Corrigendum to: The role of grass-tree *Xanthorrhoea semiplana* (Asphodelaceae) canopies in temperature regulation and waterproofing for ground-dwelling wildlife

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The editor and publisher regret that during copy editing of this paper prior to proofing the words 'pathogen *Phytophthora cinnamomi*' were replaced with 'fungal pathogen *Phytophthora cinnamomi*' in three places: once in the abstract, once in the introduction and once in the discussion. *P. cinnamomi* is an oomycete, not a fungus, so this insertion is incorrect. The error was not made by the authors, so the editor and publisher apologise for this mistake and for distress and inconvenience caused.

The role of grass-tree *Xanthorrhoea semiplana* (Asphodelaceae) canopies in temperature regulation and waterproofing for ground-dwelling wildlife

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ABSTRACT

Context. The iconic grass-trees (*Xanthorrhoea semiplana*) of Australia are used by many animal species, but their role as shelters against weather extremes is poorly known. The severe contribution of the fungal pathogen *Phytophthora cinnamomi* to grass-tree deaths and current burning practices could affect small animal conservation by exacerbating impacts of weather extremes. **Aims.** We examined the buffering role of *X. semiplana* canopies against extreme weather at four sites in the Mount Lofty Ranges, South Australia. **Methods.** We measured ambient temperature, temperatures under grass-tree canopies, and 2 m away at random locations in summer (>35°C) and in winter (<13°C) over 24-h periods at each study site. We scored soil dryness under the canopies during and after heavy rainfall. **Key results.** Temperatures under grass-tree canopies were more stable and with smaller ranges than other temperatures, and showed dramatic differences in summer when conditions were up to 20°C cooler than ambient. Temperatures were higher under grass-trees at night in winter. The soil under the largest canopies was completely dry during and after heavy rainfall. **Conclusions.** *Xanthorrhoea semiplana* buffers ground-dwelling animals against temperature extremes and rain so that the animals maintain their thermal resistance. Animals may choose foraging times based on grass-tree availability. The largest grass-trees provide the best shelter. **Implications.** Considerable grass-tree deaths from *P. cinnamomi* infestation, together with removal or burning, can have dramatic detrimental consequences for their habitat value and the survival of wildlife using them as shelter.

Keywords: bushfire, concealment from predators, cover for wildlife, foraging time, hazard reduction burning, microclimate regulation, prescribed burning, protection from rain, refuge, shade, shelter plant, thermoregulation, tree hollow, waterproofing, wildfire.

Introduction

Physiological and ecological processes influence an animal's habitat selection (Huey 1991). Shelter selection affects growth, survival and reproduction (Huey 1991), and can decrease the cost of thermoregulation (Wilkinson *et al.* 1998; Bos and Carthew 2003). The choice of an appropriate shelter is especially important in stressful climatic conditions, when temperature and relative humidity can reach fatal levels (Waudby and Petit 2017). Sunday *et al.* (2014) showed that sheltering is vital for ectotherms because extreme operative body temperatures in exposed habitats could exceed their physiological thermal limits. Shelters are also essential to protect animals from predators, which include exotic cats and foxes in Australia (Bleicher and Dickman 2020). The waterproofing value of shelters has received scant attention, yet the effect of wetting on the insulation of bird and mammal coats is dramatic, because it reduces thermal resistance by approximately half of its dry value (Webb and King 1984). Although small mammals benefit from adaptations that may assist in waterproofing (e.g. sebum – Smith and Thiboutot 2008), it is likely that long exposure to rain would have detrimental impacts on many small vertebrates if they had no access to suitable shelters. Similarly, many unsheltered invertebrates would be negatively affected by heavy rainfall.

The quality of ground vegetation that moderates temperature and wind, and that protects animals from rain and predators should have a great impact on the biodiversity of small vertebrates using an area. Not all plants perform the same services. For example, Frazer and Petit (2007) determined that the bush rat (*Rattus fuscipes*) selected grass-trees (*Xanthorrhoea semiplana* F. Muell.) over other understorey vegetation for shelter while foraging. Haby *et al.* (2013) also found a preference of the Endangered southern brown bandicoot (*Isoodon obesulus obesulus*) for *X. semiplana* habitat. In this paper, we explore the temperature and waterproofing properties of *X. semiplana* as shelter vegetation.

The endemic and iconic Australian genus, *Xanthorrhoea* (Asphodelaceae, formerly Xanthorrhoeaceae) is represented by 29 species (World Flora Online 2022); individuals of some of these species have lived for hundreds of years (Lewis 1955; Gill and Ingwersen 1976; Lamont and Downes 1979). Their stems may be arborescent or subterranean. A single inflorescence per apex consists of a long wooden scape, topped by a spike bearing numerous nectar-rich flowers; the dry scape of some species is an important nesting site for the threatened green carpenter bee (*Xylocopa aeratus*) (Leys 2000; Steen and Schwarz 2000; Glatz *et al.* 2015). The grass-trees' distinctive terminal crowns of fine, long and pointed leaves can provide shelter to a diversity of animals. In some species, including *X. semiplana*, the leaves of large individuals form a dense curving canopy and create a thick ground cover (Fig. 1). Senescent leaves dry up, but remain in the structure for a long time, unless burnt. The sheltering role of grass-tree canopies has been established for some mammals, for example bush rat (*Rattus fuscipes*) (Spencer *et al.* 2005; Frazer and Petit 2007), dasyurids (Garden *et al.* 2007), southern brown bandicoot (*Isoodon obesulus obesulus*) (Paull 1993; Haby *et al.* 2013; Robinson *et al.* 2018), several *Cercartetus* species of pygmy-possums (reviewed in Tulloch 2004), western ringtail possum (*Pseudocheirus occidentalis*) (Western Australia Department of Parks and Wildlife 2017 and references therein), Kangaroo Island dunnart (*Sminthopsis fuliginosus aitkeni*) (Gates 2001), mardo (*Antechinus flavipes leucogaster*) (Swinburn *et al.* 2007), yellow-footed antechinus (*Antechinus flavipes*) (Marchesan and Carthew 2004), silver-headed antechinus (*Antechinus argentus*) (Mason *et al.* 2017), agile antechinus (*Antechinus agilis*), bush rat, eastern pygmy-possum (*Cercartetus nanus*), and white-footed dunnart (*Sminthopsis leucopus*) (Laidlaw and Wilson 2006), heath rat (*Pseudomys shortridgei*) (Di Stefano *et al.* 2011), ash-grey mouse (*Pseudomys albocinereus*) (Smith *et al.* 2019), New Holland mouse (*Pseudomys novaehollandiae*) (Lazenby *et al.* 2008). A large amount of evidence highlights their use as food (e.g. Wanniarachchi *et al.* 2022 for some small mammal species) and shelter by many invertebrate and vertebrate species. In a review with a focus on two Queensland species, Borsboom (2005) determined that this evidence concerned over 315 invertebrate species and nearly 100 vertebrate species.

Considering their prevalence in many Australian ecosystems and their dome-shaped structure protecting a wide range of animals (also orchids, Petit and Dickson 2005), some grass-trees species are likely to be keystone (e.g. Wilson *et al.* 2020, in view of the significant association of small mammals with *Xanthorrhoea australis*, as in Laidlaw and Wilson 2006, and profound impact of grass-tree habitat loss on vertebrates, as in Cahill *et al.* 2008). Dependence of animals on grass-trees should be highest where predators are common and when temperature extremes can be fatal.

Fig. 1. Grass-tree *Xanthorrhoea semiplana* ssp. *semiplana*.

In this study, we examined the temperature microclimate and waterproofing afforded by *X. semiplana* ssp. *semiplana* in hot and cold temperature extremes and in torrential rain, respectively. We compared the maximum differences in mean temperature between locations under the canopy of grass-trees and ambient temperature, as well as temperatures at random locations. We expected that grass-trees would buffer high temperatures (shown by Keppel *et al.* 2017 on the Fleurieu Peninsula), as well as low ones (Swinburn *et al.* 2007), to a level facilitating the survival of both ectotherms and endotherms. We also determined whether soil dryness under the canopy of grass-trees was independent of canopy size. We expected that the level of protection from temperature and rainfall extremes would increase with increasing size of grass-trees.

This work is of significance because it will contribute to the mounting evidence for grass-trees as keystone species, which are highly susceptible to the key threatening fungal pathogen *Phytophthora cinnamomi* (Government of South Australia 2006; Commonwealth of Australia 2018), have suffered extensive clearance (Bickford *et al.* 2008), and are affected by soil compaction in silviculture environments (Ward *et al.* 2011). In this context, bushfires and prescribed burns are likely to have inordinate interactive or cumulative impacts on fauna by decreasing the protective functions of grass-trees as habitat.

Materials and methods

Study sites

Xanthorrhoea semiplana represents a prevalent mid-stratum habitat in the Mount Lofty Ranges of South Australia

(Armstrong *et al.* 2003), where this study took place in 2005 (Fig. 2). We worked at four sites: (1) Deep Creek National Park (Deep Creek); (2) Scott Creek Conservation Park (Scott Creek); (3) Para Wirra Conservation Park (Para Wirra); and (4) Warren Conservation Park (Warren). Deep Creek (35°39′S, 138°46′E) is located at the southern end of the Fleurieu Peninsula, 100 km south-west of Adelaide. It consists of 4554 ha of sclerophyll open forest and shrubland associations. Two open forest formations are dominated by *Eucalyptus obliqua* and *Eucalyptus fasciculosa*; common understorey species include *Banksia marginata*, *Acacia* spp., *Lepidosperma semiteres*, *Pultenaea* spp, *Hibbertia* spp, and *X. semiplana* (DENR 1997). Scott Creek (35°01′S, 138°71′E,) is located 30 km south-east of Adelaide, and supports 706 ha of native vegetation. *Eucalyptus obliqua*, *Eucalyptus cosmophylla*, and *Eucalyptus baxteri* are the dominant overstorey (Schram 1986); common understorey species are similar to those detailed for Deep Creek. Para Wirra (34°43′S, 138°48′E) is located 40 km north-east of Adelaide and covers 1409 ha. Nearby, Warren (34°44′S, 138°54′E) covers 365 ha. Both Para Wirra and Warren support low open *E. obliqua* forests over common understorey plants of *Acacia pycnantha*, *X. semiplana*, *Hibbertia exutiacies*, and *Pultenaea largiflorens* (DEP 1991). All study sites are characterised by a Mediterranean climate with warm dry summers and cool wet winters (Table 1).

Temperature under the canopy of grass-trees

At all four study sites, we measured temperature on the ground under single grass-trees ($n = 12$), which had canopies that were dense enough to cover at least 50% of the ground and were all located on the same slope and aspect. In winter at Warren $n = 10$ and at Scott Creek $n = 11$ because some data
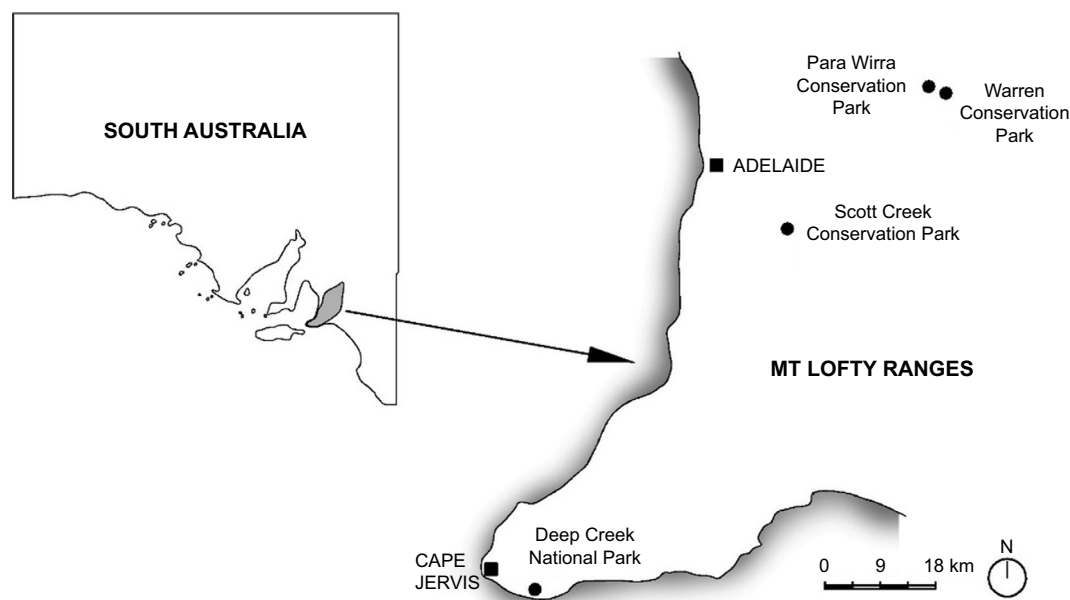

Fig. 2. Location of the study sites in South Australia.

Table 1. Mean monthly maximum and minimum temperatures and mean monthly rainfall at three weather stations near the sites: Parawa (station 023875) near Deep Creek for 1994–2021; Mount Barker (station 023733) near Scott Creek for 1861–2021 (1862 start for temperature minima and 1863 start for temperature maxima); Mount Crawford (station 023733) near Para Wirra and Warren for 1994–2021 (Bureau of Meteorology 2022a).

	January	February	March	April	May	June	July	August	September	October	November	December	Average annual	Number of years included
Parawa														
Mean maximum temperature (°C)	23.8	23.2	21.2	18.3	14.9	12.4	11.7	12.5	14.6	16.9	19.6	21.9	17.6	28.0
Mean minimum temperature (°C)	13.8	13.9	13.0	11.3	9.6	7.7	7.0	7.0	8.0	9.0	10.7	12.1	10.3	28.0
Mean rainfall (mm)	27.9	30.8	33.2	56.2	97.0	122.4	126.6	103.9	81.8	61.2	40.9	36.0	827.0	26.0
Mount Barker														
Mean maximum temperature (°C)	27.3	26.8	24.7	20.5	16.6	13.8	13.0	14.3	16.6	19.6	22.7	25.2	20.1	120.0
Mean minimum temperature (°C)	12.0	12.0	10.5	8.4	6.8	5.3	4.6	5.0	5.9	7.3	9.0	10.5	8.1	121.0
Mean rainfall (mm)	26.0	25.9	30.9	57.7	87.3	100.0	107.3	102.5	85.2	65.6	39.8	34.9	763.4	159.0
Mount Crawford														
Mean maximum temperature (°C)	27.7	26.9	23.5	19.4	14.9	11.7	11.0	12.3	15.2	18.3	22.4	25.2	19.0	27.0
Mean minimum temperature (°C)	14.0	14.1	12.2	10.6	8.6	6.5	5.9	6.1	7.3	8.5	10.7	12.2	9.7	27.0
Mean rainfall (mm)	23.1	25.8	26.9	43.8	68.6	85.8	96.8	87.0	71.2	47.1	33.7	33.0	651.9	25.0

loggers failed to record. We also measured ambient temperature in the shade and the ground temperature 2 m away from each grass-tree, in a random direction. These points away from the grass-trees were either on bare ground or under other understorey shelter.

We sampled temperature once each in summer and winter, when expected diurnal temperatures in summer were above 35°C, and below 13°C in winter. Temperature was recorded every 2 h over a 24-h period, in time intervals beginning at 08:30 hours. At each grass-tree in summer, we placed an alcohol thermometer (−10°C to 60°C; accuracy ± 0.5°C) on the ground under a dense section of the grass-tree canopy that appeared to provide good cover for vertebrate wildlife, and another at a random point 2 m away selected by spinning a compass dial. We also recorded ambient temperature in the shade (other than that provided by a grass-tree) during the same period. In winter, we used Hygrochron iButtons DS1923 (Dallas Semiconductor Corp., range from −20°C to 85°C, accuracy ± 0.5°C) instead of thermometers, but followed the same procedures. We calculated the mean temperatures for the 12 (or 10 or 11) grass-trees at each time interval. We also calculated the largest difference in mean temperature between ambient and grass-tree, and 2 m away and grass-tree for each site, the temperature range for grass-trees, ambient, and 2 m away, and plotted the temperature data. As a result of the loss of most of the raw data files after compilations of the means, we are unable to present the standard errors other than for Scott Creek in winter. However, these Scott Creek data show very small standard errors. Such small standard errors also appear in Keppel *et al.* (2017) for grass-trees in summer and Waudby and Petit (2017) for soil cracks in summer, indicating that similar shade types are associated with similar temperatures in the same environment at the same time. We are thus confident that means are fair representations of temperatures. To determine how grass-trees may buffer animals against cold in winter and heat in summer, we compared the maximum differences between the mean temperatures under grass-trees and ambient temperatures at the four sites each season, and did the same with 2-m away temperatures (night in winter, day in summer; see Supplementary Table S1). We used a paired *t*-test because this test is robust at extremely small sample sizes (de Winter 2013). SPSS (IBM Corp. 2021) was used for all statistical analyses, and we calculated effect size as recommended by Field (2013). The ranges of temperatures in the three different conditions were compared with repeated-measure ANOVA and Bonferroni *post-hoc* tests, with partial eta squared (ηp^2) indicating effect size. Temperature stability increases as the range in temperature decreases.

Soil examination during and after rainfall under grass-tree skirts

We examined the soil under *X. semiplana* ssp. *semiplana* at Scott Creek Conservation Park in June 2005. It was the wettest June between 2001 and 2021 at Longwood Alert

station (023108), 5.5 km away. It rained a total of 227.4 mm for the month compared to a June mean of 127.3 mm over the 20 years of operation of the station (Bureau of Meteorology 2022c). The study took place after it had rained 141.8 mm over 13 days and during heavy rainfall (Bureau of Meteorology 2005). East of the Bandicoot Track (Gate 3), we walked along a transect line, stopping every 10 m to sample the nearest *X. semiplana* until we had sampled 60 individuals, 20 in each canopy cover category: 0 (<50% of the ground covered by the canopy), 1 (50–90% of the ground covered), and 2 (>90% of the ground covered; after Frazer and Petit 2007). If we had already sampled 20 grass-trees of a particular canopy cover, and the nearest grass-tree to be measured at the 10-m point had the same canopy cover, we measured the next closest grass-tree in another canopy cover category. At each grass-tree, we parted the canopy and gave the soil under the canopy a score of 0 (dry, will sift through fingers when scooped; no moist clump), 1 (partially dry with wet areas; wet clumps present when soil is scooped), or 2 (saturated). We tested the independence of canopy cover and soil dryness with a two-way chi-squared test; Cramer's V indicated effect size. We also scored the soil at a randomly selected point 5 m away.

Results

Summer temperatures over 24-h periods under grass-trees

Grass-trees had a large mitigating impact over hot summer temperatures. Over the 24-h period, the mean temperature range under grass-trees was smaller at Warren, Scott Creek, Deep Creek, and Para Wirra, respectively (4.6, 2.4, 1.8, and 3.8°C; overall = 3.1°C ± s.e. 0.6) than it was for 2 m away (27.3, 11.7, 16.9, and 27.3°C; overall = 20.8°C ± s.e. 3.9) and ambient (16.0, 20.0, 14.0, and 19.0°C; overall = 17.3°C ± s.e. 1.4; $F_{2,6}$ = 16.35, P = 0.004, ηp^2 = 0.845, Bonferroni difference only between grass-trees and 2 m away, P = 0.041 and grass-trees and ambient, P = 0.007; Figs 3 and 4). The largest mean temperature differences between 2 m away and grass-trees, and ambient and grass-trees, respectively, were: 19.8 and 8.9°C (Warren), 10.9 and 19.7°C (Scott Creek), 15.2 and 14.1°C (Deep Creek), and 19.0 and 13.7°C (Para Wirra). The largest mean difference between grass-tree canopy and ambient temperatures in summer was significant (mean = −14.1°C ± s.e. 2.2; t_3 = −6.38, one-tailed P = 0.004), with a strong effect size of 0.965. The largest mean difference between temperatures under grass-tree and 2 m away was even more dramatic (mean = −16.2 ± s.e. 2.0; t_3 = −7.96, one tailed P = 0.002; effect size = 0.975).

Winter temperatures over 24-h periods under grass-trees

In winter, grass-tree canopies also provided more stable temperatures than did other areas, but the differences were

not as large as they were in summer. At Warren, Scott Creek, Deep Creek, and Para Wirra, respectively we measured mean temperature ranges under grass-trees of 0.7, 4.9, 3.9, and 2.1°C (overall = 2.9°C ± s.e. 0.9), compared to 1.4, 9.7, 10.2, and 5.4°C for 2 m away (overall = 6.7°C ± s.e. 2.1), and 1.5, 8.0, 7.0, and 3.0°C (overall = 4.9°C ± s.e. 1.6) for ambient (Figs 3 and 4). Although the difference among conditions is significant ($F_{2,6}$ = 9.13, P = 0.015, ηp^2 = 0.753), pairwise comparisons are not, possibly because of the conservativeness of the Bonferroni test and the small sample size. At these sites, the largest mean temperature differences between grass-trees and 2 m away were 1.2, 2.5, 3.0, and 3.0°C, and they were 0.8, 3.4, 2.5, and 2.6°C between grass-trees and ambient. Conditions were warmer under grass-trees during the night. The largest difference between mean temperature under grass-trees and ambient temperature was significant (mean = 2.3°C ± s.e. 0.5; t_3 = 4.24, one-tailed P = 0.012; effect size = 0.926), as was that between temperature under grass-trees and temperature 2 m away (mean = 1.8°C ± s.e. 0.4; t_3 = 4.35, one-tailed P = 0.011; effect size = 0.929).

Sampling of soil during and after heavy rainfall

Grass-tree canopy cover and soil dryness were strongly associated (χ^2_4 = 67.88, P < 0.001; Cramer's V = 0.752), with z-scores indicating the significant superiority of canopy cover 2 (>90%) in keeping the soil dry, and the significantly better performance of canopy cover 1 over canopy cover 0 as well. During and after heavy rainfall, 80% of *X. semiplana* individuals with a canopy cover of 2 provided completely dry conditions under the trees, where the soil was dry to touch. In contrast, grass-trees that had a canopy cover of 0 provided no protection from rainfall and the soil was always saturated at the base of the tree. As for grass-trees with a canopy cover of 1, the majority (65%) had partially dry soil; the soil was driest close to the trunk and became more saturated at the edge of the canopy. Another 25% of these kept the soil completely dry, and 10% had saturated soil. Soils at the location 5 m away were predominantly saturated despite the presence of other understorey vegetation; the 3% recorded as partially dry were under large specimens of wire rapier-sedge (*Lepidosperma semiteres*) (Table 2).

Discussion

Microclimate under grass-trees

This study demonstrated that the area under a thick *X. semiplana* ssp. *semiplana* canopy provides a remarkably stable temperatures in both winter and summer (Figs 3 and 4). In winter, grass-trees moderated cold extremes, with a smaller range of mean temperatures than found in other conditions, as determined also by Swinburn *et al.* (2007) for *Xanthorrhoea*
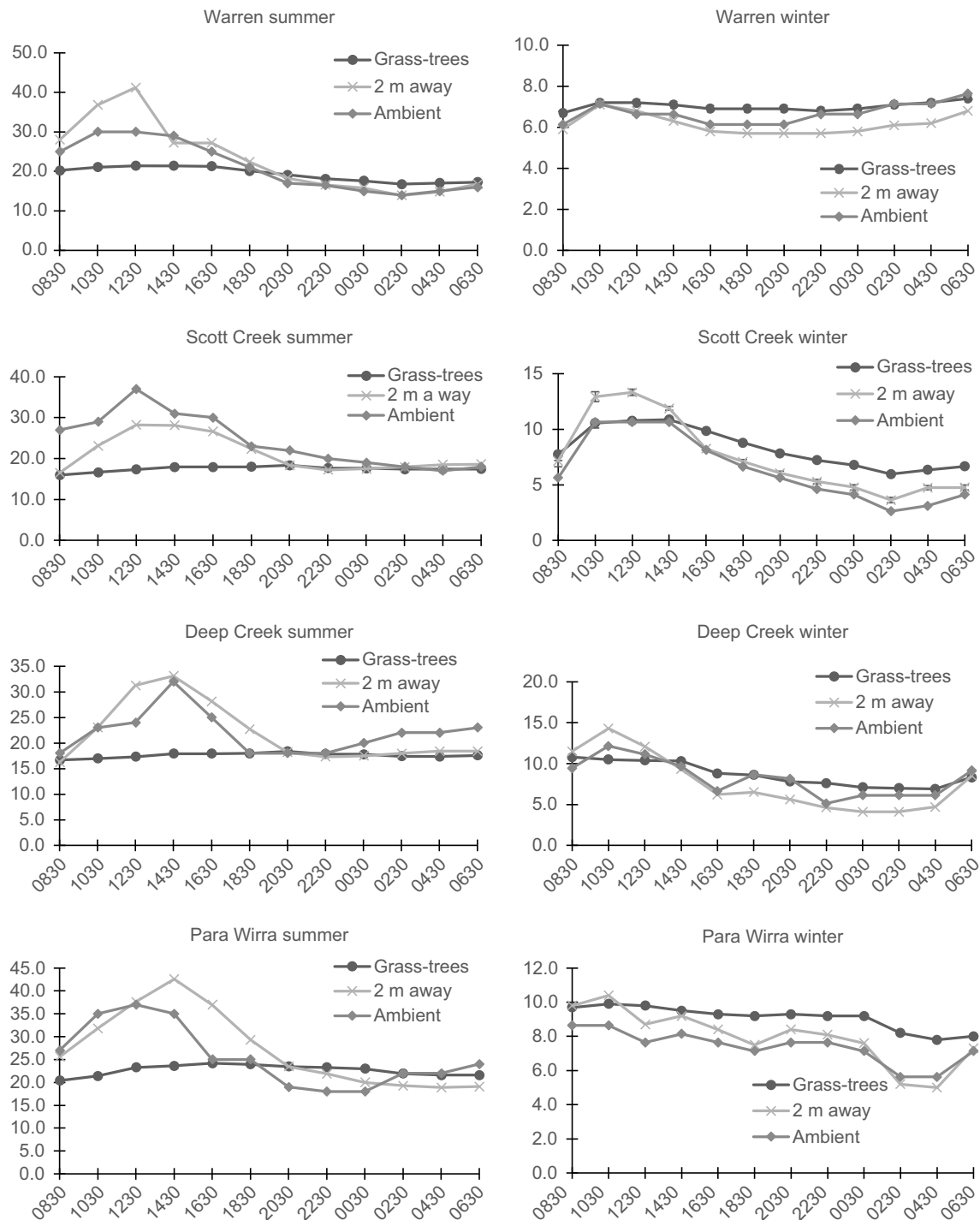
Fig. 3. Mean temperatures under grass-trees ($n = 12$, except for Warren in winter ($n = 10$) and Scott Creek ($n = 11$)), at random positions 2 m away, and in the shade (ambient) for 24-h periods in winter and summer at Warren Conservation Park, Scott Creek Conservation Park, Deep Creek Conservation Park, and Para Wirra Recreation Park. Standard errors are shown only for Scott Creek in winter (see text).

preissii. The mean of the largest difference in temperature between grass-tree and ambient for all sites was 2.3°C, representing a significant difference, which may be consequential to determine animal activity. The difference was lower between grass-trees and 2 m away, since there was a chance that some of the 2-m away temperatures could have been taken under some protection from vegetation, but it still showed a slightly higher temperature under grass-trees
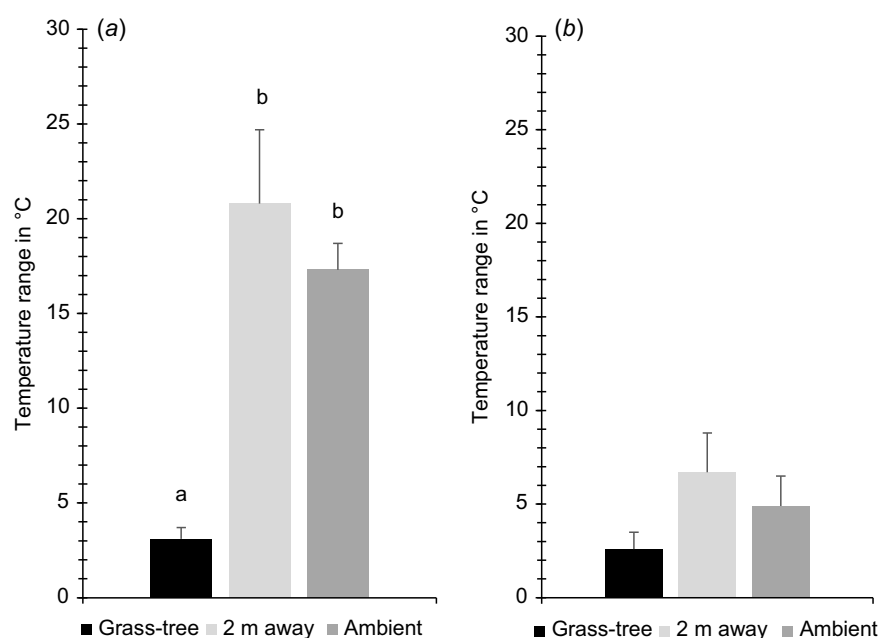
Fig. 4. Mean temperature ranges at the four parks studied (Warren Conservation Park, Scott Creek Conservation Park, Deep Creek Conservation Park, and Para Wirra Recreation Park) under the canopy of grass-trees *Xanthorrhoea semiplana* ssp. *semiplana*, at random locations 2 m away, and in the shade (ambient) in (*a*) summer and (*b*) winter. Although the differences among locations are significant overall for each season, pairwise comparisons are not for winter (see text).

Table 2. Soil condition under *Xanthorrhoea semiplana* plants with canopy covers of 0 (<50% of the ground covered by the canopy), 1 (50–90% of the ground covered), and 2 (>90% of the ground covered; after Frazer and Petit 2007) and random locations 5 m away (*n* = 60) after 13 days of, and during heavy rainfall at Scott Creek Conservation Park.

	Percentages of plants and locations 5 m away			
	Canopy cover category			**5 m away**
	2	**1**	**0**	
Soil saturated	0	10	100	96
Soil partially dry	20	65	0	3
Soil dry	80	25	0	0

(1.8°C on average). Torpor below and above minimal body temperature in animals is costly (Geiser and Broome 1993), and it is possible that the stability in temperature offered by grass-trees facilitates the maintenance of torpor in some species. Certainly, the protection of animals in torpor from predators would be enhanced by grass-trees. Species that do not use torpor could also benefit from the cover of thick skirts, the effect of which could be studied in the field with a warm animal body mimic.

The buffering role of grass-trees was strong in summer, with a maximum range for mean temperatures of 4.6°C (Warren), in comparison to random locations (27.3°C: Warren, Para Wirra) and ambient conditions in the shade (19.7°C: Scott Creek). The fact that the mean temperature at the hottest time of day for 12 grass-trees could be ~20°C lower under the grass-trees than in other shade points at their extraordinary value as shelters. For the times of largest mean differences between grass-tree and ambient temperatures for

all sites, we found a mean of – 14.10°C, which demonstrates the likely contribution of grass-trees to the survival of several animal species. This difference calculated for 2 m away reached – 16.23°C, with mean potentially lethal temperatures at Warren and Para Wirra of 41.2 and 42.6°C, respectively, whereas mean temperatures under grass-trees at those sites were 21.4 and 23.6°C. Likewise, Keppel *et al.* (2017) found a significant impact of grass-trees in moderating high temperatures, compared to ground-below-canopy sensors. Our results cannot be compared directly to theirs because methods differed, and although they did not specify the subspecies of grass-tree, it appears from a figure that they were using *Xanthorrhoea semiplana* ssp. *tateana*. It would be interesting to compare the performance of the two subspecies, which vary in growth form, with *X. semiplana* ssp. *tateana* growing elongated stems as they age.

The Adelaide Hills and Mount Lofty Ranges are sometimes subjected to temperatures >40°C in summer. For example, Mount Crawford Bureau of Meteorology Station 023878, close to Para Wirra and Warren, the temperature reached 43.7°C in January 2019 and 42.0°C in December 2019 (Bureau of Meteorology 2022b). An increase above thermoneutral temperature can cause cognitive impairment (Soravia *et al.* 2021) and be lethal to ectotherms (e.g. Spellerberg 1972) and endotherms (e.g. Ikonomopoulou and Rose 2003). Maximum body temperatures in the few small marsupial species studied were in the 38–40°C range (McKechnie and Wolf 2019). Some Australian mammals avoid high ambient temperatures by sheltering in burrows during the heat of the day (Collins 1973; Walsberg 2000; Waudby and Petit 2017), but selecting appropriate shelters to escape hot weather extremes is particularly important for small mammals that do not normally burrow, such as Peramelidae (bandicoots and bilbies),

Portoridae (potoroos and bettongs), and short-beaked echidnas (*Tachyglossus aculeatus*). We observed the entrance of vertebrate burrows hidden under the skirts of grass-trees. Echidnas radio-tracked at Warren Conservation Park sought shelter under grass-trees and in rabbit warrens (Feuerherdt 2002; L. Feuerherdt and S. Petit, unpubl. data). In Robinson's (1954) experiments, the echidna was unable to thermoregulate at a temperature of 35°C and the southern long-nosed bandicoot (*Perameles nasuta*) could not endure prolonged periods at 40°C, although Brice *et al.* (2002) showed that in Western Queensland echidnas tolerated ambient temperatures of 35–40°C in the field and Barker *et al.* (2016) confirmed evaporative water loss above thermoneutrality in *Tachyglossus aculeatus acanthion*. The eastern barred bandicoot (*Perameles gunnii*) had difficulty thermoregulating above 30°C (Ikonomopoulou and Rose 2003). Seven out of eight bandicoot species have become extinct in South Australia, leaving the last one as the focus of great conservation concern. The Endangered southern brown bandicoot was observed to nest in a cluster of grass-trees at Scott Creek Conservation Park. It also sought shelter from the radio-tracker under grass-trees and foraged in a creek line with dense grass-trees (Frazer 2005). Although these observations took place in winter, they indicated that bandicoots used grass-tree habitat there, as they did in other studies (Paull 1993; Haby *et al.* 2013; Robinson *et al.* 2018).

We did not establish the impacts of grass-trees on humidity in summer, but *X. preissii* with skirts offered a higher and more stable relative humidity than did recently burnt ones in winter (Swinburn *et al.* 2007). Grass-trees may affect evaporative water loss as do burrows (e.g. Bulova 2002), and additional research would need to establish how grass-trees may minimise this loss in summer for different local species. Keppel *et al.* (2017) showed that at a time when relative humidity was <10% away from a grass-tree on the Fleurieu Peninsula in summer, it remained above 40% under the grass-tree, although Walsberg (2000) indicated that absolute humidity is a better index, because it sets the gradient for evaporative cooling. The risk of desiccation is associated with spatiotemporal patterns of air humidity (Rozen-Rechels *et al.* 2019), and humidity should be considered in future studies that examine the role of shelter plants. Air moisture under grass-trees may be critical for some animals to survive very high temperatures, since it reduces water loss in animals, which normally benefit from humidity inside burrows (Schmidt-Nielsen and Schmidt-Nielsen 1950).

Protection from rainfall

A crucial role of grass-trees in winter comes from the extraordinary capacity of the large specimens to keep the soil conditions completely dry in torrential rainfall, and undoubtedly protect animals from the wind as well. The largest, and presumably oldest, grass-trees with canopy covers of 2 provided completely dry shelter in 80% of cases, and performed significantly better than did the other categories of 0 and 1.

Experiments conducted on cold and wet sheep showed a dramatic increase in plasma cortisol concentration before the final phase of hypothermia, accompanied by cardiac insufficiency (Panaretto and Vickery 1970, 1971). Such experiments have been mostly conducted on livestock, and we assume that small wildlife will seek shelter during downpours, considering potential impact of wetting on thermal protection (Webb and King 1984). The disappearance of grass-trees could limit dramatically the protection from wetness normally afforded to small ground-dwelling animals.

Grass-tree conservation in view of their role as shelters

Many vertebrates and invertebrates will use soil cracks, burrows, and other structures such as caves and rock crevices to avoid lethal temperatures or heavy rains. However, few plants other than those bearing hollows (e.g. Gibbons *et al.* 2002), some sedges (e.g. Happold 1976), and other dome-shaped plants (e.g. *Triodia* spp., Bell *et al.* 2021) can perform the same functions as those of grass-trees, and deliver with their foliage the remarkable stability of temperatures and waterproofing quality demonstrated for *X. semiplana* ssp. *semiplana*. Grass-trees with trunks and dense skirts also offer the benefit of a more stable microclimate than may be found away from the canopy (Swinburn *et al.* 2007; Keppel *et al.* 2017).

The availability of thermally appropriate microhabitats combined with concealment is potentially a major limiting factor affecting animal survival in degraded ecosystems, such as the Hills and Fleurieu region of Adelaide, where 41% of mammal species have already become extinct (Landscapes South Australia Hills and Fleurieu 2022). Considering the extremely high value of grass-trees as shelters for wildlife, it is likely that their availability may also affect foraging times of animals, with implications for predation.

The slow growth rate of grass-trees (e.g. Lamont *et al.* 2004 cited stem growth rates from 5 mm to 50 mm per year depending on species and condition) and the increasing value of the shelter they provide as they age make them particularly important to conserve. Although the resilience of some grass-tree species to bushfires is well known (e.g. Lamont *et al.* 2000), it may be overestimated by some. Starch loss may reduce resprouting success after fires depending on season (Korczynskyj and Lamont 2005). Tozer and Keith (2012) demonstrated that a single fire interval of 17 years resulted in the local extinction of *Xanthorrhoea resinosa*. Curtis (1998) showed that prescribed burning, which is now widely undertaken in South Australia, had a long-term deleterious impact on large *X. australis*. It also reduces tree hollow availability (Flanagan-Moodie *et al.* 2018) and could compound habitat loss. Southern brown bandicoots, vulnerable to predation after fires, established nests in dense eucalypt regrowth in New South Wales, when *Xanthorrhoea* spp. had been burnt and were unavailable (MacGregor *et al.* 2023);

although the comparison of grass-tree and eucalypt regrowth canopy was not made, the latter is more open and likely to be inferior to that of grass-trees. The re-establishment of large skirts of dry leaves is a very slow process for *Xanthorrhoea* species. Skirt burning of *X. semiplana* ssp. *tateana* is undertaken by some landholders on Kangaroo Island because they fear that the grass-trees will carry bushfires. Although some invertebrates may persist even in burning grass-trees (Brennan *et al.* 2011), this practice is likely to have a severe impact on local animal diversity, and we suggest examining how different fire intensities modify the skirts of grass-trees. Swinburn *et al.* (2007) demonstrated the loss of microclimate-stabilising properties associated with the burning of grass-tree skirts.

Long-term negative impacts of *Phytophthora cinnamomi*, a soil fungal pathogen to which grass-trees are particularly sensitive, can be dramatic for both plant and animal communities (Wilson *et al.* 2020). It has resulted in significant declines in grass-trees and associated biodiversity, with little evidence of recovery post infestation (Aberton *et al.* 2001; Laidlaw and Wilson 2003; Lamont *et al.* 2004; Casey 2022). Our recent observations of the spread of the pathogen on Kangaroo Island after the 2019–2020 bushfires are alarming. Soil compaction and its negative impacts on *X. preissii* (Ward *et al.* 2011) also indicate that special care must be taken in silviculture environments.

We recommend evaluating the relevance of grass-tree microclimate, including humidity, to specific animal taxa. The effect of grass-tree skirt availability on foraging times of animals should be examined. We also recommend the study of population dynamics of *X. semiplana* to facilitate its conservation, particularly in relation to the highly detrimental impacts of plant losses due to *P. cinammomi*, and those of fire on the temporal availability of protective foliage.

Supplementary material

Supplementary material is available online.

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