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# Landscape-Scale Impacts of Deer on Tree Ferns in South-Eastern Australia

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## ABSTRACT

Tree ferns (order Cyatheales) are a key component of wet forests globally, providing critical forest understorey structure and ecosystem functions. Tree ferns may be impacted by ungulates in novel habitats, but the extent and severity of these impacts are often uncertain. We aimed to determine the impact of introduced deer on tree ferns in wet forests of south-eastern Australia. Using both broadscale deer abundance and impact surveys and targeted tree fern assessments, we surveyed browsing impacts on tree ferns at over 200 sites across a range of wet forest types in south-eastern Australia where deer are present. Tree fern species, plant height and estimates of foliage biomass removed by browsing were recorded for over 4500 individual tree ferns including 1871 *Cyathea australis*, 2622 *Dicksonia antarctica* and 41 *Todea barbara*. Browsing impacts on tree ferns were recorded at 96% of surveyed sites, with a third to a half of tree ferns typically impacted by browsing at each site. There were no differences in recorded impact between tree fern species. Browsing of tree ferns was strongly height dependent, regardless of species, and associated with indices of deer density. Tree ferns $< 100$ cm were often highly impacted (mean $> 20\%$ foliage browsed), with impact declining approximately linearly with height to 200 cm, typically low 200 to 300 cm, and absent thereafter. The widespread and in many cases severe browsing on tree ferns recorded can be largely attributable to introduced deer. These impacts potentially threaten tree fern populations and diminish the vegetation structure and ecosystem function of these wet forests. Management interventions to reduce deer populations in the wet forests of south-eastern Australia are critical to protect forest integrity and function.

## 1 | Introduction

Tree ferns (order Cyatheales) are a distinctive component of wet forest ecosystems across eastern and south-eastern Australia, and are essential to the function and resilience of these mesic systems (Donoghue and Turner 2022). Tree ferns provide a range of ecosystem functions such as shading and temperature regulation of forest understorey and streams (Johnson 2004; Moore et al. 2005). They are a source of food, nesting materials and nesting sites for native fauna (Hollis et al. 1986; Maisey et al. 2016; Seebeck et al. 1984; Sugden 1988), and create microhabitat conditions with relatively stable temperature, light and moisture levels that are critical to the persistence of some flora species (Ough and Murphy 2004; Volkova et al. 2010). Tree ferns provide a substrate for epiphytic ferns, bryophytes and orchids (Roberts et al. 2005; Floyed and Gibson 2006) and facilitate the germination of a variety of forest understorey seedlings (e.g., banyalla *Pittosproum bicolor*; Royal Botanic Gardens Victoria 2024). The

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dense leaf litter beneath tree ferns also provides important foraging areas for superb lyrebird (*Menura novaehollandiae*; Maisey et al. 2019), which through foraging activities play a significant role in soil turnover, nutrient cycling and carbon sequestration (Maisey et al. 2021).

There are few examples where the impacts of introduced ungulates on tree fern populations have been investigated, and their findings are varied. In New Caledonia, feral pigs (*Sus scrofa*) reduced the growth and survival of tree ferns (Murphy et al. 2014), and in Hawaii, the stem density of young tree ferns increased significantly following the removal of pigs (Cole et al. 2012). In contrast, tree fern species in New Zealand appear to be largely unimpacted by the numerous ungulate species that have been introduced there (including deer and goat; Forsyth et al. 2002; Forsyth et al. 2015), which may be explained by the presence of chemical compounds in New Zealand tree fern species that deter herbivory (Cambie et al. 1961). The exception in New Zealand was a study on Secretary Island, where white-tailed deer (*Odocoileus virginianus*) and common brush-tailed possum (*Trichosurus vulpecula*) caused the loss of *Dicksonia squarrosa* tree ferns 50–200 cm in height through heavy browsing (Mark et al. 1991; Veblen and Stewart 1980).

In Australia, information on the impacts of introduced ungulates on tree ferns is similarly limited (Donoghue and Turner 2022). Several unpublished reports (Claridge 2016a, 2016b) and theses (Bennett 2008; Bowman 2014; Stockwell 2003) have reported deer browsing of tree ferns, and four published articles, each using a different survey technique, present evidence that the large deer species sambar (*Cervus unicolor*) browse tree ferns in Victoria. Peel et al. (2005) describe observations of browsed and dead *Dicksonia antarctica*, *Cyathea australis* and *Cyathea leichardtiana*; Bennett (2023) compared two sites with and without sambar populations and associated the presence of sambar with tree fern browsing; Forsyth and Davis (2011) detected minor amounts of *Dicksonia antarctica* and *Cyathea australis* in sambar rumen contents using macroscopic and microhistological analysis; and Wills et al. (2023) used differential exclosures to monitor deer browsing impacts, and demonstrated ~50% reduced cover of tree ferns in unfenced plots compared to negligible levels in fenced plots that were only accessible by smaller native herbivores.

Using broad-scale field surveys together with targeted surveys of browsing impacts on tree ferns, we aimed to better understand the scale and severity of tree fern browsing by deer across wet forest ecosystems in south-eastern Australia. Specifically, we aimed to understand: (1) how widespread is the browsing of tree ferns by deer? and (2) how does browsing vary with tree fern species and plant height? We also consider the implications of our findings for tree fern populations and the forest ecosystems in which they are found.

## 2 | Method

### 2.1 | Study Area

Our study is located in the Greater Melbourne region, primarily on Wurundjeri Woi-wurrung Country across the north and north-east of the study area, and Bunurong and Gunaikurnai Country to the south and east. Our study sites comprise a variety of widespread tall wet forest types found in south-eastern Australia including Ecological Vegetation Classes (EVC) Wet Forest, Damp Forest, Riparian Forest, Montane Wet Forest and Cool Temperate Rainforest. The region has a temperate climate, with mean maximum temperatures ranging from 6°C to 12°C in July and 20°C to 25°C in January, and mean annual rainfall ranging between 1033 and 1663 mm/year.

### 2.2 | Tree Fern and Deer Species

Three tree fern species were recorded in our surveys: Soft Tree fern *Dicksonia antarctica* Labill., Rough Tree fern *Cyathea australis* (R.Br.) Domin and Austral King-fern *Todea barbara* (L.) T.Moore. All three species have a wide geographic range in Australia, found in wet forested habitats in Tasmania, Victoria and coastal–inland habitats east of the Great Dividing Range in New South Wales and southern Queensland, with *T. barbara* also extending to northern Queensland (Donoghue and Turner 2022). *Cyathea australis* is tolerant of drier conditions than *Dicksonia antarctica*, while *Todea barbara* has a high water requirement and is only found in waterlogged soils along or in shaded watercourses and swamps (Royal Botanic Gardens Victoria 2024). In our surveys, *Dicksonia antarctica* and *Cyathea australis* were widespread, while *Todea barbara* was uncommon. In Victoria, all three tree fern species may be commercially harvested subject to permit conditions (Donoghue and Turner 2022). Our surveys were conducted on public land where commercial harvesting of tree ferns does not occur.

Three introduced deer species occur across the survey area: sambar, fallow deer (*Dama dama*) and red deer (*Cervus elaphus*). Deer are most abundant at forest-agricultural interfaces, where open habitats provide foraging opportunities, and the forest provides cover (Borkowski and Pudełko 2007; Fattebert et al. 2019; Fedrigo et al. 2024). Sambar is considered the most common deer species in the forested habitats we surveyed, although fallow deer are also present. Red deer have a scattered occurrence and are uncommon throughout the survey area.

Sambar are large, weighing 146 to 192 kg (but up to 300 kg; Forsyth et al. 2023). They are solitary or form small family groups, but larger aggregations may occur where forage is abundant (Bennett et al. 2015). Sambar consume a wide variety of food types including trees, shrubs, forbs and ferns (Forsyth and Davis 2011; Parker 2009). Sambar are found throughout eastern Victoria in a variety of habitats, including dense mountainous forests.

Fallow deer are a gregarious medium-sized dimorphic (females 36–56 kg, males 50–110 kg) species, with group size varying seasonally (Mulley 2023). They prefer woodlands or plantations (Chapman and Chapman 1980), although they do use dense habitats in proximity to open areas or pastures. Fallow deer are primarily grazers consuming mostly grasses and forbs (Parker 2009; Guy et al. 2024), but they do browse trees and shrubs (Davis et al. 2023; Guy et al. 2024). Red deer are a large (92–158 kg) gregarious species. They prefer more open habitats where they primarily consume grasses, but will also browse shrubs (Jesser 2023).



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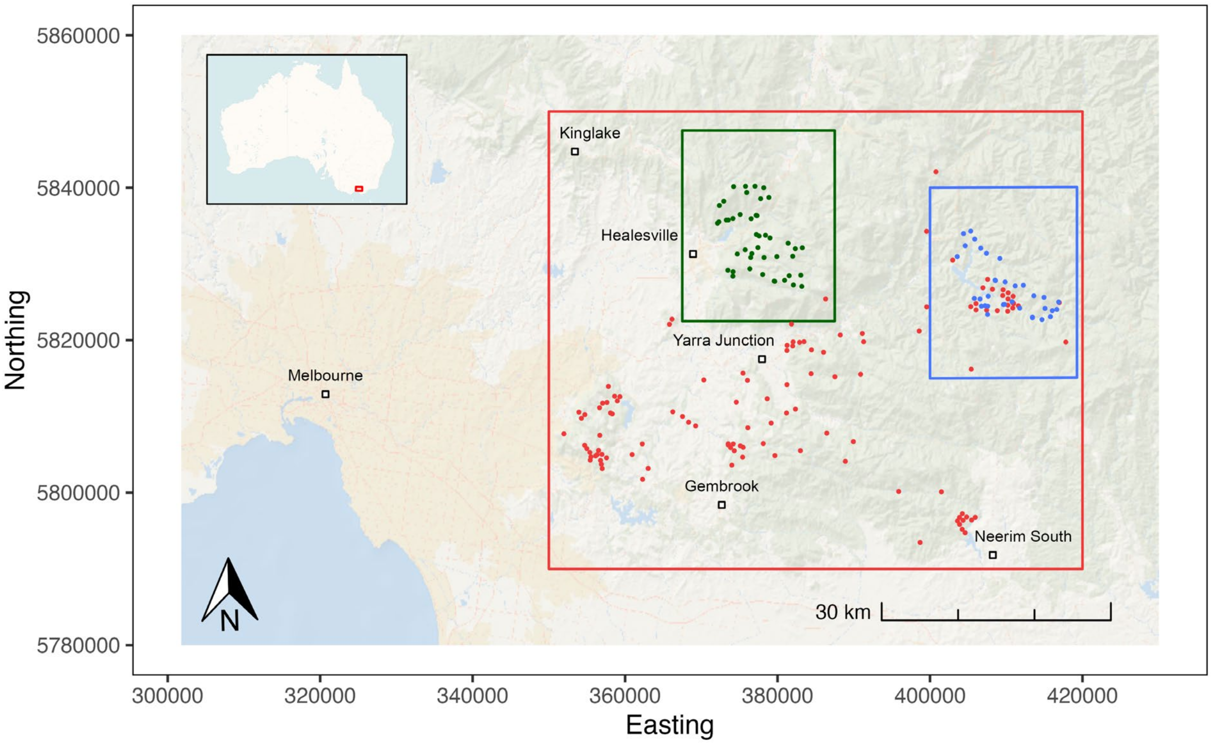


**FIGURE 1** | Location of tree fern browsing impact surveys: Deer abundance and vegetation impact assessments across the Greater Melbourne region conducted 2019–2023 (red), and rapid tree fern impact assessments in Upper Yarra (blue) and Maroondah (green) catchments conducted in 2023, Yarra Ranges National Park, Victoria.

## 2.3 | Field Survey Methods

We used two field survey methods to investigate the impacts of deer on tree ferns. First, we extracted tree fern data from a subset of 298 deer abundance and vegetation impact surveys (Bennett et al. 2022) conducted across the Greater Melbourne region (12 775 km$^2$) over 5 years (2019–2023; Figure 1). The surveys were conducted to inform the development of spatial models of deer density and impact (Fedrigo et al. 2024) and assess deer impact across this landscape (Bennett and Greet 2023, 2024). The second method was developed as an index of deer impact to assess the effectiveness of ground-shooting programmes in the Upper Yarra (33 670 ha) and Maroondah (10 400 ha) water supply catchments in the Yarra Ranges National Park (Figure 1; GHD 2023, 2024). Tree ferns were chosen as an indicator species because they are abundant in these catchments, are known to be impacted by deer in this park (Wills et al. 2023), and due to their unique growth form, can be readily and consistently surveyed.

### 2.3.1 | Landscape-Scale Deer Impact Surveys

The full methods are detailed in Bennett et al. (2022) and are only briefly described here. At each landscape-scale site, we surveyed a 150-m transect to collect information on deer abundance using faecal pellet counts and browsing impact using categorical estimates of percentage live foliage loss or damage to forest understorey trees, shrubs and tree ferns; for tree ferns, this is analogous to percentage of fronds browsed (Table 1).

**TABLE 1** | Scoring method used to estimate level of deer browsing on tree ferns (Bennett et al. 2022).

| Score | Description | |
|---|---|---|
| 0 | No impact | NA |
| 1 | Low impact | 1%–25% fronds browsed |
| 2 | Low–moderate impact | 26%–50% fronds browsed |
| 3 | Moderate–high impact | 51%–75% fronds browsed |
| 4 | High impact | 76%–100% fronds browsed |

Surveys conducted in 2019 to 2020 assessed 120 randomly selected plants on each transect, while surveys from 2021 to 2023 assessed 60 plants on each transect (Bennett et al. 2022). We extracted data on tree fern assessments from 155 transects. In total, this dataset included 3008 tree ferns comprised of three species: 1561 *Cyathea australis*, 1406 *Dicksonia antarctica* and 38 *Todea barbara*.

### 2.3.2 | Targeted Tree Fern Assessments

In total, 79 targeted assessments of deer impact on tree ferns were undertaken during 2023: 34 in Upper Yarra (644



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tree ferns: 417 *Dicksonia antarctica*, 226 *Cyathea australis* and 1 *Todea barbara*) and 45 in Maroondah (886 tree ferns: 800 *Dicksonia antarctica*, 84 *Cyathea australis* and 2 *Todea barbara*).

Each survey consisted of a 50 × 10-m belt transect located close to access tracks beyond any visible disturbance or influence of the road (usually ~10-m). Transects were generally located parallel to a gully or stream where tree ferns are most prevalent and were usually perpendicular to access tracks. Where possible, a total of 20 tree ferns between a height of 50 to 200 cm were sampled along each transect, four within each 10 × 10-m segment of the transect. To remove surveyor bias, tree ferns were selected using the point-centred quadrant method (Cottam and Curtis 1956; Mitchell 2015), where the closest tree fern to the centre point of each segment in each cardinal quadrant (NE, SE, SW, NW) was selected for assessment. Tree fern data recorded included species, height (to top of caudex; tree fern 'trunk'), count of browsed fronds and count of unbrowsed fronds. Dead tree fern fronds and dead tree ferns (no live foliage) were not recorded. Signs of deer activity within the belt transect were also recorded including faecal pellet groups, trails, rubbing, stem breakage, stream crossings, pugging and wallows. Sambar is considered the only species to occur in this National Park.

#### 2.3.3 | Data Analyses

For the landscape-scale survey data, impact scores were first converted to mid-point values (i.e., 0 = 0%; 1 = 12.5%; 2 = 37.5%; 3 = 62.5%; 4 = 87.5%; Table 1), and then averaged at the transect level by tree fern species and across all species. For the targeted tree fern assessments, average values of percentage fronds browsed (count of fronds browsed/total count of fronds) were similarly calculated. We present maps of mean values of percentage fronds browsed across all tree fern species for the different survey areas.

To assess differences in browsing by tree fern species and plant height, we used generalised additive models (GAM) of transect-level means by species for both the landscape-scale and targeted survey data, separately. Both GAM models included terms for species and height, and their interaction, and a random effect for transect; due to small sample size, *T. barbara* was excluded from these models. For the landscape-scale data, we only considered transects with ≥ 3 tree ferns and tree ferns < 300 cm in height because browsing of tree ferns above this height was rare. For the targeted surveys, only tree ferns 50 to 200 cm were surveyed. For each dataset, we present boxplots of percentage of fronds browsed by species and scatterplots of percentage of fronds browsed with GAM fitted lines by species and height.

For both survey methods used for this study, we assessed the relationships between indicators of deer density (i.e., faecal pellet counts and signs of deer activity, respectively) and percentage of fronds browsed recorded at the transect level. For the landscape-scale data, we first converted total faecal pellet counts (FPC) to FPC/$m^2$ based on the total area surveyed for pellets at each transect (i.e., 30 plots $\times \pi \times 1^2 = 94.25\,m^2$). For the targeted surveys, we summed the counts of all signs of deer activity recorded within each belt transect (i.e., total counts of faecal pellet groups, trails, rubbing, stem breakage, stream crossings, pugging and wallows). We used log-linear models to assess relationships between indicators of deer density and percentage of fronds browsed, because browsing impacts by deer have been demonstrated to increase more rapidly at lower levels of deer density (Bennett et al. 2022). We provide $p$-values and $r^2$ values (explained variance) for these models.

All analyses were conducted using the statistical software R (R Core Team 2024).

## 3 | Results

### 3.1 | Landscape Extent of Tree Fern Impacts

For the landscape-scale deer impact surveys, the heights of tree ferns surveyed ranged from 10 cm to 11 m. On average, *Cyathea australis* were tallest at 10 cm to 11 m (mean = 222 ± 4 cm), *Dicksonia antarctica* height ranged from 10 cm to 10 m (mean = 155 ± 3 cm), and *Todea barbara* were shortestat 15 to 130 cm (mean = 52 ± 5 cm).

The mean estimated percentage of fronds browsed was similar for all species: *Cyathea australis*, 11% ± 1%; *Dicksonia antarctica*, 11% ± 1%; and *Todea barbara*, 9% ± 3%. Across all species, tree ferns over 300 cm tall were typically not browsed (Figure 2), so hereafter we consider only tree ferns < 300 cm tall.

Within the landscape-scale deer impact dataset there were a total of 118 sites with 3 or more tree ferns < 300 cm, with browsing of tree ferns widespread, recorded at 113 (96%) of those sites. Across the 118 sites, we surveyed 2204 tree ferns, with a third (33%) impacted by browsing (Figure 3).

There were no significant differences in the level of browsing between species ($p > 0.05$; Figure 4A), with the mean percentage of fronds browsed comparable across species: *Cyathea*

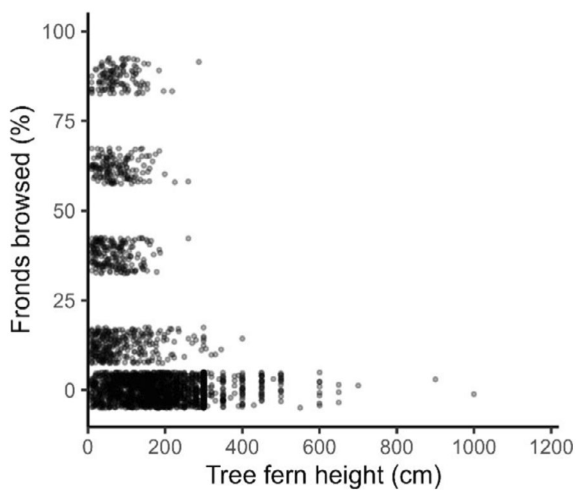


**FIGURE 2** | Browsing impact on tree ferns by height across all species ($n = 3010$ plants).



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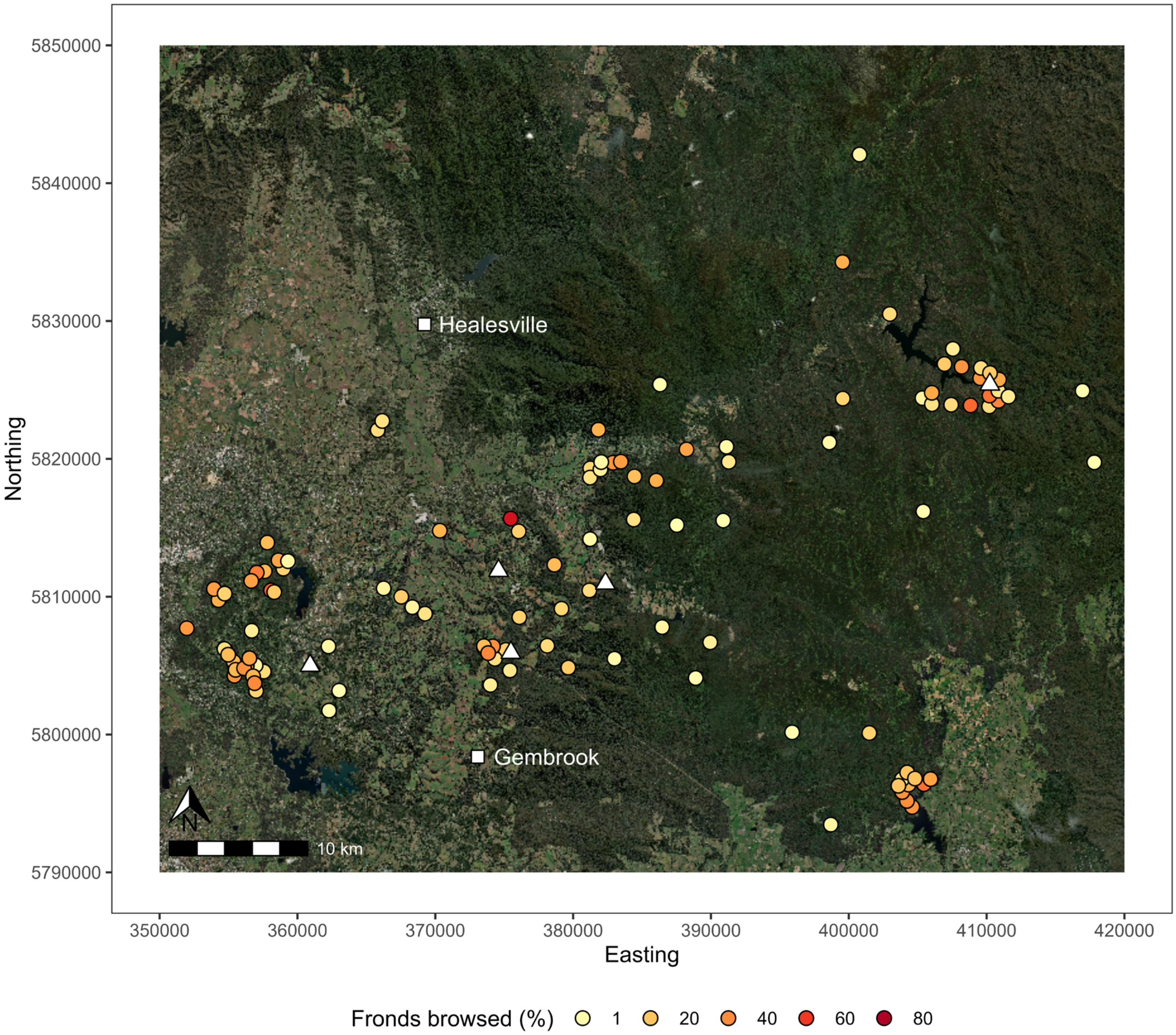


**FIGURE 3** | Sites surveyed with three or more tree ferns indicated by points ($n = 118$), with points coloured according to mean percentage of fronds browsed. White triangles indicate the few sites ($n = 5$) where no browsing of tree ferns was recorded.

*australis*, 17% ± 2% ($n = 95$ transects); *Dicksonia antarctica*, 17% ± 2% ($n = 66$ transects); and *Todea barbara*, 9% ± 8% ($n = 6$ transects).

Browsing of tree ferns was strongly height dependent, regardless of species. Tree ferns < 100 cm were typically highly impacted (> 20% fronds browsed on average); browsing was common but declined with height between 100 and 200 cm, and was typically low (~2% on average, but not always absent) from 200 to 300 cm (Figure 4B).

There was a significant albeit modest association between mean estimated percentage of fronds browsed and deer faecal pellet counts across the 118 sites surveyed ($p < 0.001$, $r^2 = 15\%$; Figure 5A).

## 3.2 | Targeted Tree Fern Surveys

Across the 79 belt transects surveyed using the targeted tree fern impact assessments in the Upper Yarra and Maroondah catchments, only two transects (in Upper Yarra) had no signs of browsing (Figure 6). Some level of browsing was recorded for 54% of the 1526 tree ferns surveyed across all the transects.

Of the 1526 surveyed tree ferns with heights 50–200 cm, 20% had half or more of their fronds browsed. We surveyed 310 *Cyathea australis* (mean height = 106 ± 1 cm; mean % fronds browsed = 26%); 1213 *Dicksonia antarctica* (111 ± 1 cm, 20%); and 3 *Todea barbara* (61 ± 6 cm, 37%). The percentage of fronds browsed was again not significantly different between species ($p > 0.05$; Figure 7A). Similar to the landscape-scale surveys, the percentage of tree fern fronds browsed was strongly height dependent regardless of species, with impacts declining roughly linearly with height between 50 and 200 cm (Figure 7B). There was a significant association between mean percentage of fronds browsed and the sum of signs of deer activity recorded during the targeted surveys across the 79 sites ($p < 0.001$, $r^2 = 27\%$; Figure 5B).

## 3.3 | Incidental Observations

Sambar were occasionally captured consuming tree fern fronds on camera traps (Figure 8A). A small proportion of surveyed



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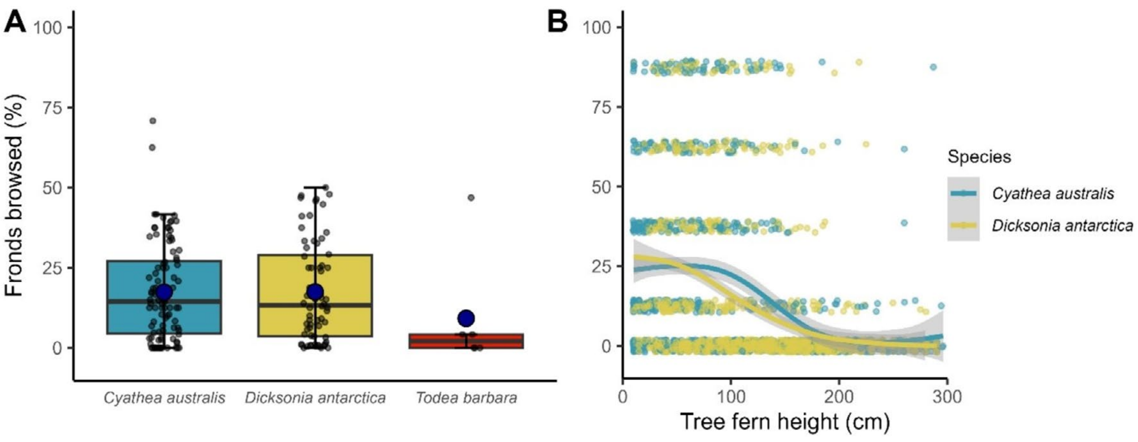


**FIGURE 4** | Percentage of tree fern fronds browsed by (A) species, and (B) species and height. Boxplots, raw data (grey points) and means (large blue point) shown in (A). Raw data and GAM fitted lines for *Cyathea australis* (blue line) and *Dicksonia antarctica* (yellow line) shown in (B). N.B. *Todea barbara* excluded from (B) due to a lack of data.

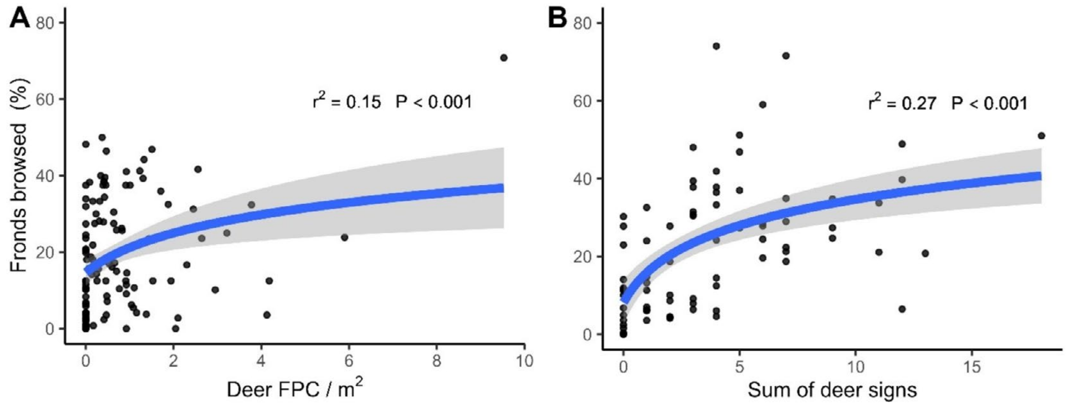


**FIGURE 5** | Relationships between tree fern browsing (%) and (A) deer faecal pellet count (FPC/$m^2$) surveyed during landscape-scale surveys ($n = 118$ sites); and (B) sum of deer signs observed during targeted tree fern surveys ($n = 79$ sites). Fitted log-linear lines (blue lines with CIs indicated by greyed areas) presented for the respective relationships between the indicators of deer density and percentage of fronds browsed.

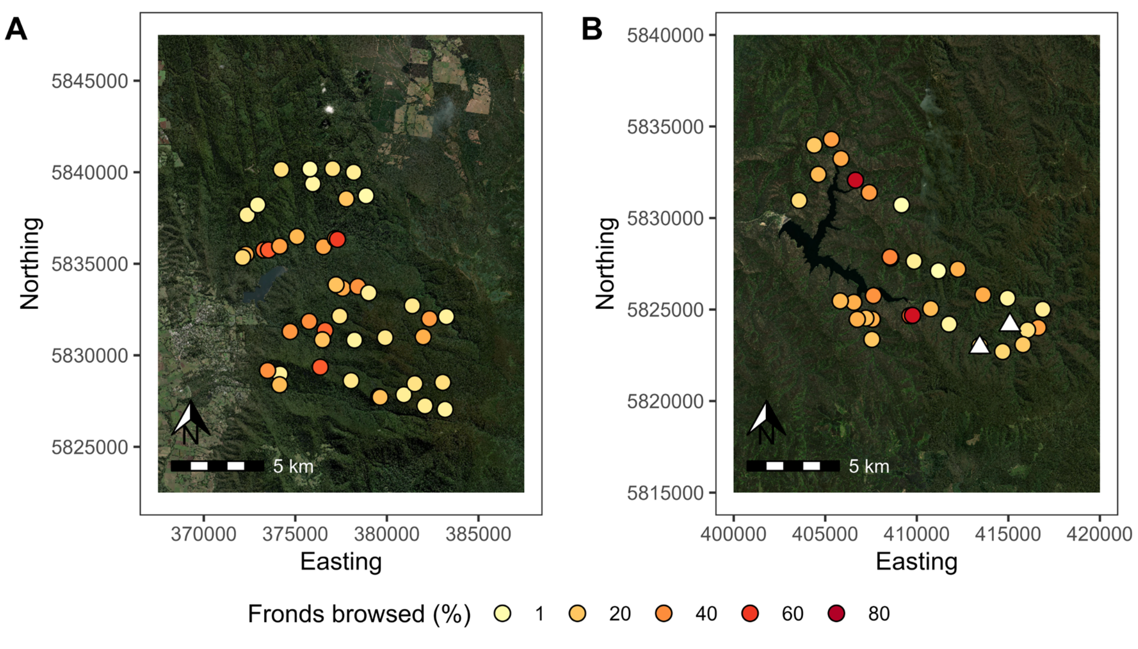


**FIGURE 6** | Sites surveyed using rapid tree fern assessment at (A) Maroondah ($n = 45$), and (B) Upper Yarra ($n = 34$), indicated by points with points coloured according to mean percentage of fronds browsed. White triangles indicate the few sites ($n = 2$) where no browsing of tree ferns was recorded.



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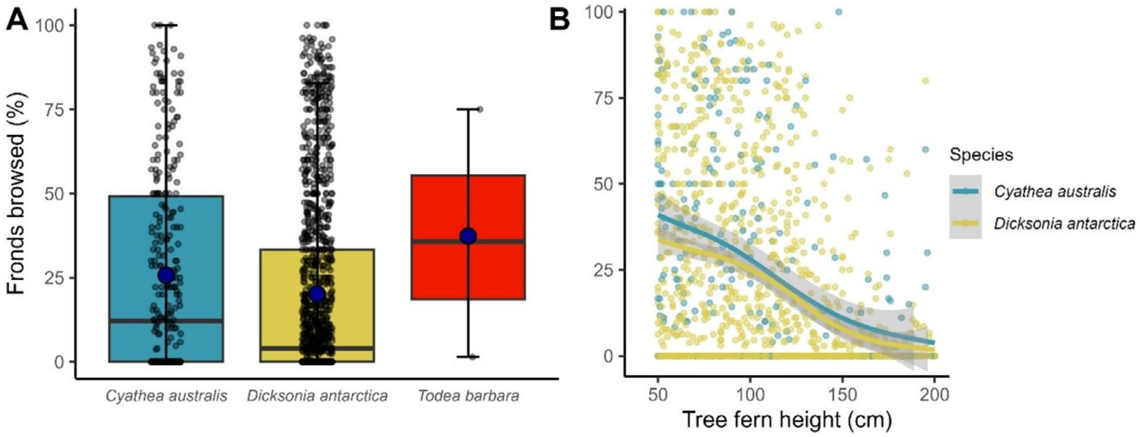


**FIGURE 7** | Percentage of tree fern fronds browsed by (A) species, and (B) species and height. Boxplots, raw data (grey points) and means (large blue point) shown in (A). Raw data and GAM fitted lines for *Cyathea australis* (blue line) and *Dicksonia antarctica* (yellow line) shown in (B). N.B. *Todea barbara* excluded from B) due to a lack of data.


**FIGURE 8** | (A) sambar browsing on a *Cyathea australis* frond in the Upper Yarra catchment (B) severely browsed *Cyathea australis* (C) dead short (< 2 m) tree ferns commonly observed throughout surveys—the cause of these deaths is uncertain, but repeated deer browsing is considered likely to have been a contributing factor.

tree ferns had up to 100% of fronds browsed (Figure 8B), but we also observed patches of similar-sized tree ferns that had all been 100% browsed. Live tree ferns that were observed in poor health apparently from repeated deer browsing seemed to produce fewer and less robust fronds; the rachis (main stem) of these fronds was narrower, frond length was shorter with overall reduced leaf area compared to that of a healthy tree fern.

Neither survey method used to collect the data for this study recorded dead tree ferns. However, during both the landscape-scale surveys and the targeted tree fern assessments, dead tree ferns < 200 cm tall were commonly observed (Figure 8C). Typically, dead fronds showing evidence of past browsing were still attached to the caudex, suggesting that repeated browsing by deer was at least a contributing factor to tree fern mortality.

## 4 | Discussion

We recorded widespread and at times severe browsing of tree ferns in wet forests inhabited by introduced deer. Browsing impacts were recorded at 96% of surveyed sites, with typically a third to half of surveyed tree ferns browsed at each site. There were no differences in recorded impact between the three species of tree fern surveyed, although comparisons of *Cyathea australis* and *Dicksonia antarctica* with *Todea barbara* were hampered by a low sample size of *Todea barbara*. Browsing of tree ferns was strongly dependent on caudex height: tree ferns < 100 cm were often highly impacted (> 20% fronds browsed) with impact declining approximately linearly with height to 200 cm, and typically minimal thereafter. For both survey methods used in this study, there were significant, albeit modest, positive relationships between indices of deer density (faecal pellet counts and signs of deer activity, respectively) and the level of browsing recorded. In areas of notable deer activity, dead tree ferns were frequently observed. The evidence we present here suggests that introduced deer pose a significant threat to tree fern populations across south-eastern Australia.

### 4.1 | Landscape-Scale Extent of Impacts on Tree Ferns

Browsing impacts on tree ferns were widespread. Site-specific studies (Bennett 2023; Wills et al. 2023) and observations (Bennett 2008; Bowman 2014; Claridge 2016a; Peel et al. 2005;



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Stockwell 2003) of tree fern browsing attributed to deer have been reported across eastern Victoria and southern New South Wales. However, this is the first study to quantify the extent and severity of these impacts at a landscape scale.

We found that across the Greater Melbourne region, a third of tree ferns had been browsed by deer. In catchment areas where deer activity is often high (Forsyth et al. 2009), over half of tree ferns had been browsed, and 20% had more than half of their fronds browsed. These stark findings demonstrate that deer browsing of tree ferns has the capacity to significantly impact local and landscape-wide populations of tree ferns and associated flora and fauna in south-eastern Australia.

## 4.2 | Impacts by Species and Height

While previous studies have indicated that deer may prefer *Dicksonia antarctica* to *Cyathea australis* (Bennett 2023; Wills et al. 2023), we did not detect any browsing preferences between *C. australis* and *D. antarctica* in this study. This is perhaps not surprising given the broad and adaptable diet of sambar (Forsyth and Davis 2011; Quin et al. 2024), the most abundant deer species in our study area. We could not confidently assess the preference and severity of deer browsing damage to *T. barbara* populations given our small sample size, but browsing damage to this species in our surveys was comparable to both *C. australis* and *D. antarctica*. Rare tree fern species such as *C. cunninghamii* and *C. leichhardtiana* (Peel et al. 2005), not surveyed in our study, may be similarly impacted.

Browsing of tree ferns was strongly height dependent, with browsing decreasing approximately linearly to 200 cm, and minimal thereafter. Browsing by deer has been demonstrated to reduce understorey vegetation particularly between 50 and 200 cm (Eichhorn et al. 2017; Veblen and Stewart 1980; Wills et al. 2023), consistent with the height of browsing impacts on tree ferns we observed. While smaller native herbivores such as swamp wallaby (*Wallabia bicolor*) and bobuck (*Trichosurus cunninghami*) potentially contributed to some of the observed browsing, this is likely to have been minimal. Swamp wallabies typically browse up to ~60 cm (Bennett 2008) and are more likely to browse frond tips rather than the whole frond (Bennett 2023), as we typically observed in this study. Furthermore, previous studies in the Upper Yarra catchment using full exclosures (exclude all terrestrial herbivores) and partial exclosures (allowing access to smaller native herbivores only) demonstrated that tree fern browsing there is almost exclusively caused by deer (Wills et al. 2023).

## 4.3 | Implications of Tree Fern Browsing by Deer

### 4.3.1 | Population-Level Impacts

Tree ferns are slow-growing and long-lived (> 200 years; Fedrigo et al. 2019). Repeated browsing by deer has the potential to severely reduce or prevent the recruitment of tree ferns into taller height classes (> 2 m) and thereby threaten the viability of tree fern populations at both local and regional scales. Over time, browsing of tree ferns by deer has the potential to limit the growth of tree ferns beyond the height threshold where deer are able to browse (generally to 200 cm but up to ~300 cm). While we did not detect any browsing preferences between tree fern species, *D. antarctica* is slower growing (33 ± 13 mm/year compared to *C. australis* 73 ± 22 mm/year; Blair et al. 2017), and thus populations of this species may be more vulnerable to long-term impacts of browsing by deer. Although there are observations of deer impacts to the less common (e.g., *Todea Barbara*; this study) and endangered (e.g., *C. leichhardtiana*; Peel et al. 2005) tree fern species, there is insufficient data on how deer populations are impacting their survival and recruitment.

### 4.3.2 | Structural and Functional Impacts

Tree ferns are vulnerable to drought (Volkova et al. 2010) and global warming effects are predicted to cause drying of the environment, with increased temperatures, reduced soil moisture and increased length of the fire season (IPCC 2023). Under these scenarios, it is likely there will be significant changes in terrestrial ecosystem structure and species range shifts (IPCC 2023), suggesting tree fern populations will undergo a significant range contraction. The impacts of deer browsing on tree fern populations are likely to exacerbate the effects of global warming on tree ferns, and threaten the resilience and persistence of wet forest ecosystems via several mechanisms, namely: (a) decrease in tree fern cover leading to a reduction in forest-floor shade, drying of the understorey and emergence of drought and fire tolerant species, and thus increasing flammability, (b) fewer moist tree fern trunks for epiphytes, bryophytes and host-specific flora to utilise, and (c) altered forest understorey structure and composition.

### 4.3.3 | Tree Ferns as a Potential Indicator Species

Given the impacts consistently observed on tree ferns in areas of notably high deer activity (Bennett 2023; Bennett et al. 2022; Wills et al. 2023 and this study), we suggest tree ferns can potentially be used as an indicator of deer impact in wet forests. Their suitability as an indicator in wet forests is because: (i) they are often locally abundant (particularly along waterways and gully areas); (ii) they are frequently browsed by deer where deer are present and the severity to which they are browsed is associated with deer abundance (Figure 5); (iii) the level of impact can be readily and consistently assessed via the counting of browsed and unbrowsed fronds; (iv) they are relatively less impacted by browsing by native herbivores compared to many understorey trees and shrubs (Wills et al. 2023); and (v) tree ferns produce new fronds annually meaning that the observed level of browsing impact is responsive to changes in deer activity from year to year (e.g., in response to changes in deer abundance).

The use of tree ferns as indicator species of deer impact is obviously limited to forest types where tree ferns are prevalent, and ideally should be monitored in conjunction with a robust measure of deer activity (e.g., faecal pellet counts or camera trapping; Bengsen et al. 2022; Forsyth et al. 2007). Furthermore, deer impacts on tree ferns may not be detected where deer are at low densities (Burns et al. 2021) and therefore tree ferns are not suitable as an indicator of deer presence, including the arrival



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of specific deer species such as sambar to a new location, but could be used in conjunction with the suite of other methods used to detect deer presence (see Gormley et al. 2011). Although research to date has highlighted sambar impact tree fern populations, we caution against assumptions that sambar are the only deer species present in Australia that will impact tree fern populations: in Tasmania, Guy et al. (2024) detected *Dicksonia antarctica* in fallow deer faecal pellets using metagenomic diet analysis, and camera trap images from our study area demonstrate fallow deer at least occasionally consume tree fern fronds.

#### 4.3.4 | Key Knowledge Gaps and Future Research

Our investigations provide insight into deer browsing of *Cyathea australis* and *Dicksonia antarctica*, but there is a lack of information on how deer browsing impacts these species in other locations and other tree fern species. Similarly, assessing the impact of other deer species on tree fern populations in the absence of sambar, e.g., fallow deer in Tasmania, would be highly informative. Landscape-wide assessments are needed to understand the scale of the issue for planning and implementation of management strategies. However, targeted field surveys are required to assess the impact of deer browsing on tree fern species that have specific habitat requirements (e.g., *Todea barbara*) or restricted distributions, e.g., the endangered prickly tree fern *C. leichardtiana* and slender tree fern *C. cunninghamii*.

Deer introduced to Australia are expanding in abundance and distribution (Davis et al. 2016). It is important to understand the potential risk to tree fern populations in locations where deer have recently or are projected to spread (Burns et al. 2023; Cunningham et al. 2022; Kelly et al. 2023; Potts et al. 2014), and where new species of deer arrive to a landscape with established populations of another deer species, potentially resulting in niche shift or resource partitioning (Whitney et al. 2011). Increases in deer abundance resulting in impacts to tree fern populations may require commercial harvest quotas to be reassessed.

A greater understanding of how the severity and frequency of repeated browsing affects tree ferns under varying climatic conditions is needed. This could be addressed by marking individual tree ferns across a range of deer densities and environmental conditions, and annually assessing their condition. This information would enable land managers to plan and implement management interventions in a timely manner.

Tree ferns that survive fire resprout new fronds shortly afterwards (Ough 2001) and may be particularly vulnerable to browsing until understorey vegetation has recovered sufficiently to provide alternative sources of forage. With predictions for increased fire activity (IPCC 2023), there is a need to better understand the cumulative impact of fire, fire frequency and deer browsing following fire on tree fern populations.

## 5 | Conclusion

Our investigations provide a stark assessment of the browsing impacts of introduced deer on tree fern populations in south-east Australia. We have demonstrated (1) deer browsing of tree ferns *Dicksonia antarctica* and *Cyathea australis* is widespread and common, and (2) deer do not preferentially browse a particular tree fern species but both tree fern height and deer abundance influence the severity of browsing on individual tree ferns. Given the widespread and often severe browsing impacts on tree ferns by deer, we suggest there is an urgent need for further investigation to better understand and manage the risks posed by deer to the wet forests of south-eastern Australia.

### Author Contributions

A.B., D.R., T.J.W., R.W.R.R. and J.G. conceived the study. A.B., T.J.W., R.W.R.R. and J.G. designed the field methods and collected data; J.G. led the analyses. A.B. led the writing of the manuscript and all authors contributed critically to drafting this manuscript and gave approval for its publication.

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### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

All data and code used in analyses for this study will be freely provided upon reasonable request.

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