjara name: tjanpi kiṯi), quandong (*Santalum acuminatum* A. DC., Pitjantjatjara/Yankuntjatjara name: mangaṯa), Maitland's wattle (*Acacia maitlandii* F.Muell., Pitjantjatjara/Yankuntjatjara name: mini-mini), waxy wattle (*A. melleodora* Pedley, Pitjantjatjara/Yankuntjatjara name: ngarkalya) and yellow flame grevillea (*Grevillea eriostachya* Lindl., Pitjantjatjara/Yankuntjatjara name: kaliny-kaliny(pa)) (see Table 1). Four of these species were focal species: mulga, desert oak, desert myrtle and soft spinifex. Surveys of these four species incorporated the following: (1) estimates of survival rates; (2) measurements of canopy/hummock size and stand density; and (3) counts of seedling numbers. For the remaining four species (quandong, Maitland's wattle, waxy wattle and yellow flame grevillea), survival rates were assessed but no estimates of plant size, stand density or seedling numbers were made.

Soft spinifex is a hummock-forming, long-lived grass that dominates grasslands in arid and semi-arid regions across the northern half of Australia. This grass varies considerably across Australia in terms of its fire response (i.e. whether it regenerates vegetatively or from seed after fire), but the form occurring at UKTNP is fire killed and only regenerates from seedlings after burning (Rice et al., 1994). Mulga is a long-lived (>50 years [Friedel et al., 1994]) shrub or small tree that is highly variable in form, height and phyllode characteristics. It dominates woodlands on red earth soils across c. 20% of Australia (i.e. c. 1.5 million km^2). It resprouts from epicormic shoots under low-intensity burning (Wright & Clarke, 2007b), although a rare form occurring at UKTNP, known as 'blue mulga', is capable of resprouting from underground buds even after high-intensity crown fires. Desert oak is a long-lived, slow-growing tree that is widely distributed on spinifex-dominated dune and sandplain systems through the southern Northern Territory, the far north-west of South Australia, and the north-east of Western Australia. Both adult and juvenile desert oaks resprout strongly after fire. Desert myrtle is a small shrub that forms dense, structurally simple stands on dune crests, slopes and sometimes swales of spinifex-dominated dune fields. Desert myrtle is extremely fire sensitive and does not resprout under any burn conditions (Wright et al., 2019).

Quandong is a small (4–6 m) hemi-parasitic tree that occurs widely across arid and semi-arid Australia. It occurs in a wide variety of habitats, including creek lines, gravelly plains, sandplains and dune fields. Quandong is a culturally important species and, being listed as 'vulnerable' in the Northern Territory, is a focus for park management at UKTNP. Maitland's wattle is a spindly, open shrub that grows to 2–2.5 m and occurs on sandy soils in arid regions across all mainland Australian states except Victoria. Waxy wattle is a spindly open shrub with relatively erect main stems that grows to 2–2.5 m and almost always occurs alongside spinifex grasses. It occurs on deep sands, sandy/stony loams and clay loams and has a distribution similar to Maitland's wattle. Yellow flame grevillea is a shrub that grows to 1.5–2 m tall and has colourful green-yellow flowers with a torch-like appearance. It occurs primarily on red and yellow sandy soils throughout arid Western Australia, the southern Northern Territory and the far north-west of South Australia.

TABLE 1 List of culturally important plants surveyed at Uluru-Kata Tjuta National Park during drought conditions in 2021.

Species	Family	Common name	P/Y name	Uses	References
Acacia aneura	Fabaceae	mulga	wanar̲i	Seeds eaten as a paste, tool manufacture, firewood, ashes mixed with *Nicotiana* spp. for narcotic use, shrubs provide important habitat for culturally important honey ants (*Cumponotus influtus* Lubbock).	Cleland and Tindale (1959); Kalotas (1989); Walsh (1990)
Acacia maitlandii	Fabaceae	waxy wattle	mini-mini	Seeds eaten as a paste.	Napangardi et al. (2021)
Acacia melleodora	Fabaceae	maitland's wattle	ngarkalya	Seeds eaten as a paste, edible grubs found in roots.	Kalotas (1989)
Allocasuarina decaisneana	Casuarinaceae	desert oak	kurkar̲a	Seeds eaten, tool manufacture, firewood and ashes mixed with *Nicotiana* spp. for narcotic use.	O'Connell et al. (1983), James, R. pers. comm (2020).
Aluta maisonneuvei	Myrtaceae	desert myrtle	purkar̲a	Nectar used to sweeten water.	Napangardi et al. (2021)
Grevillea eriostachya	Proteaceae	desert grevillea	kaliny-kalinypa	Nectar from flowers consumed directly from plant.	Kalotas (1989)
Santalum acuminatum	Santalaceae	quandong	mangat̲a	Edible fruit and tool manufacture.	Nash (1984)
Triodia pungens	Poaceae	soft spinifex grass	tjanpi-kit̲i	Seeds used to make nyuma (edible seed cake) and resin from leaves used to make spinifex wax (kirti).	Cane (1987); Gamage et al. (2012); Long (1971)

Vegetation sampling

Field surveys took place in May and June 2021. Two replicate plots dominated by each of the four focal species were sampled at each of 10 randomly selected sites (see Supplementary Figure S2 for site locations). This resulted in a total of 80 plots being sampled, with 20 plots being sampled for each of the 4 focal species. Locations of individual plots were assigned using randomly generated points selected remotely from high-resolution Landsat MSS satellite imagery (subject to certain exclusion criteria outlined below). The stands of the focal species could be readily discerned from the imagery. All sites were located >20 m from road edges to avoid enhanced soil moisture conditions that commonly occur on roadside verges. All sites were selected in long unburnt habitats only (i.e. >20 years time since fire) as this ensured that any observed mortality would not relate to burning. Permission was obtained from traditional owners from UKTNP to conduct vegetation sampling at all sites.

At each plot, square-shaped quadrats were used to count alive versus dead individuals of the focal species within plots dominated by that species (i.e. desert oaks were counted in 'desert oak' plots, mulga individuals were counted at ‘mulga’ plots, etc.). The size of the quadrats varied between species according to the approximate size and typical population densities of the plants. Accordingly, all desert oak plots were sampled with quadrats with an edge length of 40 m, mulga shrubs were sampled with quadrats with an edge length of 20 m and desert myrtle and spinifex were sampled with quadrats with an edge length of 10 m. Surveys of the remaining four non-target species (quandong, Maitland's wattle, waxy wattle and yellow flame grevillea) were sampled opportunistically whenever they occurred in any of the 80 plots. As good rains (c. 130 mm) had occurred at UKTNP between January and April 2021 (see Figure 2), seedling recruitment of the focal species was also counted at each plot. Seedlings of woody species were classed as non-reproductive individuals that were <10 cm in height. For soft spinifex, a seedling was classed as a non-reproductive individual that was <20 cm in diameter.

Plants were categorized as ‘alive’ if they satisfied one or more of the following survival indicators: (1) green leaves were present; (2) above-ground stems were flexible and showed green hues or evidence of dampness when broken (for non-spinifex species only) and (3) a bark ‘scratch’ test whereby a single small incision was made into the cambium layer at the base of the shrub/tree, and this incision showed evidence of greenness or moisture (for woody species only). Initially, a root scratch test was also applied to the woody species on roots ca. 5 cm below the soil surface. However, this test was later abandoned as plants that failed the above-ground scratch test inevitably also failed the root scratch test. Plants were categorized as ‘dead’ if they failed all survival indicator tests.

During the vegetation survey, as a means of controlling for the possibility that plants classified as dead may have been killed by non-drought-related factors, all plants classified as ‘drought-killed’ met the following requirements: (1) they showed retention of some dead leaves on stems ≥10 mm (this would reflect recent death as arid trees and shrubs usually shed all dead leaves within 2–3 years of plant mortality); (2) they showed no evidence of fire-related injury or death (e.g. blackened stems/trunks) and (3) they showed no evidence of exposed aged white sapwood or deep bark cracking that would reflect a long time period since shrub/tree death. Photo points taken in 2017–2018 of live plants were used to assess leaf retention on dead plants of the various species confirmed as having been alive prior to the drought. This visual information was used to inform the expected amount of retention of dead leaf material for plants killed by the 2018–2021 drought.

Statistical analyses

All analyses were carried out using R statistical software (R Core Team, 2021). Data exploration for the various analyses followed the protocols described by Zuur et al. (2013). For the plant survival data, analyses were carried out on two datasets: (1) a ‘multi-species’ dataset that incorporated survival data for the four focal species plus survival data for the four non-focal woody species sampled within the plots; and (2) a ‘mortality drivers’ dataset comprising the survival data for the four focal species plus the plant size and stand density data associated with these species.

Data exploration of the multi-species survival dataset revealed three outliers in the desert myrtle data (see red stars in Figure 5). These data points were retained in the analysis, as they represented real variability in the data, and modelling with or without the outliers did not change the overall significance of the results. Data exploration also revealed very low sampling numbers for yellow flame grevillea, Maitland's wattle, waxy wattle and quandong. Given this, it was unlikely that statistical testing would return significant results for these species. Nevertheless, these species were retained in the analysis as the data provided preliminary estimates of their drought resilience. Proportional survival rates of the eight species were initially modelled using a binomial generalized linear model (GLM) in the R base package. Species were incorporated as a fixed categorical variable in this analysis. Site was also incorporated as a fixed categorical factor to assess whether overall mortality between species differed between sites. The initial binomial GLM model was overdispersed (overdispersion statistic = 4.33). Subsequently, a quasibinomial GLM was used to model the extra variance not accounted for by the binomial model. The model was of the form:

$$\mathrm{Survival}_{ij} \sim \mathrm{Bin}\left(\pi_{ij}\right)$$

$$\mathrm{E}\left(\mathrm{Survival}_{\mathrm{ij}}\right) \sim \pi_{ij} \text{ and } \mathrm{var}\left(\mathrm{Survival}_{\mathrm{ij}}\right) = \pi_{ij} \times \left(1 - \pi_{ij}\right)$$

$$\mathrm{logit}\left(\pi_i\right) = \mathrm{Species}_i + \mathrm{Site}_j$$

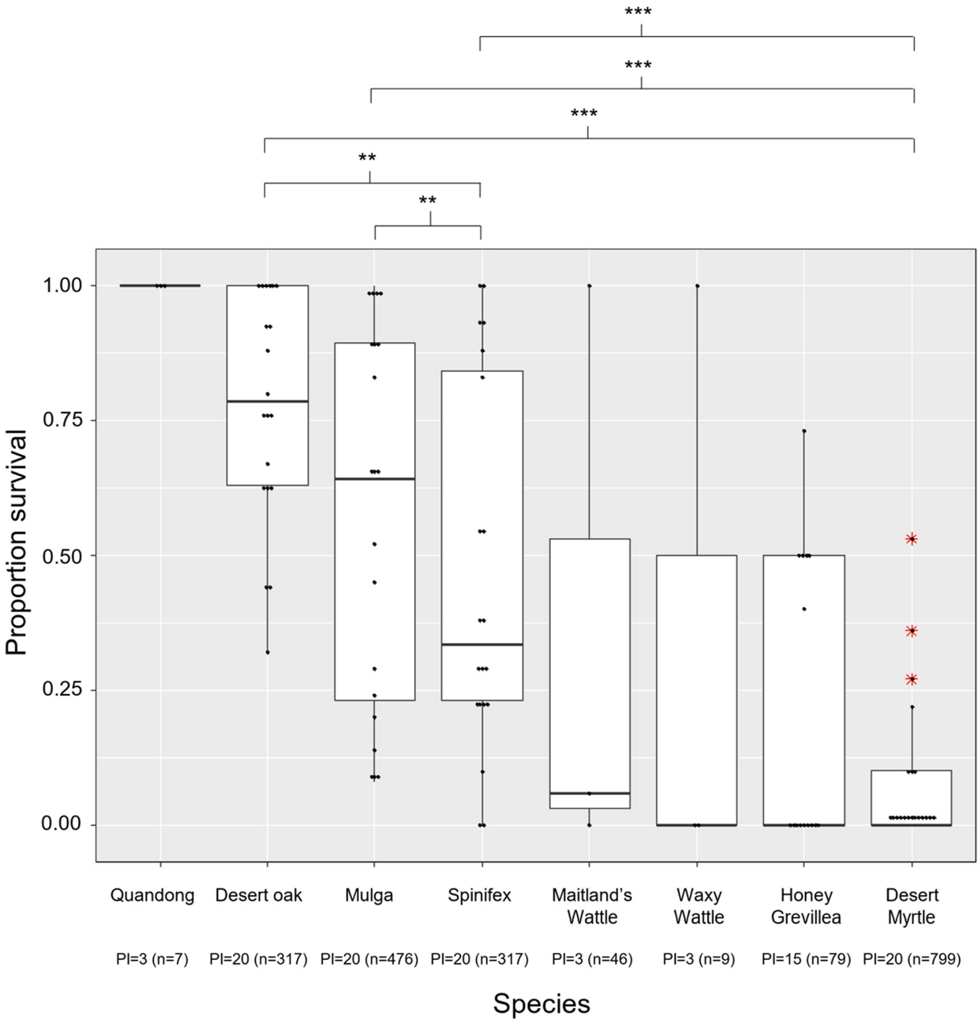

FIGURE 5 Boxplot of survival rates of eight arid zone plants at Uluru-Kata Tjuta National Park during the 2018–2021 drought. Central lines and top and bottom box extremities of the boxes indicate medians and interquartile ranges of the data respectively. Red stars indicate outliers in dataset. Points are jittered observations of plot-level proportional survival for each species. On the X-axis labels, (Pl) indicates number of plots where species were present and sampled and (*n*) indicates total number of individuals sampled across all plots. At the top, significance codes indicate statistically significant differences in proportional survival between the species encompassed by brackets. Significant differences in proportional survival are given by the codes '***' = $p < 0.001$; '**' = $p < 0.01$.

where Survival$_{ij}$, the binomial response variable, was the proportional survival of species i at site j, where i= 1, … 8 and j= 1, … 10. Following model fitting, post-hoc comparisons with Bonferroni corrections were made using the 'mcp' function in the 'multcomp' package (Hothorn et al., 2008). After model fitting, model validation was applied whereby Pearson residuals were plotted against fitted values of the model.

For the mortality drivers' dataset, a Bernoulli generalized linear mixed model (GLMM) was used to model proportional survival of mulga, spinifex, desert oak and desert myrtle as a function of plant size and stand density. For this model, species, plant size and stand density were incorporated as fixed continuous covariates. Site was incorporated as a random categorical covariate to account for site-specific variability in survival rates and to focus the analysis on the variables of interest (species, plant size and stand density) rather than on-site effects. Two-way interaction terms included in this model were species × plant size and species × stand density. The model for the Bernoulli GLMM had the following form:

$$\mathrm{Survival}_{ij} \sim \mathrm{Bin}\left(\pi_{ij}\right)$$

$$\mathrm{E}\left(\mathrm{Survival}_{ij}\right) \sim \pi_{ij} \text{ and } \mathrm{var}\left(\mathrm{Survival}_{ij}\right) = \pi_{ij} \times \left(1 - \pi_{ij}\right)$$

$$\mathrm{logit}\left(\pi_i\right) = \mathrm{Species}_{ij} + \text{Plant diameter}_{ij} + \text{Stand density}_{ij} + \mathrm{Species}_{ij} \times \text{Plant diameter}_{ij} + \mathrm{Species}_{ij} \times \text{Stand density}_{ij} + a_j$$

$$a_j \sim N\left(0, \sigma_j^2\right)$$

where Survival$_{ij}$, the binary response variable, was the survival of a plant of species i at site j, where i= 1, … 0.4 and j= 1, …. 10 sites. The residual term a_j was the random site effect, which was assumed to be normally distributed with a mean of 0 and variance of σ^2_{Site}. Following model fitting, overdispersion was checked for and a likelihood ratio test was used to assess the significance of the covariates. Model validation was applied whereby Pearson residuals were plotted against fitted values and against the covariates.

Given the absence or extremely low seedling numbers of mulga, desert oak and desert myrtle, no analysis of seedling counts between species was conducted. However, the raw data for these species and spinifex are presented in a box plot (Figure 7). As there were high numbers of spinifex seedlings, an analysis was carried out to assess the relationship between seedling number and the density of dead adult plants at a plot. It was hypothesized that plots with more dead adult spinifex would permit more seedling recruitment as competition for soil moisture at such plots should be less. As the data comprised count data, a Poisson generalized linear model (GLM) was initially carried out. However, this model was badly overdispersed (overdispersion statistic = 25.02). Subsequently, a negative binomial (NB) GLM was applied, and this model was not overdispersed (overdispersion statistic = 1.34). The NB GLM had the following form:

$$\mathrm{Seedlings}_i \sim \mathrm{NB}\left(\mu_i, k\right)$$

$$\mathrm{E}\left(\mathrm{Seedlings}_i\right) \sim \mu_i \text{ and } \mathrm{var}\left(\mathrm{Seedlings}_i\right) = \mu_{ij} + \frac{\mu_{ij}}{k}$$

$$\log\left(\mu_i\right) = \mathrm{intercept} + \mathrm{Seedlings}_i$$

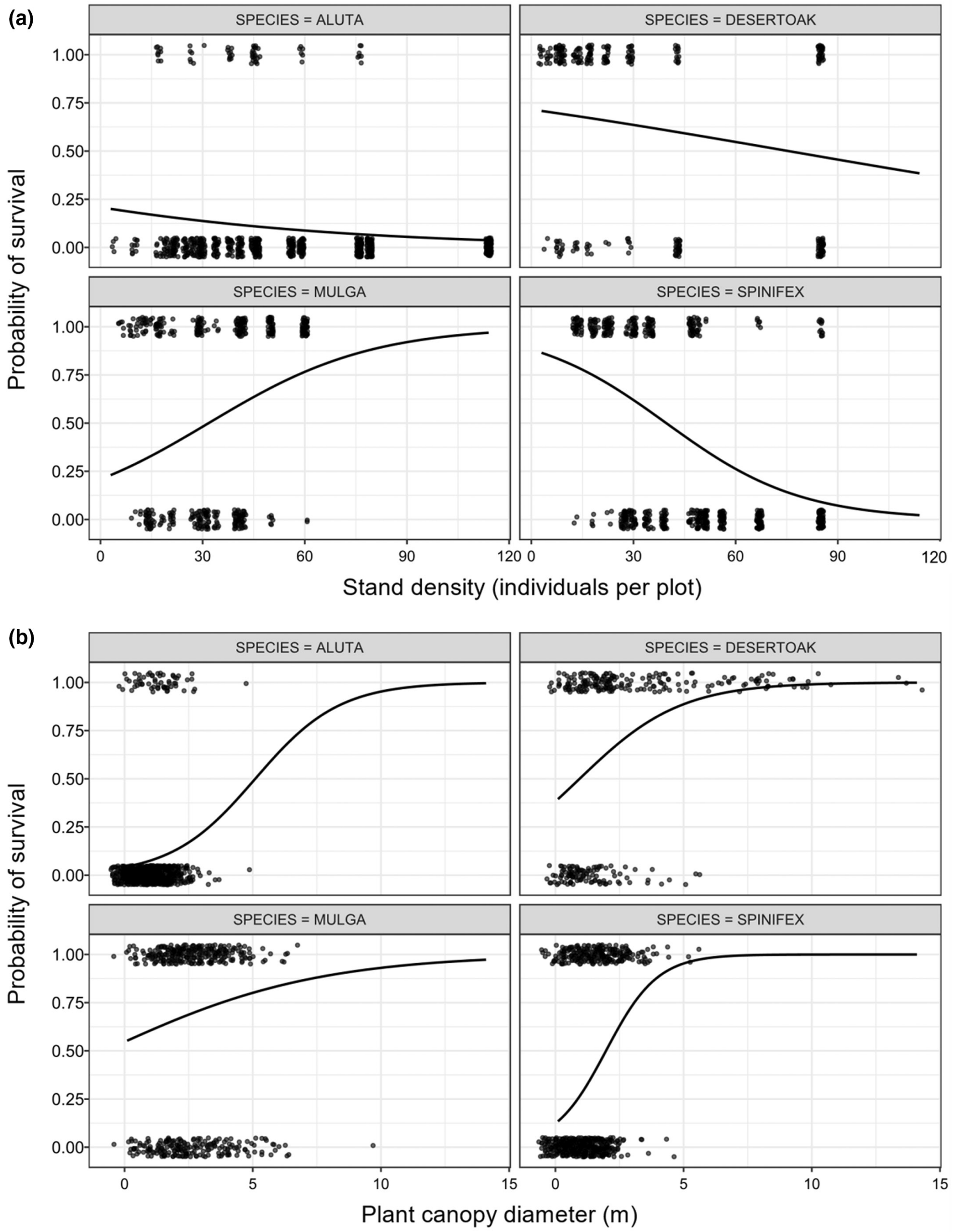

FIGURE 6 Conditional survival slopes from binomial GLMs showing significant two-way interactions between species and plant density (per plot) (a), and species and plant size (canopy diameter for trees and shrubs; hummock diameter for spinifex grasses) (b). Raw binary survival data are plotted and jittered to aid visualization of relationships between species survival and plant size/density.

where Seedlings$_i$ was the number of observed seedlings at plot i, where i = 1, …. 20. Data exploration and model validation for the NB GLM seedlings analysis followed the protocols used for the previous analyses.

RESULTS

Drought survival rates in 2021 among the eight examined plant species were highly variable. Post-hoc testing of the multi-species GLM indicated that desert myrtle had significantly lower mean proportional survival ($\bar{x}$ =0.09, SE = 0.05) compared to mulga ($\bar{x}$ =0.58, SE = 0.11), spinifex ($\bar{x}$=0.47, SE = 0.11) and desert oak ($\bar{x}$ =0.78, SE = 0.07) (Pr(>|z|) < 0.001

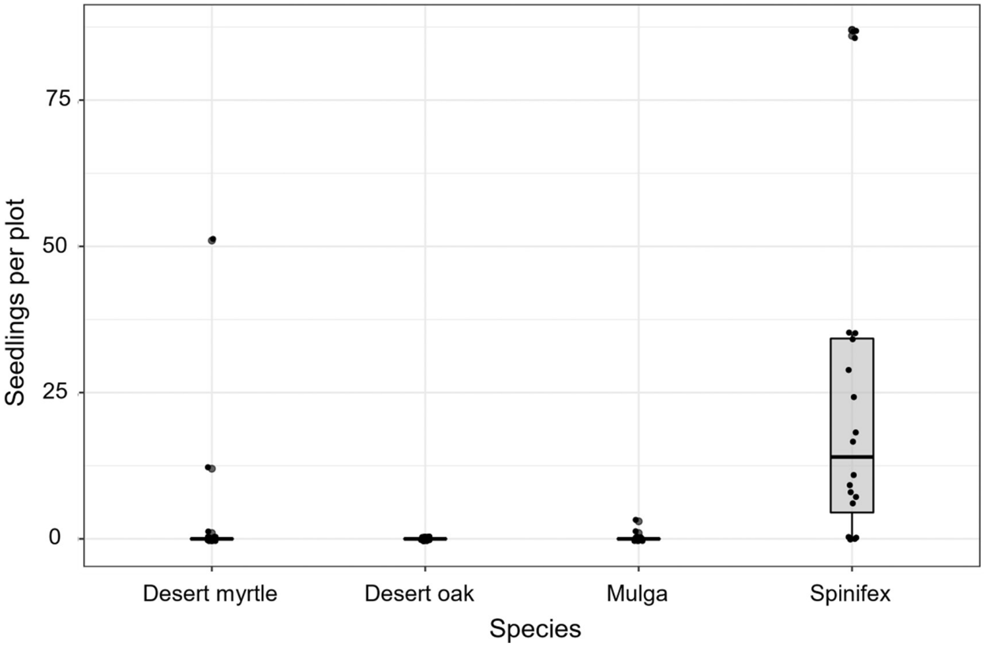

FIGURE 7 Boxplot of seedling recruitment per dead adult plant for the four focal species at Uluru-Kata Tjuta National Park during 2018–2021 drought period. Central lines and upper and lower extremities of the boxes indicate medians and interquartile ranges of the data respectively. Points are jittered observations of plot-level seedling recruitment for each species.

for all post-hoc comparisons) (Figure 5). Post-hoc testing also showed that spinifex had lower survival rates compared to desert oak and mulga (Pr(>|z|) = 0.008 and Pr(>|z|) = 0.002, respectively). Low mean proportional survival rates were observed for Maitland's wattle ($\bar{x}$ =0.35, SE = 0.18), waxy wattle ($\bar{x}$ =0.33, SE = 0.18) and yellow flame grevillea ($\bar{x}$=0.21, SE = 0.09) (Figure 5). However, post-hoc testing did not indicate significant differences between these and other species, possibly due to low sampling numbers for these species. No dead quandongs were observed, although the sample size for this species was very low (*n* = 7). In addition to inter-species variability in survival, the multi-species GLM indicated that plant survival varied across sites (LRT = 98.58, Pr(>Chi) = <0.001), with post-hoc comparisons showing that sites 2, 3 and 4 had significantly higher survival than the other sites (Figure S3).

The analysis of the mortality drivers dataset indicated significant two-way interactions between species and plant size (LRT = 20.92, Pr (>Chi) < 0.001), and between species and stand density (LRT = 110.67, Pr (>Chi) < 0.001). This indicated that the relationships between survival and plant size, and between survival and stand density, differed between species. Figure 6 illustrates these relationships. In Figure 6a, the survival curve for desert myrtle (*Aluta*) and desert oak is relatively flat across the range of stand densities, indicating no or minimal relationship between survival and stand density. In contrast, survival of spinifex declined with increasing stand density, while mulga showed increased probability of survival as stand density increased. For mulga, this effect was driven largely by high survival rates at the following two plots with high stand densities: plot 2 at site 2 (92% survival, *n* = 50 shrubs) and plot 1 at site 3 (97% survival, *n* = 60 shrubs) (Figure 6a). As seen in Figure 6b, all species showed an increase in probability of survival as plant size increased. The positive relationship between survival and plant size was strongest for desert oak, with no dead adults observed once canopy diameter exceeded 6 m (Figure 6b).

Minimal seedling recruitment was observed at plots for desert oak ($\bar{x}$ = 0 seedlings/plot), mulga ($\bar{x}$ = 0.2 seedlings/plot, SE = 0.8) and desert myrtle

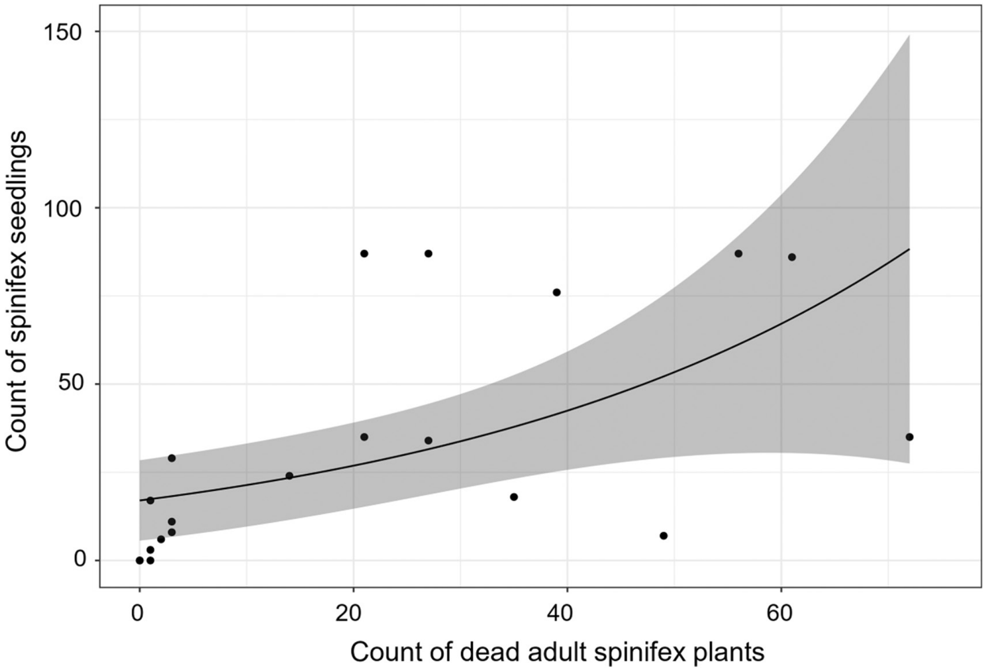

FIGURE 8 Fitted values (plus data points) for relationship between *Triodia pungens* seedling occurrence and number of dead adults across 40 plots (10 × 10 m) at Uluru-Kata Tjuta National Park during the 2018–2021 drought period. Shaded bands indicate 95% confidence intervals of the negative binomial (NB) generalized linear model.

($\bar{x}$ =3.4 seedlings/plot, SE = 3.4) (Figure 7). Only spinifex showed recruitment levels that offset adult deaths, with mean seedling recruitment per plot of 24.7 (SE = 5.4) (Figure 7). For the analysis of spinifex seedling counts as a function of the density of dead adult spinifex plants, a significant positive relationship was found between seedling numbers and the number of dead adults (LRT = 206.8, Pr(>Chi) < 0.001). Figure 8 illustrates this relationship, showing that the number of spinifex seedlings per plot increased as the number of dead plants increased.

DISCUSSION

Vegetation mortality rates

Uluṟu-Kata Tjuṯa National Park experienced substantial losses in woody flora and spinifex cover during the 2018–2021 drought, although mortality rates were highly variable between species. The mean percentage of mortality was 53% across the eight species we sampled, with percentage mortality ranging from very low in species such as quandong (0%) and desert oak (12%) to very high in species such as yellow flame grevillea (79%) and desert myrtle (91%). Variability in drought susceptibility between species was not an unexpected result and may have been due to any of the following: (1) between-species variation in the capacity of stem morphologies to resist cavitation; (2) differing root characteristics between species and (3) adaptations in certain species to aid in reducing water loss during transpiration (e.g. reduced leaf sizes [mulga] or having cladodes rather than true leaves [diminished, photo-synthetic stems such as in desert oak]) (Anderegg et al., 2016; Crouchet et al., 2019; Fensham et al., 2009; Fensham & Fairfax, 2007). Studies on the drought susceptibility of semi-arid and savanna flora in Australia and of arid zone flora in other parts of the world have shown similar variability to drought mortality among plant species (Fensham et al., 2009; Koepke et al., 2010; Vicente-Serrano et al., 2020). For quandong, high rates of drought survival could also relate to hemi-parasitism if soil moisture resources from host trees facilitated survival.

In addition to between-species variability in drought susceptibility, we observed significant intra-species variability in survival rates across sites. Some of this variability may have been driven by patchiness of rainfall that can occur during small, non-general, rainfall systems that sometimes pass through inland Australia (Acworth et al., 2016). In addition to patchiness of rainfall, it is possible that between-site variability in soil conditions and depth of underlying regolith may have affected access of plant rooting systems to soil moisture (Fensham et al., 2015; Koepke et al., 2010; Renne et al., 2019). This hypothesis is supported by observations at the plot level of patches of live plants inter-mixed with patches of plants that were mainly dead. Such observations could be explained by localized variability in soil conditions but would be unlikely to relate to variability of rainfall at such scales.

The results of the 'mortality drivers' analysis showed that across species, survival during drought was consistently related to increasing plant size. In other regions globally, contrasting results have been found in studies of drought vulnerability and plant size. Some studies have found increased drought-linked death in larger trees (Bennett et al., 2015; Olson et al., 2018; Phillips et al., 2010). Others have found increased mortality in smaller trees (Nolan et al., 2021). In the UKTNP system, increased survivability of larger plants probably relates to greater root reach enabling increased stem water storage capacity (Fensham & Fairfax, 2007). The significant survival × stand density interaction from the same analysis is more difficult to explain. Drought-linked density-dependent mortality has been reported in some studies in Australia (Dwyer et al., 2010) and overseas (Guarin & Taylor, 2005; Savage, 1997), although a previous study on drought death in mulga in western Queensland did not (Fensham et al., 2012). At UKTNP, desert myrtle showed no relationship between survival and stand density, which is likely due to the apparently high susceptibility of this species to drought, with high rates of mortality occurring even at low stand densities. In contrast, drought mortality for soft spinifex increased with increasing sward density, presumably because competition for soil moisture resources was higher in plots with higher sward densities. Interestingly, mortality rates of mulga decreased at plots where stand density increased. This trend is difficult to explain. It is possible that this result reflects a sampling artefact, with the high-density mulga plots that we sampled having by chance been growing in areas with improved site quality and/or having been subjected to higher rainfalls than other plots at crucial times. At UKTNP, there is a trend for rainfall systems to pass to the south and south-west of the Kaṯa Tjuṯa Mountain system in the western region of the park. As a result, rainfall conditions in the east of the park are commonly drier than in more western areas. Sites 2, 3 and 4 were in the central and western portion of UKTNP and could have been affected by these rainfall trends. This might explain the high rates of survivability of mulga observed at sites 2 and 3, despite high mulga stand densities at these sites.

It has previously been suggested that coppicing (i.e. resprouting) evolved among certain Australian arid woody flora because it enables post-drought recovery rather than post-fire regeneration (Hodgkinson & Griffin, 1982). This may hold true for certain arid zone species; however, our results do not support this hypothesis for at least two of the four non-focal species — Maitland's wattle and yellow flame grevillea. Both these shrubs display strong post-fire resprouting from well-insulated below-ground bud banks, even under high-intensity summer fires (Wright & Clarke, 2007a, 2007b) (Figure S4). Despite this, both species showed high susceptibility to drought death in our study, with neither showing any resprouting from the below-ground bud banks that normally enable regeneration after fire. Instead, any drought-linked sprouting that did occur in these species came from above-ground epicormic buds. This observation suggests post-fire resprouting from underground buds in these species is an evolved fire response trait, rather than a fire exaptation that evolved under drought. The conclusion that both fire and drought could have played evolutionary roles in resprouting in these plants is consistent with recent research showing that fire has been an evolutionary driver of plant selection in Australia since the Cretaceous, well before northward continental drift resulted in increasing aridity in inland regions during the Miocene (Lamont et al., 2018; Lamont & He, 2017).

Seedling regeneration

This study provided a preliminary assessment of seedling regeneration dynamics during drought for the four long-lived focal species. No recruitment was observed for desert oak, and this was not unexpected. This species does not maintain a persistent soil-stored seed bank but instead stores its seeds in woody cones in the canopy (i.e. the tree is serotinous). The seeds are large and non-toxic and, therefore, likely to be highly attractive to granivores (R. James, pers. Comm. 2020). For strong germination and recruitment of desert oak to occur, fire or canopy death is necessary as this enables large quantities of seeds to be synchronously released from cones to the soil surface. After seed release, good follow-up rain is required for recruitment, and the timing of follow-up rain must be closely synchronized with seed release since seeds are rapidly depredated by granivores once they reach the soil surface (Wright, 2007). As the plots we sampled had not been burnt for >20 years, no fire-triggered seed release would have occurred recently. Therefore, an absence of desert oak seed in the soil may explain why no recruitment was observed despite good rains in early 2021. In June 2021, many desert oaks were seen with large quantities of unopened pods in their canopies. It is possible that if the present drought continues and these trees die in the future, pods will then release seeds and some recruitment may occur.

Recruitment for desert myrtle in 2021 was minimal at all but two sites. Desert myrtle usually maintains dense and persistent soil seed banks (c. 200 viable seeds/m^2 [Wright, 2018; Wright et al., 2019]), and large pools of seed were observed on the soil surface at all desert myrtle sites visited during the study. Germination conditions for this species are quite specific, requiring seed ageing, warm incubation temperatures during germination and prolonged wetting (Wright et al., 2019). Additionally, germination rates are enhanced by smoke inoculation. Given the complete absence of seedlings at all except two sites, it is likely that insufficient warm-season rainfall and soil wetting had occurred to allow germination of the seed bank to occur at most sites. Localized rainfall at sites 7 and 9, where good recruitment was observed, was presumably sufficient to allow for seed germination from the seed bank to occur.

Very low rates of recruitment were observed for mulga. This species has seed banks that fluctuate considerably in density in response to the rare synchronized production of large seed crops among populations (i.e. masting) (Wright et al., 2015; Wright & Fensham, 2018; Wright & Zuur, 2014). Like desert oaks, the seeds of mulga are favoured by granivores, and seed populations in soils rapidly decline following seed bank pulses that occur during mast years. As no mulga seed production was observed at UKTNP for many years (T. Guest, pers. Obs.), low seed bank densities may explain low seedling recruitment for this species in 2021. It is also possible that an absence of appropriate germination stimuli minimized mulga recruitment, as none of the sites we visited were burnt and mulga seeds are strongly promoted to germinate by soil heating to between 80 and 100°C during fire (Fox, 1985; Wright et al., 2015). Nevertheless, in any mulga seed crop, a low proportion (c. 1–5%) of seed will germinate without any heat cue (Fox, 1985; Wright et al., 2015). Consequently, with heavy rainfall that results in protracted soil wetting, good seedling regeneration may occur even in the absence of fire (as reported by Silcock et al., 2017). In our UKTNP study, the complete absence of recruitment observed at all but two sites might be explained by a combination of a lack of landscape fire and inadequate rainfall.

Recruitment rates for soft spinifex were considerably higher than for any other species. Like mulga, soft spinifex is a masting species with seeds favoured by granivores and with seed banks that fluctuate strongly in response to rare rainfall-triggered mast events (Wright & Fensham, 2016, 2018). Good rainfalls occurred at UKTNP in 2016 (532.8 mm) and masting for this species was observed in 2017 at populations close to the Alice Springs airport where similar quantities of rainfall had occurred (Australian Government Bureau of Meteorology, 2021; Wright & Fensham, 2018). Given these good rains, it is possible that soft spinifex populations at UKTNP had also masted in 2017, and that seed bank densities were still high in 2021 because of this mast year. Although germination of soft spinifex seed is enhanced by a fire-related cue (smoke), a proportion of the seed bank still germinates in the absence of smoke (Davidson & Adkins, 1997; Lewandrowski et al., 2018; Wells et al., 1999). This may explain why good recruitment was observed even in the long-unburnt plots of our study. It is also possible that prolonged drying and high soil temperatures during the drought had broken down *T. pungens* seed dormancy by rupturing the florets that enclose the seeds on dispersal (which typically impede germination [Lewandrowski et al., 2017]), thereby facilitating the good spinifex recruitment that occurred after rains in early 2021.

Although quandong was not one of the focal species chosen for targeted seedling sampling at UKTNP, no seedlings of quandong were observed beneath any of the individuals sampled during the vegetation survey component of this study. Viability testing of seed from the UKTNP quandong population has previously occurred at the Australian National Botanic Garden and shown the seed to have moderate-to-low viability (Guja, L., pers. Comm. 2021). This might suggest that the absence of recruitment we observed for this species after the early 2021 rains could relate to low viability of the soil seed bank. Alternatively, as the seeds are dormant on dispersal and require a complex combination of conditions to alleviate dormancy (e.g. wet–dry cycling and cracking of the woody coat [Chong, 2018]), it may be that the absence of recruitment we observed related to an absence of appropriate germination stimuli.

For future research on drought-linked impacts on arid plants, we encourage conducting investigations of other local, and/or landscape-scale drivers of plant survival/mortality, as well as broadening the suite of Australian arid zone species that are assessed for drought resilience. At UKTNP, other culturally and biologically important plants that require drought assessment include the rare Mt Connor wattle (*Acacia ammobia*), witjuti bush (*Acacia kempeana*), desert corkwoods (*Hakea* spp.) and various species of mallee (*Eucalyptus* spp.). Another important area of research would be assessing whether an interactive effect of fire and drought on plant survival exists. Field observations in recently burnt areas in UKTNP suggest that survival of plants in habitats that had been burnt prior to the onset of the drought was higher than in long-unburnt areas. This may have been because fire removed the cover of large, old spinifex grasses, thereby reducing competition for soil moisture and increasing survival rates of plants during the drought. Further research is required to test this hypothesis.

CONCLUSION

This study provides an initial assessment of the impacts of high-intensity drought and heatwave conditions on arid zone plants at Uluṟu-Kata Tjuṯa National Park. Overall, our results indicate that extreme water deficits coupled with heatwave conditions during the current drought have driven extremely high rates of vegetation loss in most UKTNP vegetation communities. Further disruption to ecosystem function and restructuring of plant communities in the park is likely to occur in the long term if drought severity/frequency and summer temperature conditions continue to increase with anthropogenic climate change. These impacts are likely to be exacerbated by competition with invasive weed species, exotic herbivore pressure and altered fire regimes due to anomalous climate change-linked weather conditions. High rates of plant mortality during the current drought should serve as a warning that urgent and proactive climate change action needs to be taken to mitigate escalating temperatures and increasingly severe drought conditions forecast in arid Australia.

AUTHOR CONTRIBUTIONS

Boyd Wright: Conceptualization (equal); data curation (equal); formal analysis (lead); investigation (equal); methodology (equal); writing – original draft (lead); writing – review and editing (equal). **Tracey Guest:** Conceptualization (equal); investigation (equal); methodology (equal); project administration (equal); writing – original draft (supporting); writing – review and editing (equal). **Sam Merson:** Conceptualization (equal); methodology (equal); writing – original draft (supporting); writing – review and editing (equal). **Nathan Nipper:** Conceptualization (equal); methodology (equal). **Martin Nipper:** Conceptualization (equal); data curation (equal); methodology (equal).

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DATA AVAILABILITY STATEMENT

Data to be stored on Dryad open-access data repository

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SUPPORTING INFORMATION

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

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