

Quantifying variations in browsing pressure caused by feral deer for a range of threatened ecological communities and plant growth forms

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Abstract Globally, high-density populations of feral deer have been associated with a range of negative ecological consequences. Within Australia, limited quantitative research has assessed the impacts of deer, particularly in threatened ecological communities (TECs). Our study aimed to quantify the impact of feral deer on the herbivory of a range of woody plant species, non-woody growth forms and TECs; and assess whether feral deer increase herbivory in TECs above background rates caused by native herbivores. We surveyed 356 transects across 89 sites representing eight TECs and collected herbivory data for woody and non-woody plants. At each site, we recorded the presence or absence of deer sign and abundance of macropod pellets to account for variations in herbivory between groups of sympatric species. Generalised linear mixed models were developed to predict: (i) proportion of individual plants browsed (or grazed); and (ii) average browsing (or grazing) intensity for woody plant species and non-woody plants. Controlling for macropod abundance, we found the average grazing intensity and proportion of non-woody plants grazed was higher when deer were present compared to absent.

Specifically, grazing pressure on rushes, cycads, sedges and grasses was significantly higher where deer were present. In contrast, we did not observe a significant impact of deer on woody plant species. The presence of deer resulted in higher grazing intensity in coastal saltmarsh, freshwater wetland, littoral rainforest and bangalay sand forest TECs. Although the deer population across our study region generally appears to be at low density compared to neighbouring regions, their presence is resulting in grazing pressure above that caused by native herbivores for a range of non-woody plants. Our results contribute to a growing body of research about the ecological impacts of feral deer in Australia and can be used as a baseline for ongoing regional monitoring of deer impacts in TECs.

Key words: Australia, herbivory, introduced species, macropod.

INTRODUCTION

Various species of deer have been introduced to every inhabited continent (Dolman & Wäber 2008), and in recent decades global patterns have emerged to identify the key ecological impacts resulting from this expansion. High-density deer populations can cause significant ecological damage including intensive browsing of native plant species, rubbing or ring-barking trees, thrashing saplings, exacerbating soil erosion and reducing water quality through the creation of wallows (Akashi & Nakashizuka 1999; Côté *et al.* 2004; Keith & Pellow 2005; McDowell 2007; Bilney 2013; Davis *et al.* 2016).

Globally, high densities of deer have caused measurable and sometimes significant reductions in plant species diversity (Gill & Beardall 2001) and created simplified vegetation community structures (Côté

et al. 2004). High-intensity browsing can affect the recruitment and age structure of vegetation communities. For example, young seedlings are highly palatable and often browsed by deer (Tanentzap *et al.* 2009). This can stunt regeneration (Husheer *et al.* 2006; Frerker *et al.* 2014) and limit the proportion of individuals reaching reproductive maturity (Côté *et al.* 2004). Individuals that do reach the mature stage may be limited in their potential for seedling dispersal and establishment by opportunistic browsing on reproductive organs (Peel *et al.* 2005; Dvorak & Catalano 2016). Although complete herbivore exclusion often assists regeneration (Nilar *et al.* 2019), vegetation communities can take decades to recover from the effects of intense browsing while low densities of feral deer are still present (Tanentzap *et al.* 2009).

Although deer have broad diets, certain plant species are preferred over others due to their increased palatability. This hierarchy leads to preferential browsing of certain species, and can greatly reduce

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Accepted for publication April 2021.

the abundance of palatable plant species in areas of high deer density (Gill & Beardall 2001). With continued browsing, communities can shift towards non-palatable species and eventually lead to the emergence of a new stable state (Côté *et al.* 2004). Such community shifts can make it difficult for palatable species to re-establish even in the event of reduced browsing intensity (Côté *et al.* 2004; Tanentzap *et al.* 2009).

Feral deer have been linked to significant ecological damage in Australia (Davis *et al.* 2016), and since their introduction in the 1800s six species have successfully established viable populations and expanded their range (Gormley *et al.* 2011; Potts *et al.* 2015; Forsyth *et al.* 2019). Australia has no native ungulates, and feral deer often have dietary overlap with a range of sympatric native herbivores (Moriarty 2004; Davis *et al.* 2008).

Although Australian native plants are not a natural part of their diet, deer are opportunistic feeders and their broad diet has adapted to include a wide range of Australian native species (Keith & Pellow 2005; Davis *et al.* 2008; Forsyth & Davis 2011; Claridge 2016). The complete range of plants consumed by any feral deer species has not been recorded or catalogued in Australia; however, rumen content analyses have directly identified dietary components for rusa deer (*Cervus timorensis*; Moriarty 2004), hog deer (*Axis porcinus*; Davis *et al.* 2008) and sambar deer (*Cervus unicolor*; Forsyth & Davis 2011). Rusa deer consumed material from most functional groups surveyed, although quantities of each functional group varied with habitat type (Moriarty 2004). Hog deer also consumed material from all functional groups surveyed, with most of their diet consisting of forbs and shrubs (Davis *et al.* 2008). Sambar deer consumed a range of plant species from various functional groups and demonstrated high dietary variability between individuals, indicating a level of dietary plasticity.

Impacts of deer herbivory on native Australian plant species and vegetation communities is consistent with findings from elsewhere in the world. For example, rusa deer browsed on shoots, foliage, reproductive material and bark of 88% of native species surveyed in Royal National Park, South-eastern Australia and intense browsing negatively impacted long-term regeneration and recruitment for these species (Keith & Pellow 2005). Additionally, rusa deer in Royal National Park affected the structure and composition of heathlands, and reduced coverage of grasses, sedges and low vegetation (Crowther *et al.* 2016). Coverage of medium and tall shrubs also varied with fire history and the presence of rusa deer (Crowther *et al.* 2016).

Deer are widespread across the eastern coast of Australia, yet very limited research has been

conducted on how deer impact endangered vegetation, including threatened ecological communities (TECs; Davis *et al.* 2016). Moriarty (2004) found that littoral rainforest, which is classified as a TEC in New South Wales, had over 50% fewer plant species in areas with high deer density compared to areas with low deer density. Groundcover species and saplings were particularly negatively affected (60–70% and 50–60% lower in high-density areas, respectively; Moriarty 2004). Dietary analysis revealed that in rainforest communities deer most commonly consumed trees and shrubs (Moriarty 2004). More recent work by Nilar *et al.* (2019) assessed the impacts of herbivory on a range of regenerating species in endangered Illawarra escarpment subtropical rainforest. Differences in browsing pressure between fenced and unfenced plots provided valuable insight into the browsing preferences of resident herbivores, namely the swamp wallaby (*Wallabia bicolor*) and rusa deer. Additionally, there were more native species and fewer alien species when all herbivores were excluded (Nilar *et al.* 2019). These studies focussed primarily on rainforest communities, and the impacts of deer on a variety of other TECs remain unquantified. As a result, local land managers often lack information to effectively prioritise deer management or control in these areas.

In this paper we aimed to: (i) quantify the impact of herbivory by feral deer on a range of woody plant species, non-woody growth forms and threatened ecological communities; and (ii) assess whether feral deer increase herbivory in threatened ecological communities above background rates caused by native species.

MATERIALS AND METHODS

Study area

Our study area comprised the South Coast of NSW, lying between the coastal city of Nowra (34.88°S, 150.60°E) in the north and the Victorian border (37.49°S, 149.97°E) in the south, extending inland to approximately the top of the coastal escarpment. Within this area, our research focussed on eight well defined TECs: bangalay sand forest, coastal saltmarsh, freshwater wetlands on coastal floodplains, littoral rainforest, river-flat eucalypt forest on coastal floodplains, swamp sclerophyll forest on coastal floodplains, swamp oak floodplain forest, and *Themeda* grassland on sea cliffs and coastal headlands. The annual average rainfall is variable across the study area, ranging from 600 to 1000 mm year⁻¹ in the south to 1000–1500 mm year⁻¹ in the north. The mean annual temperature for this region is 12–15°C. Five species of deer are present: Fallow deer (*Dama dama*) and sambar deer are widespread throughout the region, while red deer (*Cervus elaphus*), rusa deer and chital deer (*Axis axis*) are more patchily distributed (D. McCreery, pers. comm., 2019). Quantitative data on each

species are scarce, but anecdotal reports suggest general abundances are greater along the coastal escarpment and near the Victorian border. A sixth species, hog deer, may occur but there are no definitive records at the time of writing.

Field surveys

Field surveys were conducted only within National Parks and Wildlife Service (NPWS) estate and were limited to the eight TECs listed above. These TECs were nominated by NPWS because they are poorly represented in current research about the ecological impacts of deer, and anecdotal evidence suggested the impact of deer in these areas is increasing. To ensure sites were evenly distributed, the study area was further stratified into three geographic regions of roughly equal area. We used ArcMap (v.10.7.1; Esri 2019) to randomly allocate sites within the predicted distribution of TECs (New South Wales National Parks & Wildlife Service 2019) and NPWS estate (State Government of NSW & Department of Planning Industry & Environment 2017). Although we attempted to sample vegetation communities at a rate proportional to their available area, some TECs were harder to access and, therefore, remained under-sampled. Sites were excluded if they were not easily accessible by 4WD vehicle or did not contain the predicted TEC. Each TEC was sampled with 7–28 sites except *Themeda* grasslands, which were sampled with two sites because they are only found in small patches within Eurobodalla National Park (Table 1). In total, 89 sites were surveyed between April and July 2019.

Evidence of herbivory

We sampled herbivore damage to plants at each of 89 sites using four transects, each transect 50 m in length ($n = 356$ transects in total) and a maximum of 50 m apart. Whenever possible, transects were aligned with areas where the

Table 1. Area (km²) represents the total predicted area of each TEC within NPWS estate

| Threatened ecological community | Area (km ²) | Sites | Sites with deer present |
|---|-------------------------|-------|-------------------------|
| Bangalay sand forest (BSF) | 36.46 | 28 | 1 |
| Coastal saltmarsh (CSM) | 7.19 | 13 | 3 |
| River flat eucalypt (RFE) | 3.57 | 11 | 7 |
| Swamp sclerophyll floodplain forest (SSF) | 2.31 | 11 | 0 |
| Freshwater wetland (FWL) | 31.73 | 9 | 6 |
| Swamp oak floodplain forest (SOF) | 19.38 | 9 | 0 |
| Littoral rainforest (LRF) | 11.16 | 7 | 1 |
| <i>Themeda</i> grassland (THL) | 0.25 | 2 | 0 |

The abbreviations used for each TEC in the statistical analysis are shown in parentheses.

probability of detection for deer sign was likely to be highest, such as near waterways and along wildlife trails (Gormley *et al.* 2011). When well-defined trails were not evident, transects were located randomly. We sampled each transect using the step-point method (Evans & Love 1957) with points established at every metre (a total of 50 points per transect). At each point we recorded: (i) species of woody vegetation present; (ii) if woody vegetation was present, the minimum browsing intensity of each plant (from 0% to 100%); (iii) non-woody plant groups (grass, rush, sedge, forb, cycad, fern, vine, moss and samphire); (iv) if non-woody vegetation was present, the minimum grazing intensity of each plant was recorded (from 0% to 100%). Species names for woody vegetation are consistent with NSW PlantNET (Royal Botanic Gardens & Domain Trust 2021).

A plant was recorded as ‘present’ if it touched a two-metre segment of rope starting at ground level and extending perpendicular to the ground at each point. We calculated minimum browsing (or grazing) intensity as the percentage of available foliage and woody material that had been consumed for each individual. Plants were assumed to have reasonably normal shapes (i.e. no abnormally large or outlying branches) and when there was evidence of herbivory (i.e. scars on stems or missing foliage) the quantity of vegetation removed was estimated based on differences between the remaining plant material and the average size of surrounding unbrowsed stems or branches. For large trees and shrubs that continuously intersected the transect for multiple sampling points, the total length of the plant was broken down into one-metre segments and browsing intensity was recorded for each segment. For continuous groundcover that could not be assessed as individual plants, grazing pressure was averaged across one-metre segments of vegetation directly intersecting the transect.

The vegetation surveyed was limited to individuals with growth below two metres in height to restrict the sample to only vegetation within the notional browsing range of sambar deer (Peel *et al.* 2005). As there are no proven methods to distinguish herbivory by deer from herbivory by macropods, all evidence of herbivory was recorded. Similarly, as both deer and the swamp wallaby (a common macropod in our study area) are both browsers and grazers (Moriarty 2004; Davis *et al.* 2008; Forsyth & Davis 2011), estimates of browsing intensity included both woody stems and leafy material. This method may have led to certain instances of herbivory (i.e. the complete consumption of a plant) being under-reported, and as a result, our measurements may underestimate the true level of browsing or grazing intensity. A single observer (HB) sampled vegetation transects and recorded minimum browsing (or grazing) intensity on plants at all 89 sites to minimise observer bias.

Deer presence

At each site, surveys were conducted to assess the presence (and absence) of deer using searches for sign along the same transects used to assess herbivory, as well as an additional 200-m transect (cumulative transect length = 400 m). We walked each transect with the aim of detecting the following signs of deer within 1 m on either side (total area surveyed = 800 m²): faecal pellet

groups, rubbed trees, tracks and cast antlers (Gormley *et al.* 2011). Although there are many ways to measure deer presence and activity, including looking at the density of scats (Moriarty 2004; Forsyth 2005), we chose to simply record the presence or absence of faecal pellet groups due to their limited abundance at many sites.

Other herbivory

In Australian landscapes, herbivore niche overlap creates one of the largest limitations to determining the impact of herbivory by deer. Deer have highly versatile diets and records show they consume a wide range of native and non-native vegetation (Moriarty 2004; Davis *et al.* 2008; Forsyth & Davis 2011). This often includes varying degrees of overlap with the diets of sympatric macropods (Moriarty 2004; Davis *et al.* 2008), making it difficult to attribute herbivory to a particular species. The only way to provide more certainty about the impacts of herbivory by specific species or groups is to conduct experiments with long-term exclusion plots (Moriarty 2004; Goetsch *et al.* 2011), which we did not have the time nor resources to do. To account for herbivory by other species, we also counted pellet groups for macropods (i.e. swamp wallaby, eastern grey kangaroo (*Macropus giganteus*), and red-necked wallaby (*M. rufogriseus*)), the common wombat (*Vombatus ursinus*), and European rabbit (*Oryctolagus cuniculus*) using the same methods as searches for deer sign. Macropod scat was present at 86 of 89 sites, and pellet group counts were used as an index of macropod abundance. As there are many sympatric macropod species in our study area and it is difficult to differentiate scat at a species level, all macropod scat was grouped together. Scat from other herbivores, such as wombats and rabbits, was not present at most sites and was, therefore, not included in our analysis.

Statistical analysis

Using R Studio (R Core Development Team 2018; RStudio Team 2019) we fit two generalised linear mixed models (GLMMs) to explore relationships between two measures of herbivory: average grazing intensity of non-woody plants

and average browsing intensity of woody species. We also fit two linear mixed models (LMMs) to explore relationships between the proportion of non-woody plants grazed and the proportion of woody species browsed. In all four models (two GLMMs and two LMMs), we fit four potential explanatory variables: TEC, deer presence, macropod pellet abundance, and plant type (for non-woody plants) or species (for woody plants). We added non-woody plant type as a fixed effect with seven levels: grasses, sedges, rushes, forbs, ferns, cycads and vines. Mosses and samphire were excluded because they were represented by a very small number of individuals. We added woody species as a fixed effect with 12 levels representing the dominant species. These 12 species (*Acacia dealbata*, *A. implexa*, *A. longifolia*, *Acronychia oblongifolia*, *Banksia spinulosa*, *Callistemon citrinus*, *Casuarina cunninghamiana*, *Dodonaea triquetra*, *Leucopogon parviflorus*, *Pimelea axiflora* and *Phyllanthus gummii*) were selected from the original 119 species recorded during our study because there were not enough degrees of freedom to run models with more species. Species were selected if they had >5% average browse and >10 individuals recorded. In each model, we fitted site as a random effect because herbivory was recorded separately for multiple plant types (or species) at each location. For models predicting the proportion of plants browsed (or grazed) we assumed a binomial distribution; for models predicting the average browsing (and grazing) intensity we assumed a Gaussian distribution. Average grazing intensity values were log-transformed for non-woody plants to ensure those data were normally distributed. Non-woody plant type or woody species data at the transect level was combined, and models were run using pooled data at the site level. In each GLMM, we specified a range of models (see Tables 2–6) with varying combinations of TEC, deer presence, macropod pellet abundance, plant type (or species) and/or an interaction between deer presence and plant type (or species) as fixed effects and ranked them using Akaike's Information Criterion for small samples (AICc) to select the best model. We also calculated marginal R^2 values for each model based on methods described in Nakagawa and Schielzeth (2013). We did not include TEC and plant type (for non-woody individuals) or TEC and species (for woody individuals) in the same model because the two variables were highly correlated (i.e. some plant types or species are more likely to occur in certain TECs).

Table 2. The best model (weight = 0.85, $R^2 = 0.243$) predicting the proportion of non-woody individuals grazed contained macropod pellet, deer presence, and non-woody plant type as independent variables

| Explanatory variable | Estimate | 95% confidence interval | Pr (> z) |
|----------------------|----------|-------------------------|--------------|
| Intercept | -1.33 | (-1.63, -1.03) | 0.000001*** |
| Deer presence | 0.82 | (0.44, 1.20) | 0.03* |
| Fern | -0.64 | (-0.89, -0.39) | 0.01* |
| Forb | -3.28 | (-3.58, -2.98) | <2 e-16*** |
| Grass | -1.07 | (-1.31, -0.83) | 8.6 e-6*** |
| Rush | -2.05 | (-2.32, -1.78) | 6.62 e-14*** |
| Sedge | -0.67 | (-0.94, -0.40) | 0.014* |
| Vine | -3.04 | (-3.57, 2.51) | 7.27 e-9*** |
| Macropod pellets | 0.012 | (0.008, 0.016) | 0.012* |

This table includes estimates ($\pm 95\%$ confidence intervals) and significance levels for each explanatory variable in the best model. Estimates associated with each plant type represent contrasts with cycads.

Table 3. The best model (weight = 0.77, $R^2 = 0.18$) predicting the average grazing intensity of non-woody plants contained deer presence, non-woody plant type, and a deer presence:non-woody plant type interaction as independent variables

| Explanatory variable | Estimate | 95% confidence interval | Pr ($> t $) |
|----------------------|----------|-------------------------|---------------|
| Intercept | 2.30 | (1.70, 2.89) | 0.0002*** |
| Deer presence | 1.74 | (0.28, 3.21) | 0.24 |
| Fern | -0.63 | (-1.27, 0.01) | 0.33 |
| Forb | 0.06 | (-1.06, 1.18) | 0.96 |
| Grass | -1.47 | (-2.09, -0.85) | 0.019* |
| Rush | -1.57 | (-2.26, -1.28) | 0.025* |
| Sedge | -1.96 | (-2.64, -1.28) | 0.005** |
| Vine | -1.25 | (-2.23, -0.28) | 0.20 |
| Deer presence:Fern | -1.65 | (-3.20, -0.09) | 0.29 |
| Deer presence:Forb | -3.13 | (-5.12, -1.15) | 0.12 |
| Deer presence:Grass | -0.70 | (-2.20, 0.80) | 0.64 |
| Deer presence:Rush | -0.32 | (-1.89, 1.25) | 0.84 |
| Deer presence:Sedge | -0.10 | (-1.74, 1.54) | 0.95 |
| Deer presence:Vine | -1.43 | (-3.56, 0.69) | 0.50 |

This table includes estimates ($\pm 95\%$ confidence intervals) and significance levels for each explanatory variable in the best model. Estimates associated with each plant type represent contrasts with cycads and Deer:cycad interactions.

We also used data collected during our field surveys to test the hypothesis that herbivore pressure varies across TECs. The initial modelling described above resulted in non-woody plant type (or species), rather than TEC, being included in the best model. This indicates that plant type (or species) is a more important predictor of herbivore pressure than TEC; however, results relating herbivore pressure and TEC may be easier to apply to

landscape-scale management decisions. Due to the high correlation between plant type (or species) and TEC, these two variables could not be included in the same model, therefore additional models were required to test this hypothesis. Using R Studio (R Core Development Team 2018; RStudio Team 2019) we similarly generated two LMMs and two GLMMs to examine this more closely. Each model explored the relationships between average grazing intensity of non-woody plants, and average browsing intensity of woody species, the proportion of non-woody plants grazed, and proportion of woody plants browsed (calculated using the same methods as previous models) and three potential explanatory variables: TEC, deer presence and macropod pellet abundance. We recorded macropod abundance and deer presence (or absence) in the same way as the previous analysis. In each model, we fitted site as a random effect because herbivory was recorded separately for many individual plants at each location. In each GLMM, we specified a range of models with varying combinations of TEC, deer presence and/or macropod pellet abundance as fixed effects and ranked them using AICc to select the best model. In all models, we plotted predictions for individual variables while holding the other continuous variables at their mean and categorical variables at their mode.

RESULTS

We measured 356 transects at 89 sites across eight TECs. Signs of deer were recorded at 19 of the 89 (21.3%) sites. Deer pellets were found at 12 (13%) sites, tracks were present at six sites (7%), rubbed trees were present at seven sites (8%), and wallows were found at one (1%) site. Macropod scat ranged from 0 to 181 pellet groups per site (mean = 19.8 pellet groups).

Table 4. The best model (weight = 0.93, $R^2 = 0.23$) predicting the proportion of woody species browsed contained deer presence, macropod pellets, and woody species as independent variables

| Explanatory variable | Estimate | 95% confidence interval | Pr ($> z $) |
|---------------------------------|----------|-------------------------|---------------|
| Intercept | 0.41 | (-0.25, 1.07) | 0.54 |
| Deer presence | 0.24 | (-0.23, 0.71) | 0.61 |
| <i>Acacia implexa</i> | -1.01 | (-1.74, -0.28) | 0.17 |
| <i>Acacia longifolia</i> | -0.62 | (-1.28, 0.04) | 0.35 |
| <i>Acronychia oblongifolia</i> | -1.87 | (-2.70, -1.04) | 0.02* |
| <i>Pimelea axiflora</i> | -0.62 | (1.67, 0.43) | 0.56 |
| <i>Banksia spinulosa</i> | -18.68 | (-2392, 2354) | 0.99 |
| <i>Bursaria spinosa</i> | -0.77 | (-1.71, -0.13) | 0.23 |
| <i>Callistemon citrinus</i> | 1.37 | (0.11, 2.63) | 0.28 |
| <i>Casuarina cunninghamiana</i> | -3.46 | (-4.23, -2.69) | 6.25 e-6 *** |
| <i>Dodonaea triquetra</i> | -0.56 | (-1.32, 0.20) | 0.46 |
| <i>Leucopogon parviflorus</i> | 0.33 | (-0.76, 1.42) | 0.76 |
| <i>Phyllanthus gunnii</i> | 0.90 | (-0.39, 2.19) | 0.49 |
| Macropod pellets | 0.06 | (0.04, 0.08) | 0.01* |

This table includes estimates ($\pm 95\%$ confidence intervals) and significance levels for each explanatory variable in the best model. Estimates associated with each plant type represent contrasts with *Acacia dealbata*.

Table 5. The best model (weight = 0.76, $R^2 = 0.30$) predicting the average browsing intensity for woody species contained deer presence and woody species as independent variables

| Explanatory variable | Estimate | 95% confidence interval | Pr ($> t $) |
|---------------------------------|----------|-------------------------|---------------|
| Intercept | 19.86 | (14.75, 24.97) | 0.0008*** |
| Deer presence | -12.30 | (-18.86, -5.74) | 0.07 |
| <i>Acacia implexa</i> | -6.28 | (-10.49, -2.07) | 0.19 |
| <i>Acacia longifolia</i> | -4.57 | (-9.08, -0.06) | 0.34 |
| <i>Acronychia oblongifolia</i> | 5.48 | (-0.05, 11.46) | 0.39 |
| <i>Pimelea axiflora</i> | -8.93 | (-13.54, -4.32) | 0.10 |
| <i>Bursaria spinosa</i> | 1.59 | (-1.75, 4.93) | 0.65 |
| <i>Callistemon citrinus</i> | 0.14 | (-6.16, 6.44) | 0.98 |
| <i>Casuarina cunninghamiana</i> | -9.88 | (-14.86, -4.90) | 0.09 |
| <i>Dodonaea triquetra</i> | -2.96 | (-9.18, 3.26) | 0.65 |
| <i>Leucopogon parviflorus</i> | 29.48 | (23.09, 35.87) | 0.001** |
| <i>Phyllanthus gunnii</i> | 2.50 | (-1.92, 6.92) | 0.59 |

This table includes estimates ($\pm 95\%$ confidence intervals) and significance levels for each explanatory variable in the best model. Estimates associated with each plant type represent contrasts with *Acacia dealbata*.

Impacts of deer on non-woody vegetation

A total of 1251 individuals of nine non-woody plant groups (rush, sedge, vine, cycad, fern, forb, grass, samphire and moss) were identified during field surveys. The impact of deer on non-woody vegetation was assessed using two measures of grazing pressure: average grazing intensity of seven non-woody plants and the proportion of non-woody individuals grazed. The model with the lowest AICc predicting the proportion of non-woody individuals grazed contained 'macropod pellet', 'deer presence' and 'non-woody plant' as fixed effects (Table 2). The proportion of non-woody plants grazed was higher where: deer were present (Fig. 1a), in areas with a higher abundance of macropod pellets (Fig. 1b), and for certain plants (cycads, ferns and sedges; Fig. 1c). The model with the lowest AICc predicting average grazing intensity of non-woody plants contained 'deer presence', 'non-woody plant type' and an interaction between deer presence and non-woody plant type as fixed effects (Table 3). Where deer were present, average grazing intensity was greater for grasses, rushes, sedges and cycads (Fig. 2). TEC was not included as a fixed effect in the best model of proportion of individuals grazed nor average grazing intensity because of correlations between the occurrence of some non-woody plants and certain TECs.

Table 6. The best model (weight = 0.63, $R^2 = 0.17$) predicting average grazing intensity for non-woody plants across eight TECs contained deer presence, TEC, and a deer presence:TEC interaction as independent variables

| Explanatory variable | Estimate | 95% confidence interval | Pr ($> t $) |
|------------------------------------|----------|-------------------------|---------------|
| Intercept | 1.04 | (0.85, 1.23) | 0.000001*** |
| Deer presence | 0.48 | (-0.55, 1.51) | 0.64 |
| Coastal saltmarsh | 1.12 | (0.63, 1.61) | 0.025* |
| Freshwater wetlands | 0.08 | (-0.75, 0.91) | 0.92 |
| Littoral rainforest | -0.27 | (-0.81, 0.27) | 0.63 |
| River-flat eucalypt | 0.12 | (-0.36, 0.60) | 0.81 |
| Swamp oak floodplain forest | -0.21 | (-0.64, 0.22) | 0.63 |
| Swamp sclerophyll forest | -0.51 | (-0.9, -0.12) | 0.19 |
| <i>Themeda</i> headlands | 0.85 | (-0.14, 1.84) | 0.39 |
| Deer presence: coastal saltmarsh | 0.12 | (-1.14, 1.38) | 0.92 |
| Deer presence: freshwater wetlands | 0.62 | (-0.74, 1.98) | 0.65 |
| Deer presence: littoral rainforest | 1.48 | (0.05, 2.91) | 0.31 |
| Deer presence: river-flat eucalypt | -0.68 | (-1.87, 0.51) | 0.57 |

This table includes estimates ($\pm 95\%$ confidence intervals) and significance levels for each explanatory variable in the best model. Estimates associated with each plant type represent contrasts with bangalay sand forest.

Impacts of deer on woody vegetation

Of 119 woody plant species identified in the browse survey (Appendix S1), 74 species (61.1%) experienced some level of browsing by herbivores. Of this subset, 31 had an average browsing intensity at or above 5%. The model with the lowest AICc predicting the proportion of woody plant individuals browsed contained 'woody species', 'macropod pellet' and 'deer presence' as fixed effects (Table 4). The model of best fit indicated that the proportion of woody individuals browsed was not significantly higher where deer were present (Fig. 3a), increases with increasing macropod pellet abundance (Fig. 3b), and was higher for some species (Fig. 3c). The model with the lowest AICc predicting average browsing intensity of woody species contained 'deer presence' and 'woody species' as fixed effects (Table 5). Average browsing intensity for woody species was not significantly affected by the presence of deer (Fig. 4a) but was higher for some species (Fig. 4b). TEC was not included as a fixed effect in the best model of proportion of individuals browsed or average browsing intensity because of correlations between the occurrence of some woody species and TECs.

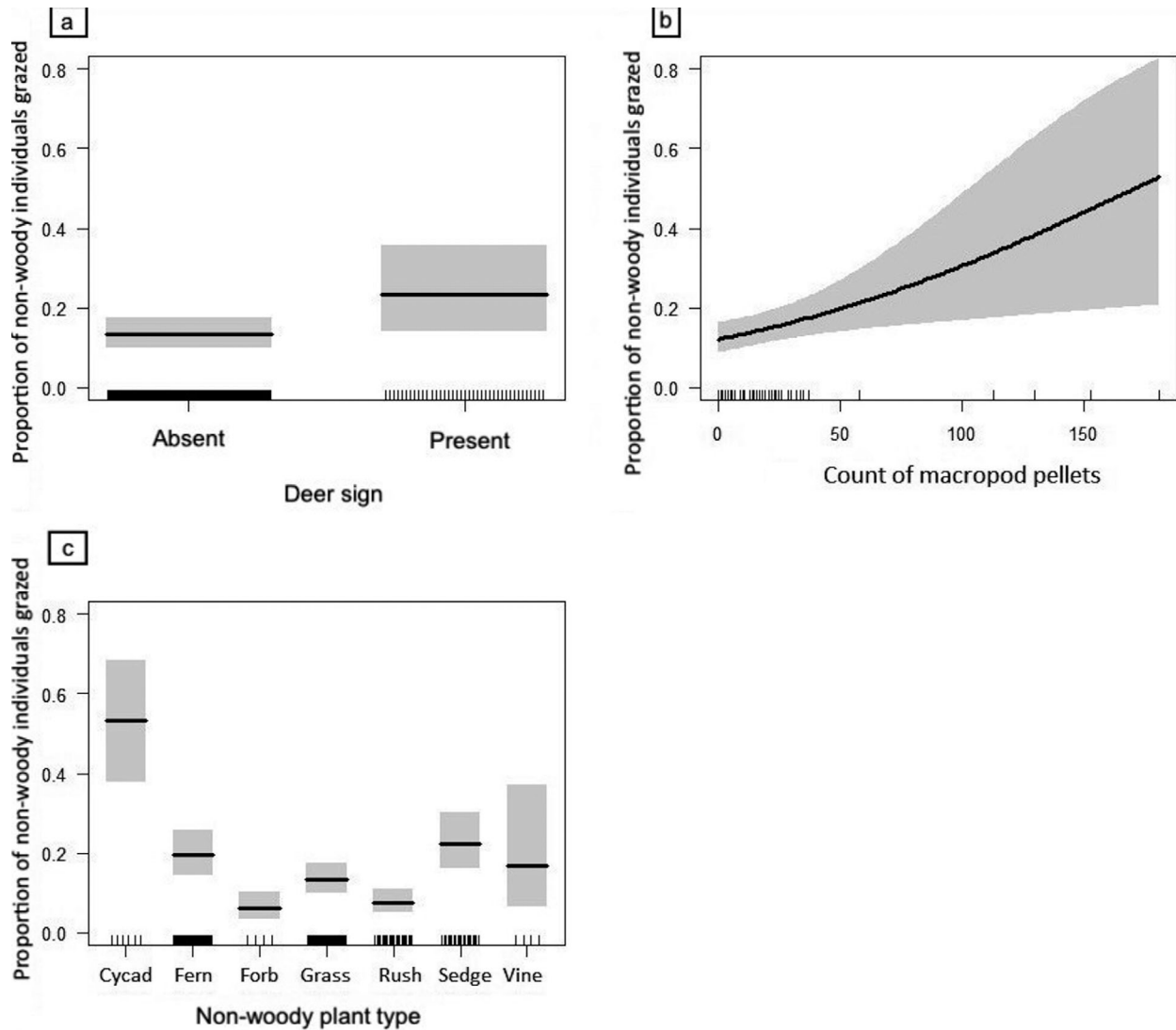


Fig. 1. (a) The predicted mean ($\pm 95\%$ confidence interval) proportion of non-woody individuals grazed where deer sign was present and absent (b) as a function of macropod pellet counts and (c) for seven non-woody plant growth forms.

Impacts of deer on TECs

Four alternative models were tested using GLMMs to predict the average browsing (or grazing) intensity and proportion of individuals browsed (or grazed) for both woody species and non-woody plants across the different TECs. The model with the lowest AICc predicting the average grazing intensity of non-woody plants contained 'deer presence', 'TEC', and an interaction between deer presence and TEC as fixed effects (Table 6). **Where deer were present, average grazing intensity for non-woody plants was significantly increased in bangalay sand forest, coastal salt-marsh, freshwater wetland and littoral rainforest TECs (Fig. 5).** The presence of deer did not significantly affect the proportion of woody species browsed or the average browsing intensity of woody species in

this analysis. The model with the lowest AICc predicting the proportion of non-woody plants grazed did not contain TEC as a fixed effect. The models exploring impacts on TECs did not include 'woody species' or 'non-woody growth form' as potential fixed effects because of correlation between some plant types and species and certain TECs.

DISCUSSION

Our research aimed to: (i) quantify the impact of feral deer on herbivore pressure for a range of woody plant species, non-woody plant growth forms and TECs; and (ii) assess whether feral deer increase herbivore pressure in TECs above background rates caused by native herbivores. Grazing impact on non-

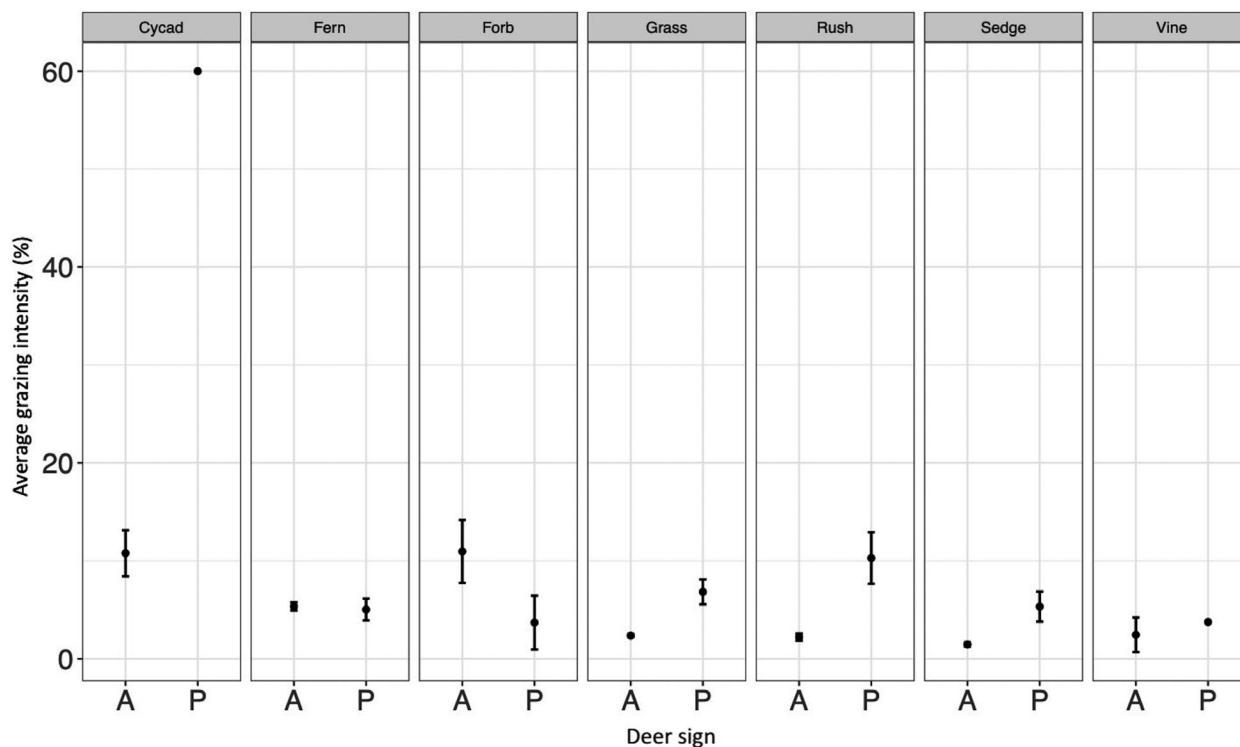


Fig. 2. The predicted mean ($\pm 95\%$ confidence interval) grazing intensity for rushes, sedges, vines, cycads, ferns, forbs and grasses where deer sign was present and absent.

woody plants was higher when deer were present compared to absent. Specifically, grazing intensity was higher for rushes, cycads, sedges and grasses where deer were present. In contrast, the average browsing intensity and proportion of woody plant species browsed was not demonstrably increased by the presence of deer. Where deer were present, coastal saltmarsh, freshwater wetland, littoral rainforest and bangalay sand forest experienced higher grazing pressure than other TECs.

Grazing of non-woody vegetation

The presence of deer increased the proportion of non-woody plants grazed while controlling for macropod density (Fig. 1a). This indicates that deer have an additional impact on the level of grazing over and above background rates. Research within Australia (Moriarty 2004; Davis *et al.* 2016) and internationally (Augustine & McNaughton 1998; Rooney & Waller 2003; Côté *et al.* 2004) consistently shows that deer can create large-scale changes to vegetation communities with the quantity or quality of vegetation they consume. For example, a study in Royal National Park estimated that a single deer consumes as much plant material as nearly four adult swamp

wallabies on a daily basis (Moriarty 2004), which means even a low-density deer population could raise herbivory above background rates.

Our results indicate that ferns, cycads, and sedges were more likely to be grazed in the presence of deer compared to other plants such as rushes (Fig. 2). Previous studies of feral deer (Moriarty 2004; Davis *et al.* 2008; Forsyth & Davis 2011) and macropod (Moriarty 2004; Davis *et al.* 2008) diets, with techniques such as pellet and rumen content analysis, indicate that ferns and sedges are routinely within the dietary ranges of both herbivores. Crowther *et al.* (2016) also observed that the coverage of sedges and grasses was lower at sites where deer were present, compared to sites where deer were absent. Cycads have not been frequently recorded as components of either deer or macropod diets, making it unclear which group is responsible for the recorded grazing pressure. The lower proportion of grasses grazed may be due to difficulties associated with measuring low-intensity grazing, rather than a lack of preference by either deer or macropods. Grasses have been identified in the diets of feral deer, kangaroos and wallabies (Moriarty 2004; Davis *et al.* 2008; Forsyth & Davis 2011; Claridge *et al.* 2016).

Our model predicting the grazing intensity on non-woody plants included an interaction between plant

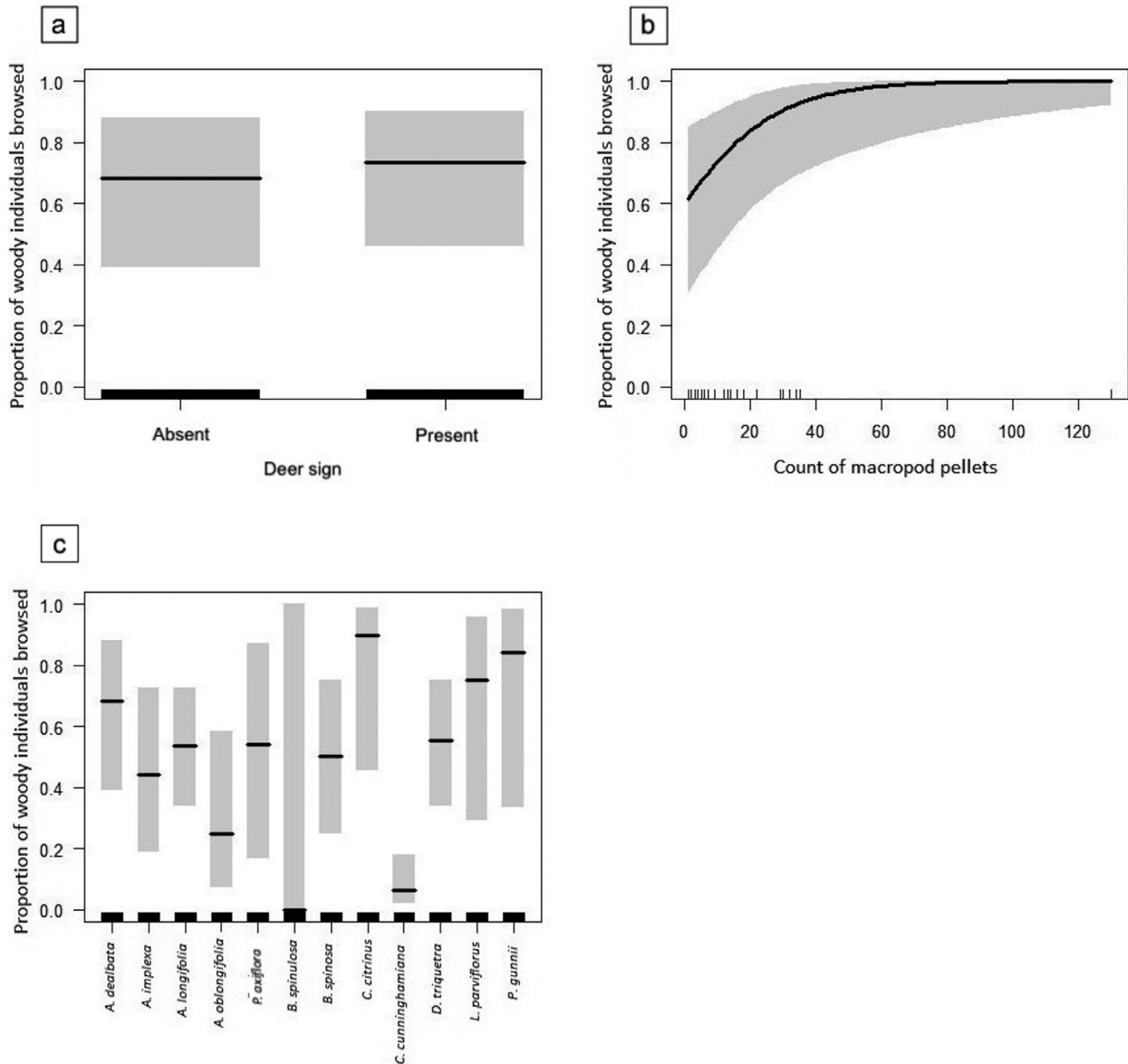


Fig. 3. (a) The predicted mean ($\pm 95\%$ confidence interval) proportion of woody individuals browsed where deer sign was present and absent. (b) As a function of macropod pellet counts and (c) for 12 woody plant species.

growth form and deer presence. Rushes, cycads, sedges and grasses had higher average grazing intensity values at sites where deer were present compared to sites where deer were absent, suggesting deer preferentially graze rushes, sedges, cycads and grasses over most other plant types. Deer have highly versatile diets, and rushes, sedges and grasses have been frequently recorded in the diets of deer throughout eastern Australia (Moriarty 2004; Davis *et al.* 2008; Forsyth & Davis 2011). Cycads, as previously mentioned, have not been recorded. However, anecdotal reports indicate that cycads may be more heavily grazed at sites where deer are present (J. Miles, pers. comm., 2019).

Differences in results for the proportion of non-woody plants grazed and grazing intensity of non-woody plants could have multiple implications. Herbivory by deer may increase average grazing intensity for some plant types, while the proportion of non-woody individuals grazed indicates this increased pressure is currently focussed on a small proportion of plants. Anecdotal evidence suggests that the density of deer across most of our study area is still low compared to other areas of south-eastern Australia, and it is likely that there are only low numbers of deer at each of the sites where they were recorded. A small number of deer might be heavily consuming a small number of individuals of each of

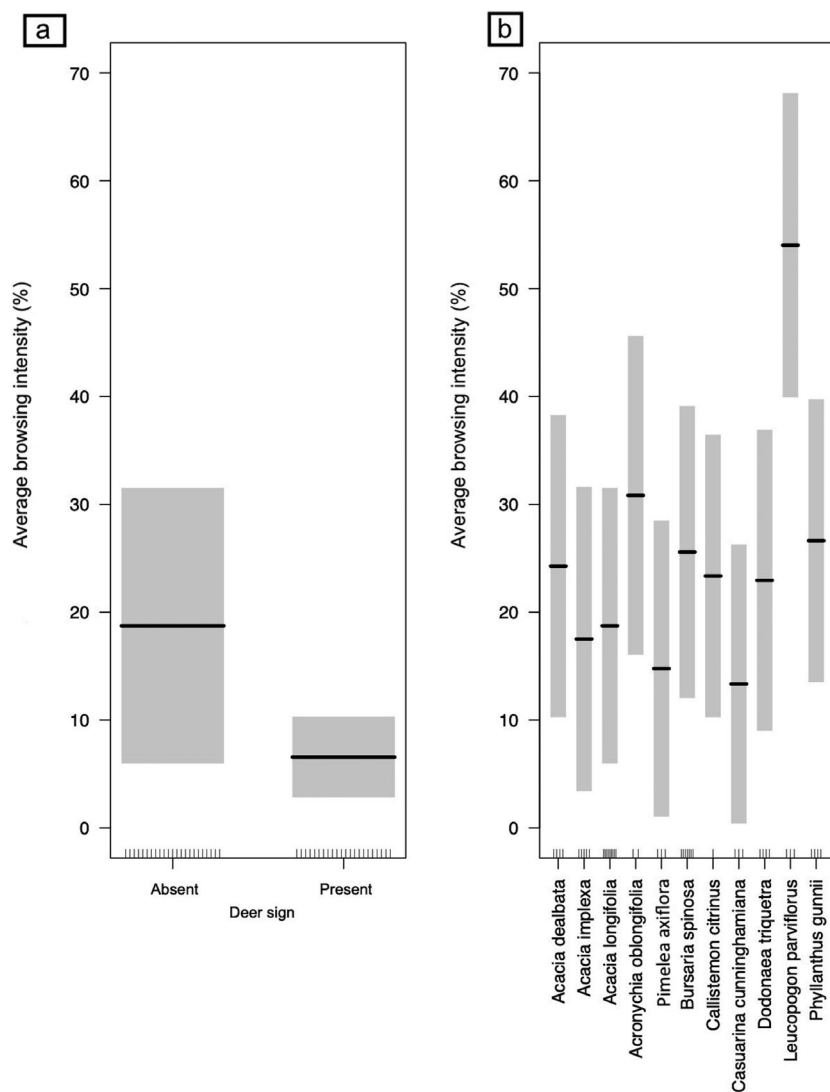


Fig. 4. (a) The predicted mean ($\pm 95\%$ confidence interval) browsing intensity of woody plants where deer sign was present and absent (b) for 12 woody species where deer sign was present and absent.

the preferred plant types. As the density of deer increases though, the proportion of individuals grazed and total volume of non-woody plants consumed is likely to increase (Gill & Beardall 2001; Côté *et al.* 2004).

Browse damage to woody vegetation

In contrast to non-woody plants, the average browsing intensity and proportion of woody individuals browsed were not significantly affected by the presence of deer. This is unsurprising, as anecdotal reports suggest the density of deer in our study area is low. Additionally, deer may have seasonal variations in their diets. Forsyth and Davis (2011) reported sambar deer in Victoria to graze more in summer and autumn and shift towards browsing in

winter and spring. As our data were collected in autumn and early winter the results may underestimate true browsing pressure in the region. Additional studies conducted in winter and spring months are necessary to confirm or refute this theory.

When the presence of deer and abundance of macropods was held constant, browsing intensity and proportion of individuals browsed varied across woody species. *Callistemon citrinus*, *L. parviflorus* and *P. gunnii* had the highest proportions of individuals browsed, while *B. spinulosa* and *C. cunninghamiana* had the lowest. Average browsing intensity was relatively similar across all species, except for *L. parviflorus* which was significantly higher than all other species. Two rainforest species, *Ficus coronata* and *Glochidion ferdinandi* were browsed at high intensities in a similar area (Nilar *et al.* 2019), but experienced very low browsing pressure in our study (1.88% and

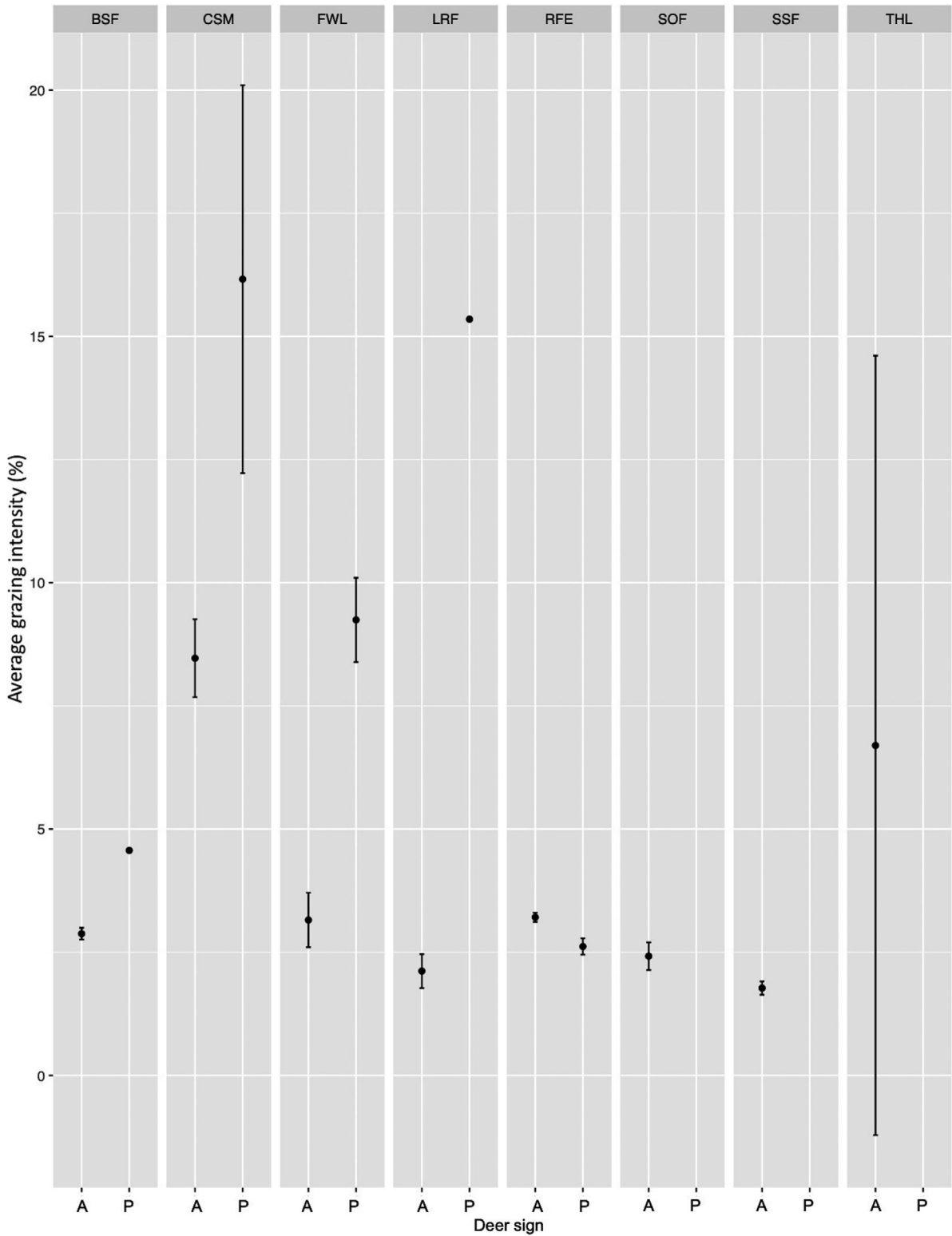


Fig. 5. The predicted mean ($\pm 95\%$ confidence interval) grazing intensity of all non-woody plants in eight TECs: bangalay sand forest (BSF), coastal saltmarsh (CSM), freshwater wetland (FWL), littoral rainforest (LRF), river-flat eucalypt (RFE), swamp oak floodplain forest (SOF), swamp sclerophyll floodplain forest (SSF) and *Themeda* grasslands (THL), where deer sign was present (P) and absent (A). Swamp oak floodplain forest, swamp sclerophyll floodplain forest and *Themeda* grassland TECs have no present data as deer sign was not found at any sites for these TECs.

0% respectively; Appendix S1). A third rainforest species, *Pittosporum undulatum*, was browsed at low intensity in both studies (Nilar *et al.* 2019), indicating it may be resistant to herbivory by both native species and feral deer.

Although our results indicate the impact of deer on woody species was not significant, other research indicates that most of the species identified in our analysis are browsed by deer in other areas of Australia. Using rumen content analysis of sambar deer in Victoria, Forsyth and Davis (2011) identified traces of *A. dealbata* and *B. spinulosa* along with other unidentified *Acacia* species. Keith and Pellow (2005) also concluded rusa deer were likely browsing on *L. parviflorus*, *P. gummii*, *Acacia longifolia*, *Acacia implexa* and *A. oblongifolia* in Royal National Park. Anecdotal evidence also suggests that browsing on *A. oblongifolia* is higher in areas where deer are present (J. Miles, pers. comm., 2019). Without an interaction between woody species and deer presence, herbivory by deer cannot be isolated from herbivory by other sympatric species to explain differences in browsing pressure between woody plant species in our study.

Herbivory by native macropods

Our methods did not distinguish between types of macropod scat, and as such, our analysis deals with all macropods rather than specific species. However, in our study area, there are two abundant macropod species likely responsible for most of our recorded herbivory: the eastern grey kangaroo (*M. giganteus*) and the swamp wallaby (*W. bicolor*). Swamp wallabies can consume a range of both woody and non-woody species, potentially explaining the positive relationship between pellet counts and all types of herbivore damage (Moriarty 2004; Davis *et al.* 2008; Di Stefano & Newell 2008). In contrast, eastern grey kangaroos are primarily grazers (Davis *et al.* 2008), and likely only contributed to the grazing pressure recorded for non-woody plants. As feral deer are likely to occur in most habitat types in the region (Burns 2019), it is likely that both swamp wallabies and eastern grey kangaroos are sympatric with feral deer in our study area. Although Moriarty (2004) found swamp wallaby densities were greater in areas with low rusa deer density, we found no significant difference in the number of macropod pellet groups at sites where deer were present, compared to sites where deer were absent (Appendix S2).

Herbivory in threatened ecological communities

There was significantly greater average grazing intensity of non-woody plants in bangalay sand forest,

coastal saltmarsh, freshwater wetland and littoral rainforest TECs where deer were present. Although deer were only present at one littoral rainforest site in our study, herbivory by deer in rainforest communities has been examined elsewhere in Australia with similar results. Nilar *et al.* (2019) found that in Illawarra escarpment subtropical rainforest, another TEC, the exclusion of native herbivores and rusa deer promoted regeneration for a range of species and significantly increased the mean foliage cover for a number of non-woody herbs and graminoids. The increased average grazing intensity of non-woody plants in coastal saltmarsh and freshwater wetland TECs where deer were present is likely due to their vegetation composition; both TECs are made up of a high proportion of grasses and rushes, which our previous results indicate experience greater average grazing intensity when deer were present. However, as there are no data available on the level of herbivore pressure these TECs are able to sustain, we are unable to conclude whether the increased grazing pressure indicated by our results places any of these sites at significant risk. Non-woody plants in bangalay sand forest TECs also had significantly greater average grazing intensity when deer were present, but the limited sample size (1 site) and lack of data available for this TEC make it difficult to draw conclusions about the broader applications of this finding.

CONCLUSION

In the South Coast Region of New South Wales, herbivory was greater when deer were present. Specifically, deer increased the average grazing intensity of grasses, sedges, rushes and cycads. There was no significant increase in browsing pressure on woody species when deer were present.

The average grazing intensity of non-woody plants in bangalay sand forest, coastal saltmarsh, freshwater wetland and littoral rainforest TECs also increased where deer were present. The results from our studies of herbivore pressure can be used to help create effective management plans in the South Coast region, and direct future monitoring efforts focussed on detecting changing vegetation composition resulting from feral deer herbivory. Additionally, our results can be used to indicate areas where feral deer may have negative impacts on vegetation elsewhere in south-eastern Australia.

ACKNOWLEDGEMENTS

The New South Wales National Parks Service (NPWS) provided funding for this research through the *Saving Our Species Program*. We would like to

thank David McCreery from New South Wales NPWS for his logistical support throughout the study. In addition, various NPWS Service field staff helped facilitate field work and sharing their local knowledge about deer and landscapes in the South Coast of New South Wales.

AUTHOR CONTRIBUTIONS

Heather Burns: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (lead); Writing-original draft (lead); Writing-review & editing (equal). **Philip Gibbons:** Conceptualization (supporting); Formal analysis (supporting); Funding acquisition (lead); Methodology (supporting); Project administration (supporting); Resources (equal); Supervision (lead); Writing-review & editing (equal). **Andrew Claridge:** Conceptualization (supporting); Methodology (supporting); Project administration (supporting); Resources (equal); Supervision (supporting); Writing-review & editing (equal).

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

FUNDING

Funding for this research was provided by the New South Wales National Parks and Wildlife Service through the *Saving Our Species* program.

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SUPPORTING INFORMATION

Additional Supporting Information may/can be found online in the supporting information tab for this article.

Appendix S1. Average browsing intensity and abundance (count) for all 118 woody species recorded.

Appendix S2. Differences in mean macropod pellet group count where deer sign is present and absent.