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Deep tree hollows: important refuges from extreme temperatures

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Tree hollows constitute crucial habitats for fauna and can buffer ambient environmental conditions. The latter property should be especially relevant during extreme weather conditions, which are forecast to increase under anthropogenic climate change. We investigated the buffering capacity of *Eucalyptus oleosa* F.Muell. ex Miq. subsp. *oleosa* tree hollows in semi-arid southern Australia for 28 days under a wide range of ambient temperatures. Tree hollows provided more stable microclimates than ambient conditions, maintaining lower temperatures and higher humidity during the day and higher temperatures and lower humidity during the night. Daytime buffering capacity increased slightly with depth and we recorded a maximum buffering of 15.1°C below ambient temperatures. Maximum day time buffering capacity increased at a rate of approximately 0.6°C per 1°C increase in ambient temperature, meaning that maximum buffering capacity was reached during the hottest periods. The high buffering capacity of tree hollows suggests that old trees with deep hollows are important in facilitating the persistence of fauna during extreme weather events. Therefore, protecting old-growth forests and vegetation remnants that are rich in tree hollows is an important strategy for mitigating the impact of climate change on fauna.

Tree hollows provide important habitat for fauna, offering protection from predators and extreme temperatures. They also provide a safe environment for rearing offspring (Sedgeley 2001, Isaac et al. 2008, Bryant et al. 2012). In Australia, about 15% of native vertebrate animal species make use of, or rely upon, tree hollows and clearing of woodlands and forests has contributed to faunal declines, with a third of hollow-using species presently threatened (Gibbons and Lindenmayer 2002). Tree hollows most frequently occur in old and dead trees and their formation is stimulated by external factors, such as fire, disease or insect infestation (Wormington and Lamb 1999, Eyre 2005, Koch et al. 2008, Haslem et al. 2012, McLean et al. 2015). Tree size and species can also affect hollow formation (Inions et al. 1989, Wormington et al. 2003, Rayner et al. 2014).

Hollow microclimate is important for animal species and influences hollow selection by many species including bats, birds, possums and reptiles (Sedgeley 2001, Goldingay 2009, Bryant et al. 2012). The climatic buffering provided by tree hollows is affected by hollow height, opening size and stem size (Isaac et al. 2008). Tree hollows can reduce maximum day temperature by 1.6–2.9°C, and increase night time minimum temperatures by about 2.3°C (Sedgeley 2001, Isaac et al. 2008).

This ability to buffer ambient environmental conditions will become especially important under forecast temperature increases as a result of anthropogenic climate change, with extreme temperature events predicted to increase (IPCC 2013). For example, in semi-arid Australia days with temperatures above 35°C are predicted to more than double, if global warming exceeds 4°C (Braganza et al. 2013). Such extreme weather events can have disastrous consequences for wildlife (Jiguet et al. 2006, Welbergen et al. 2008). While tree hollows are known to provide microclimates that are more stable than ambient conditions (Sedgeley 2001, Scheffers et al. 2014) little is known about their buffering capacity under extreme temperatures.

Here we investigate the buffering capacity of tree hollows in the red mallee, *Eucalyptus oleosa* F.Muell. ex Miq. subsp. *oleosa*, for 28 days during spring in semi-arid southern Australia, with ambient temperatures ranging from about 0–40°C. Using microsensors, we determine the capacity of tree hollows to buffer extreme temperatures and humidity fluctuations. We also investigate, if buffering capacity increases with depth in tree hollows and with increasing ambient temperatures. We expected that temperature and humidity would be more stable inside tree hollows, compared to ambient conditions, and that this stability would increase with depth inside a hollow. We further predicted that buffering provided by tree hollows (the difference between internal and ambient temperature) would increase with ambient temperature because cooler air is heavier, retaining cooler air inside the hollow.

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Methods

The study was conducted at Brookfield Conservation Park (Fig. 1), ~130 km northeast of the city of Adelaide, South Australia (DEH 2005). The study site receives low, reliable winter rainfall and a mean annual rainfall of 248 mm year⁻¹, the minimum at which mallee woodlands occur (Sparrow 1989). Mallee trees are *Eucalyptus* species with reduced height (usually ≤ 8 m), multiple stems and subterranean swellings (lignotubers) composed of stem tissue. Mallee woodlands experience seasonal drought, extreme heat ($> 35^{\circ}\text{C}$) and frequent fires (Burbidge 1950). Five mallee species commonly occur within the Brookfield Conservation Park: *E. gracilis* F.Muell., *E. incrassata* Labill., *E. leptophylla* F.Muell. ex Miq., *E. oleosa* F.Muell. ex Miq. and *E. socialis* F.Muell. ex Miq. (DEH 2005). Prior to protection, parts of the park were used for agriculture and its present mallee woodlands consist of small (< 1 ha), old-growth remnants among a matrix of 60–70 year old regrowth.

Using proximity to pre-determined GPS points, 50 old-growth trees (stems with diameter at breast height (dbh) > 15 cm) were selected in 'chenopod mallee', a vegetation association dominated by *Eucalyptus oleosa* subsp. *oleosa* and *E. gracilis* in the canopy layer and by shrubs in the family Chenopodiaceae in the understory (Sparrow 1989, Haslem et al. 2012). The 50 trees had 126 stems with dbh > 15 cm,

which contained 161 hollows with an opening of diameter ≥ 3 cm². Of these 49 had a hollow with an opening ≥ 226 cm², belonged to *E. oleosa* subsp. *oleosa* and were located in remnant stands of old-growth mallee. These 49 hollows were then ranked using random numbers and the first four that had openings located < 3 m above the ground depth > 40 cm were selected.

The four tree hollows were on different stems of three individuals and varied in dimensions (Table 1). Each hollow was equipped with five microsensors (ibuttons; CS215 CSL; manufacturer: Campbell Scientific Australia Pty. Ltd.), which were programmed to record temperature and humidity every 20 min from 3 October to 3 November 2013. One microsensor was placed externally, just beside the hollow opening in an inverted plastic cup that was insulated with duct tape, to record the ambient conditions. The other four microsensors were placed at 10 cm intervals, starting at a depth of 10 cm inside the hollow. These internal ibuttons were placed into metal tea strainers attached by thread and hung into the hollow in positions not receiving direct sunlight.

Minimum and maximum temperatures were determined for the period of 3–31 October following the protocol of the Australian Bureau of Meteorology (BOM); minimum temperature being the lowest recorded temperature in the 24 h to 9 a.m., and maximum temperature the highest in

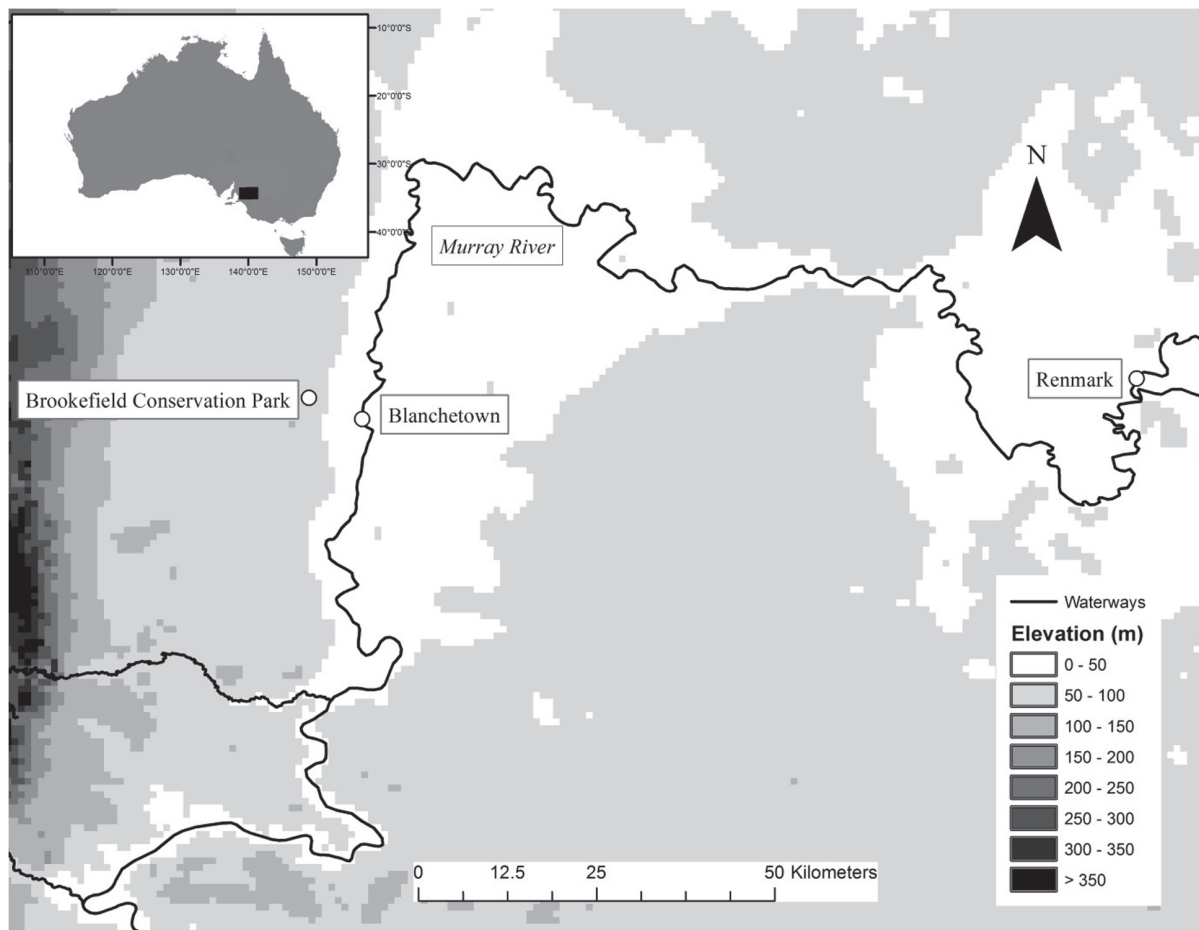


Figure 1. Location of Brookfield Conservation Park and Renmark climate station. The black rectangle in the inset map indicates the location of the larger within Australia.

Table 1. Location, diameter at breast height (dbh) of supporting stem, circumference of opening, depth, internal diameter at the opening, elevation above the ground and aspect for the four tree hollows studied. The distances between the three trees were 1157 m for trees 66–82, 1170 m for trees 82–87, and 2120 m for trees 66–86.

Tree	Location	dbh (cm)	Opening circumference (cm)	Depth (cm)	Internal diameter (cm)	Stem elevation	Aspect (°)
66	34°20'33.9504S, 139°31'24.1284E	41.7	31.5	64	14	100.94	300
82A	34°19'55.3584S, 139°31'26.3964E	36.6	11.8	113	6.5	96.4	240
82B	34°19'55.3584S, 139°31'26.3964E	23.6	10.2	52	25	96.4	180
87	34°19'22.9362S, 139°31'41.7246E	45.2	73.5	56	29	95.67	80

the 24 h from 9 a.m. Temperatures recorded by the external ibuttons were compared to those of the closest weather station (Renmark airport weather station, 34.20°S, 140.68°E, ca 120 km east of Brookfield Reserve; Fig. 1; (BOM 2015).

To determine the buffering capacity, we divided the dataset into night (sunset to sunrise) and day (sunrise to sunset) time temperatures, using sunset and sunrise times from BOM. We used the data sets to determine mean night and day temperatures, and the standard deviation around the mean. We then calculated the mean and maximum buffering provided by tree hollows at different depths by subtracting the temperature of the internal ibutton from that of the external one and disregarding the first hour before and after sunset and sunrise to allow time for equilibration. Hence for each internal sensor, we calculated the diurnal and nocturnal buffering capacity.

To investigate the relationship between maximum buffering and ambient conditions, we regressed the maximum diurnal buffering provided by the four tree hollows at 40 cm depth each day against ambient temperatures. We quantified the strength of the relationship using Pearson's correlation coefficient and determined p-values. Assuming a linear relationship, a line of best fit was added using the method of least squares in Microsoft Excel. The slope of this line provided an estimate of the rate of buffering in relation to ambient temperatures.

Results

Temperature range and reliability of microsensors

Temperatures at the Renmark weather station within the 28 days ranged from 0.1 to 39.7°C, while the ambient temperatures recorded by the external ibuttons ranged from 0.5 to 40.1°C. The daily maximum and minimum temperatures recorded were mostly within 2°C of and strongly correlated ($r^2 > 0.86$, $p < 6.4 \times 10^{-9}$) to those at the Renmark climate station (Supplementary material Appendix 1). Furthermore, an ANOVA test found no significant variation among the daily maximum ($F = 0.15$, $p = 0.93$) and minimum ($F = 0.70$, $p = 0.55$) ambient temperature values for the ambient temperatures of the four hollows. This suggests that values from the external ibuttons provided a reasonable measure of local ambient temperatures. There were differences among the maximum temperatures recorded by external ibuttons, likely caused by differences in microclimate.

Buffering capacity

Tree hollows provided warmer temperatures at night and cooler temperatures during the day (Fig. 2, Supplementary material Appendix 2, 3). Mean buffering during the day was 2.5–4.0°C below average ambient temperatures and

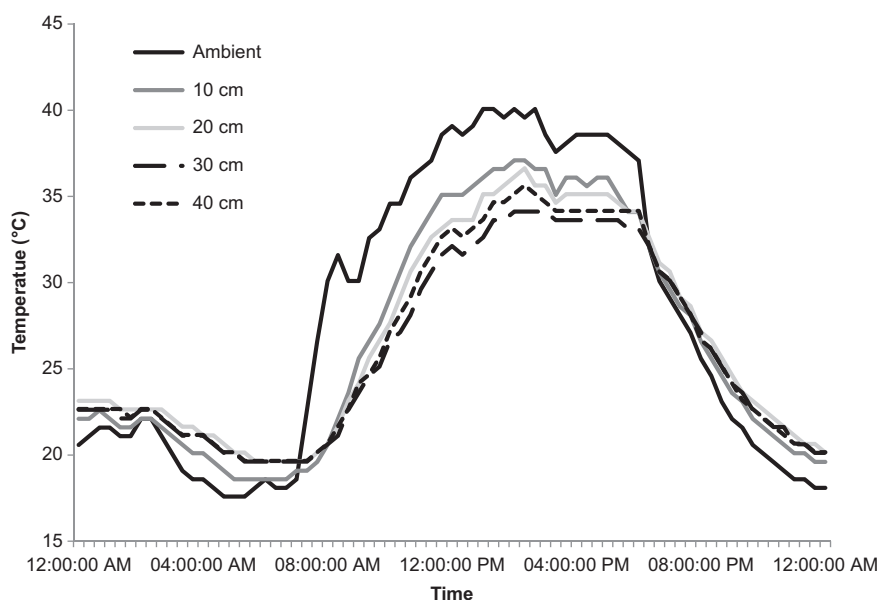


Figure 2. Illustration of daily fluctuations in ambient and hollow (at 10, 20, 30 and 40 cm depths) temperatures for a selected tree (82B) for a 24 h period from 12 a.m., 20, to 12 a.m., 21 October 2013, the hottest day during the study period.

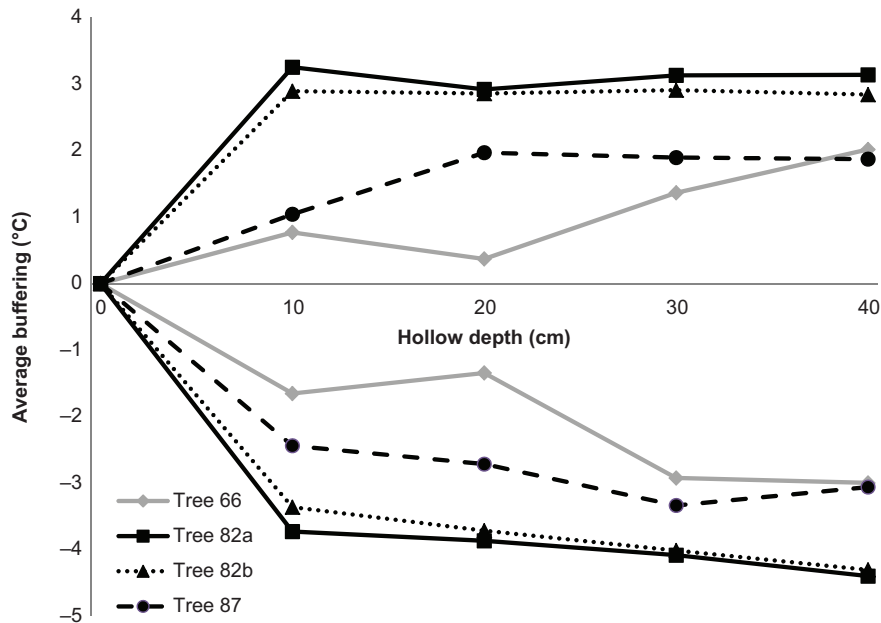


Figure 3. Average buffering provided by tree hollows at different depths during night (positive values above the x-axis) and day (negative values below the x-axis) for 28 days (3–31 October 2013).

increased slightly with depth (Fig. 3). During the night, mean buffering was 2.0–3.2°C above ambient temperatures but did not seem to increase with depth. Similarly, tree hollows retained more stable humidity than ambient conditions (Table 2). Maximum buffering increased with increasing ambient temperatures ($p = 1.8 \times 10^{-3}$), at a rate of about 0.6°C per every 1.0°C (Fig. 4). This rate (as estimated by the regression's slope) ranged from 0.36 to 0.71 (Fig. 4). The maximum buffering recorded was 15.1°C below the ambient temperature recorded.

Discussion

Tree hollows have a high capacity to buffer extreme temperatures. This capacity increases with increasing ambient temperatures. The maximum buffering recorded here greatly exceeds that reported in previous studies for tree hollows and other microhabitats (Sedgeley 2001, Isaac et al. 2008).

Our study corroborates a previously reported increase in day time buffering for tree hollows at a rate of 0.66°C per 1°C increase in ambient temperature (Scheffers et al. 2014). These rates are based on the assumption of a negative linear relationship between maximum buffering and maximum ambient temperature. However, this relationship could also be exponential, with buffering plateauing at higher temperatures.

Day time buffering capacity increases with depth, suggesting that hollow depth plays an important role in determining the maximum buffering a tree hollow can provide. In addition, hollow width, tree diameter and hollow height above ground (possibly related to hollow depth) have previously been identified as important factors affecting hollow microclimate (Isaac et al. 2008). The reason that night time buffering did not display consistent increases in buffering with depth, may be related to cooler, heavier night time air sinking to the bottom of hollows, breaking the thermal stratification within hollows.

Table 2. Mean (for 28 days, 3–31 October 2013) percentage humidity external to and within four tree hollows at different depths (10 cm, 20 cm, 30 cm and 40 cm) during the day (sunrise to sunset) and night (sunrise to sunset).

Tree	Humidity (%)				
	External	10 cm	20 cm	30 cm	40 cm
Day					
66	36.0 (± 19.0)	39.5 (± 20.4)	39.7 (± 20.4)	43.8 (± 20.8)	42.9 (± 20.5)
82A	38.5 (± 21.8)	42.4 (± 21.7)	43.1 (± 21.7)	42.8 (± 21.3)	45.7 (± 21.7)
82B	36.0 (± 20.5)	42.8 (± 21.5)	43.3 (± 21.1)	42.9 (± 21.0)	43.8 (± 21.1)
87	33.8 (± 19.8)	37.3 (± 20.6)	38.3 (± 21.0)	39.3 (± 21.2)	39.8 (± 21.3)
Night					
66	50.3 (± 16.3)	49.0 (± 12.7)	51.4 (± 13.5)	49.2 (± 8.0)	46.5 (± 8.6)
82A	53.9 (± 14.9)	49.0 (± 12.7)	47.9 (± 11.5)	45.9 (± 9.7)	48.1 (± 8.4)
82B	60.5 (± 19.8)	51.4 (± 13.6)	54.6 (± 14.8)	54.7 (± 14.7)	56.0 (± 14.6)
87	57.4 (± 19.0)	53.3 (± 16.4)	51.6 (± 15.4)	51.3 (± 14.7)	52.6 (± 13.8)

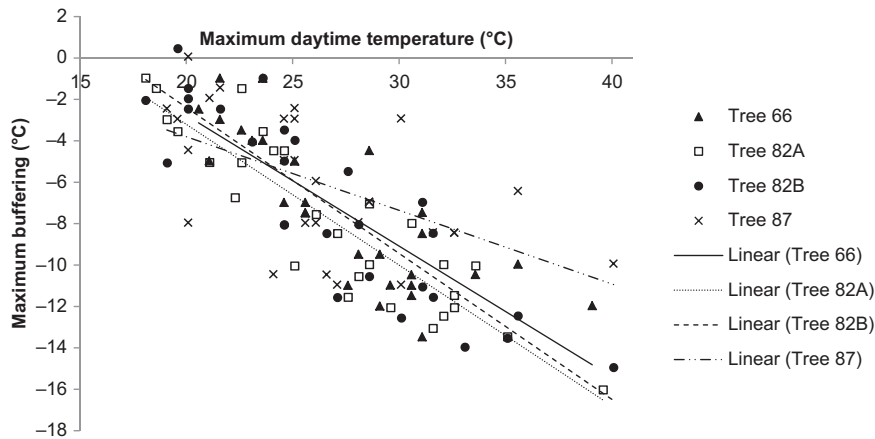


Figure 4. Maximum day time buffering provided by four tree hollows at depth 40 cm in relation to ambient maximum temperatures for 28 days (3–31 October 2013). Note that temperatures below 15°C are excluded from the x-axis, as no maximum daytime temperatures below 18°C were recorded. Assuming and fitting a linear relationship with negative slopes resulted in highly significant Pearson's correlation coefficients (tree 66: $y = -0.632x + 9.867$, $r^2 = 0.80$, $p = 2.7 \times 10^{-7}$; tree 82A: $y = -0.680x + 10.405$, $r^2 = 0.90$, $p = 3.9 \times 10^{-11}$; tree 82B: $y = -0.705x + 11.715$, $r^2 = 0.88$, $p = 5.0 \times 10^{-10}$; tree 87: $y = -0.356x + 3.319$, $r^2 = 0.56$, $p = 1.8 \times 10^{-3}$).

Our findings highlight the importance of tree hollows in mitigating extreme weather events, which are predicted to increase under anthropogenic climate change (IPCC 2013). They support the high value of older, larger, hollow-bearing trees as important refuges for wildlife, and calls to conserve hollow-rich habitats immediately (Gibbons and Lindenmayer 2002, Isaac et al. 2008, Manning et al. 2013). This is especially true in mallee woodlands, where tree hollows take 100 to 400 years to form (Clarke et al. 2010, Manning et al. 2013). In this environment, the formation of deep tree hollows would take even longer, possibly exceeding half a millennium.

Tree hollows and other microhabitats therefore may play an important role in facilitating the persistence of fauna under anthropogenic climate change by mitigating the impacts of extreme events (Shoo et al. 2010, Bryant et al. 2012, Schefers et al. 2014). However, the microclimatic effects created by these refuges are not considered when the impacts of future climate change on animal species are modelled (Vos et al. 2008, Garden et al. 2015), meaning that hollow-using species may have higher resilience to climate change than previously predicted. Therefore, similar to refugia at a larger scale (Ashcroft et al. 2012, Keppel et al. 2012, 2015), tree hollows may have the ability to mitigate the impacts of landscape-level climatic changes. It is therefore important to protect old-growth forests and vegetation remnants that are rich in tree hollows, as these may assist the in-situ survival of fauna under climate change.

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Supplementary material (available online as Appendix wlb-00210 at <www.wildlifebiology.org/appendix/wlb-00210>). Appendix 1–3.