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Article

The Fire and Fodder Reversal Phenomenon: Vertebrate Herbivore Activity in Burned and Unburned Tasmanian Ecosystems

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Abstract: Very few multi-species or ecosystem comparisons of post-fire vertebrate herbivore activity and food preference exist to inform fire-management and conservation strategies. We inferred post-fire (1-3 years) native and introduced vertebrate herbivore activity and attraction to six diverse temperate vegetation communities (grassland to rainforest) from scat counts. We hypothesised that where fire reduced herbaceous and grassy vegetation ('fodder'), vertebrate herbivores would decline, and that post-fire preferences of native versus exotic herbivores would differ significantly. Instead, we found evidence for a 'fire and fodder reversal phenomenon' whereby native macropod *and* exotic rabbit scats were more abundant *after* fire in consistently 'fodder-poor' vegetation types (e.g wet forests) but more less abundant after fire in previously fodder-rich vegetation communities (e.g. grassland). Fodder cover predicted native macropod, wombat, and introduced deer activity and bareground cover was strongly associated with introduced herbivore activity only, with the latter indicating post-fire competition for food sources due to their abundance in high altitude open ecosystems. We therefore found environmental and vegetation predictors for each individual species/group and suggest broadscale multi-environment, multispecies observations to be informative for conservation management in potentially overlapping post-fire niches.

Keywords: Tasmania; Australia; herbivory; macropods; soil moisture; grazing; blazing

1. Introduction

To adequately conserve the biota of protected areas, fire-environment-herbivore interactions need to be examined in different ecosystems. Fire is a physical consumer, which can exhaust above-ground biomass rapidly, whereas herbivory is a more constant, biological driver of biomass consumption [1,2]. Though fire and herbivory exert significant influences on biophysical parameters in ecosystems, their interaction is less understood than their singular effects. Importantly, interactions within the few years post-fire are likely to be the most critical.

The food resources in the post-fire environment can be greater than those available before fire, attracting vertebrate herbivores (henceforth herbivores) from adjacent, unburned vegetation [3-8]. Post-fire regrowth, often rich in nitrogen, can be a critical resource for herbivores, particularly in areas that experience long dry seasons [1,9]. However, post-fire conditions are not always more attractive to herbivores. For instance, two years after fire there were more macropod scats in unburned grassy vegetation than in burned grassy vegetation in lowland Tasmania, while in highland vegetation and that dominated by sedges and shrubs there were more scats in the burned vegetation [10], suggesting that fire reduces food resources where the vegetation is rich in them (Fig 1).

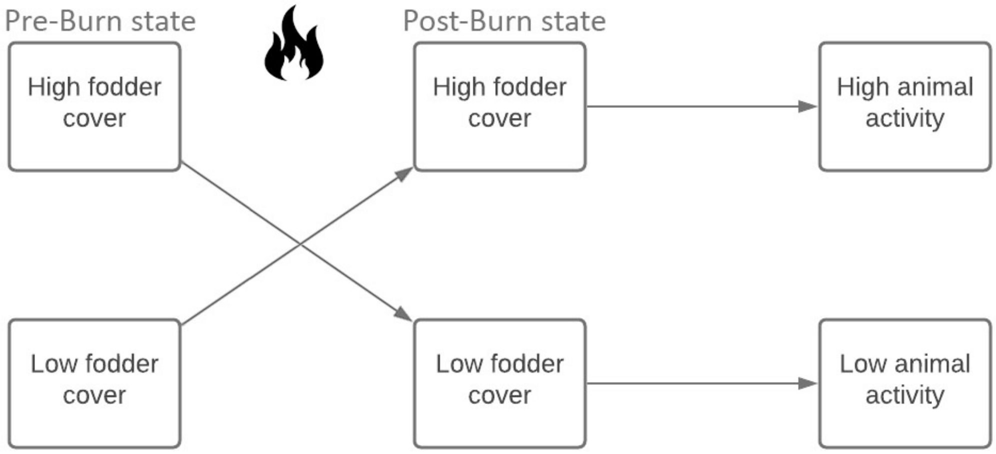


Figure 1. In certain ecosystems, the relative abundance of fodder before and after a fire event can have meaningful impact on local vertebrate herbivore activity.

The effects of recent fire on populations of introduced herbivores may exacerbate conservation problems associated with their grazing and browsing, as in the elimination of *Allocasuarina verticillata* by rabbits in South Australia [11,12]. Alternatively, grazing pressure in recently burned grasslands can create lawn grasslands from tussock grasslands, increasing their conservation significance [10,13].

Different herbivore species in the same area usually have different dietary preferences, as with the short-grass and generalist grazers of the South African savannas [14], and the marsupial macropod grazers in Australia [15,16]. Fire could therefore be considered a singular point-source disturbance in an otherwise complex environmental matrix that can be further preferentially modified by grazing herbivores with different needs.

The counting of scats (dung/faeces/faecal pellets) has been widely used as a bio-indicator of herbivore activity. Scat counting is a highly effective technique to infer presence and/or abundance for many herbivores, including rabbits [17], macropods [18], deer [19], cattle [20], and elephants [7,21].

Contemporaneous comparisons of the effects of burning on herbivore scat counts in different vegetation types are restricted to macropods in grasslands, sedgelands and dry eucalypt forests [10]. In the present study, we extended upon the previous investigation of the effects of recent fire on the attractiveness of three Tasmanian vegetation communities to macropods, to the effects on six vegetation types and four vertebrate grazing animal groups, two of which are exotic.

We hypothesised that the effects of fire on herbivore abundance would increase with decreasing abundance of food plants in the unburned vegetation and that the native macropods and common wombats *Vombatus hirsutus* (Perry) would respond differently to the environmental effects of fire than the introduced rabbit *Oryctolagus cuniculus* (Linnaeus) and fallow deer *Dama dama* (Linnaeus).

2. Study Area

Tasmania is a mid-latitude, temperate island state of Australia featuring high geodiversity, maritime superhumid to semiarid climates, with no point in Tasmania further than 115 km from the ocean [22]. Overall, 21% of Tasmania is currently protected as World Heritage Area, and another 21% is preserved in National Parks and other protected areas [23].

Vegetation ranges from coastal heathland to alpine fjaeldmark, from tussock grassland to rainforest. Most of the native vegetation of the island is dominated by either trees in the genus *Eucalyptus* or hummock sedges in the genus *Gymnoschoenus*. There is negligible top-down pressure from large predators and a relative tectonic stability, meaning that most of the native vegetation is shaped by climate, topography, soils, fire, and herbivory. The most widespread plant communities of Tasmania are (Figure 2):

Dry eucalypt forests - flora has many scleromorphic plants and an open understorey. Bushfire is critical to the regeneration of scleromorphic plants, such as those in the genus *Eucalyptus* [24].

Highland treeless vegetation – This ecosystem is typically dominated by scleromorphic shrubs that are not well-adapted to fire [25].

Grasslands - in Tasmania, grasslands are typically dominated by native tussock grasses and have low forb and shrub cover. Both fire and grazing can be important in preventing invasion of woody plants [26].

Moorlands, sedgelands, and rushlands - These ecosystems dominated by sedges, rushes and other hard graminoids predominantly occur in areas with high rainfall and low fertility. Fire can burn in any season after as little as 1 –2 rain-free days [27].

Scrub, heathland, and coastal complexes Occurring near the coast, this vegetation grouping has little else in common, with heath and scrub being scleromorphic vegetation occurring largely on infertile soils, with the latter replacing the former in the absence of fire [28], and the latter being the vegetation within the fertile saltspray zone, variously dominated by large-leaved shrubs and sand-binding grasses [29].

Wet eucalypt forests are characterised by understoreys dominated by rainforest trees, broad-leaved small trees or by tree ferns [30], They occur in areas of high rainfall with reliable summer rain. Ignition is infrequent and undesirable due to accumulation of large fuel loads and the potential for catastrophic loss of biota.

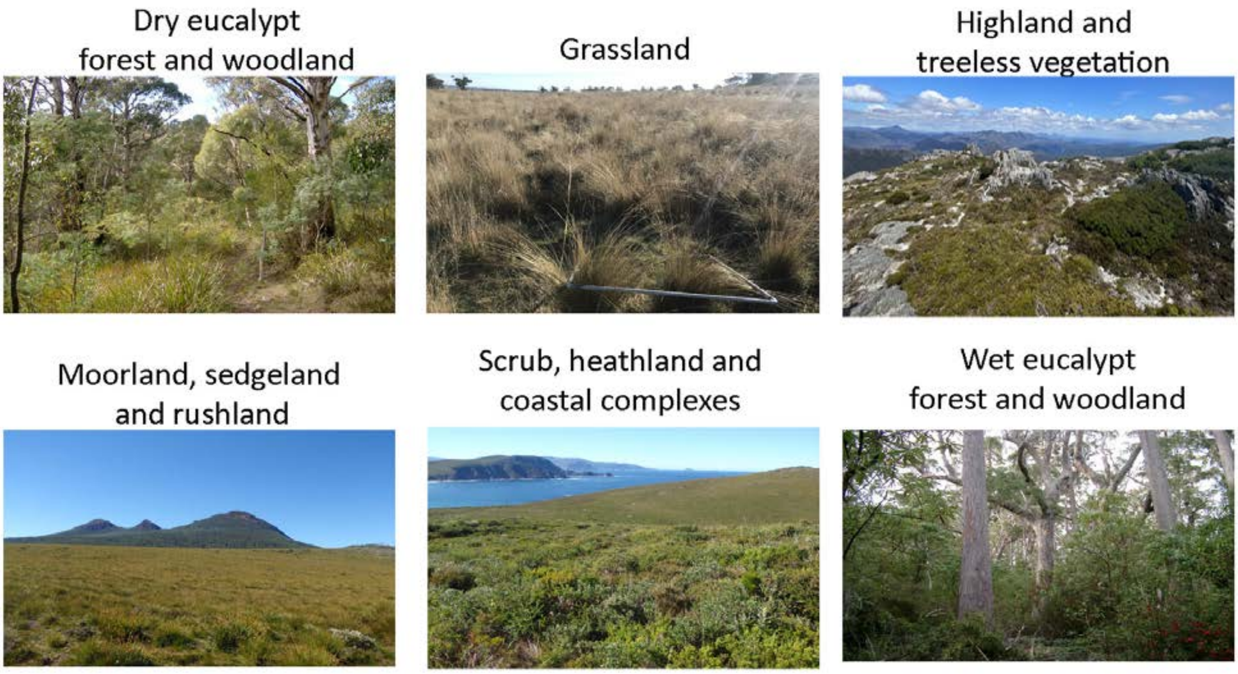


Figure 2. Images of the six vegetation types. Photographs: top left – Jamie Kirkpatrick, top middle – David Heaton, top right – Melinda McHenry, bottom row – Jamie Kirkpatrick.

Native and introduced vertebrate herbivores of Tasmania

The most widespread and abundant macropods in Tasmania are the Tasmanian subspecies of Bennett's wallaby *Notamacropus rufogriseus* (Desmarest) and the Tasmanian pademelon *Thylogale billardierii* (Desmarest). Pademelons select the dense understorey of native forests and plantations for shelter, whereas the Bennett's wallaby has a greater home-range area, often in eucalypt forests with open understoreys [16,31]. Wallabies and pademelons preferentially consume grasses, though pademelons also consume broad-leafed forbs [15] where these are available and shrubs, including many weeds [32]. Both species browse the lower branches of trees [33]. Bennett's wallabies occur from sea level to the highest peaks in Tasmania, while pademelon are absent only from the true alpine zone (Figure 3).

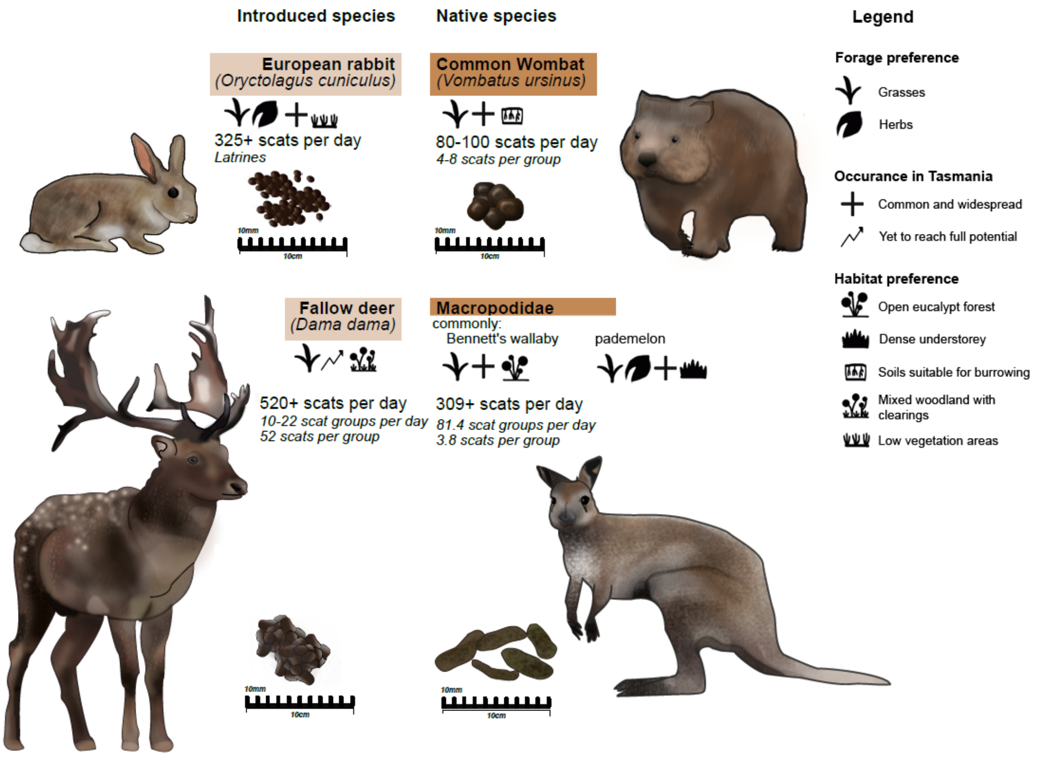


Figure 3. Approximate defecation rate and habits for the four herbivore groups in this study. Included here are forage preferences, population occurrence, and habitat preference in Tasmania. These results are taken from previous papers as discussed in the following sections.

Johnson *et al.* [34] estimated the average defecation rate of the Bennett's wallaby to be 81.4 per 24 hours (3.82 pellets per defecation). Scat deposition typically occurs directly where the individual feeds, with most feeding occurring around dawn and dusk [34]. This means scat location and abundance can provide insight into macropod feeding behaviour. Wiggins & Bowman [31] found 90% of macropod scats persisted undecomposed in the landscape for five months, with greater than 50% persisting over an 11-month period.

Wombats create burrow systems or shelter in caves from sea level to the highest peaks of Tasmania. Wombats have a strong preference for grasses in their diet [35-37]. Wombats will also feed on sedges, rushes, and lilies, using adapted upper incisor teeth and hypsodont molars to gnaw through tougher vegetation [36]. In a single night, a wombat will commonly produce 80-100 scats. They are usually placed in latrines, away from forage plants [37].

Fallow deer were introduced to Tasmania in 1829 [39], and mainland Australia in the 1880s. Deer have not yet reached their potential range in Tasmania [40]. Deer are ruminants, predominantly grazing on softer grasses, though they may browse upon soft bark, new shoots, seed heads, leaves and flowers [41,42]. Over-population of deer has caused vegetation degradation across the globe [43-46].

Deer pellet production ranges between 10 groups per day in spring to 22 groups per day in summer [46]. These groups typically occur where deer feed, consisting of approximately 52 scats. Scats can be dispersed by trampling, or through aeolian processes, so individual deer scats must be counted. Deer scat groups can persist in the Tasmanian landscape up to 17 months after defecation [42].

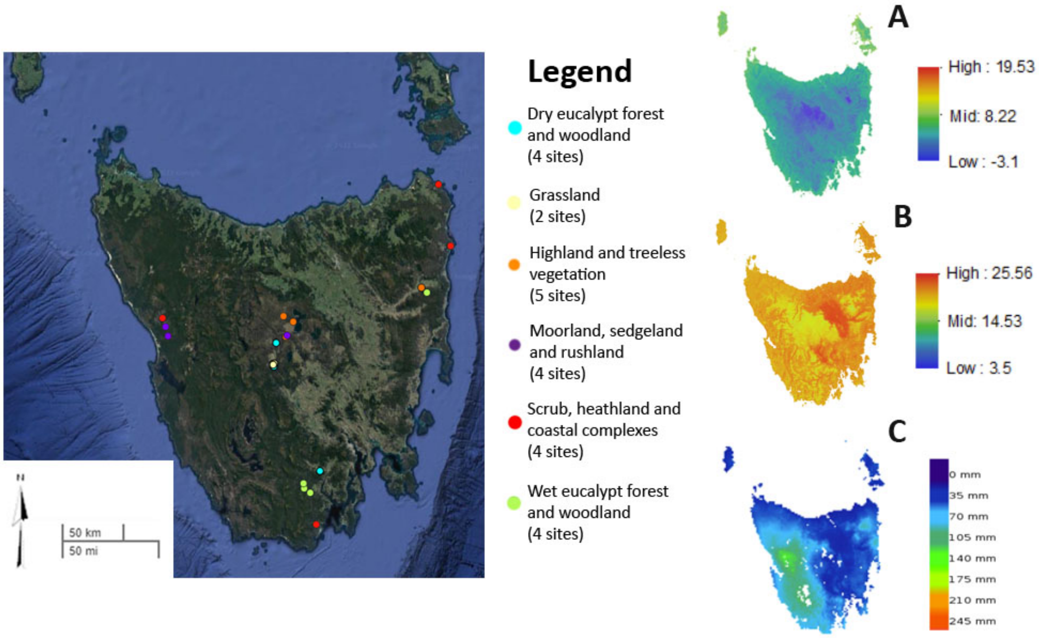
Since their introduction to Tasmania, rabbits have become common and widespread, particularly in low vegetation with deep soils suited to building warrens. Rabbits generally prefer grasses and forbs [47]. Groups of rabbits (3-11 individuals) build warrens and may consume the roots and seeds of grasses, which may lead to soil erosion and the loss of native plant species [48]. Such degradation has inspired the common labelling of the species as Australia's most destructive pest [49].

Like other species of the *Leporidae* family, rabbits produce both soft and hard scats, ingesting the former which are rich in protein and vitamins [50]. Estimations of total scats per day vary with diet, location, and climate, with groups of rabbits often piling scats at latrine sites [51]. Wood [52] recorded an average of 325 hard scats per rabbit per day, fluctuating between 276 in winter and 448 in spring, with 99.3% persisting over seven weeks, and 95% over a 14-week period.

3. Materials and Methods

Site selection

The *Fire History* layer [53] was used to identify the most recent fire event between January 2018 and November 2020. This area was intersected with each of the following vegetation layers in *TASVEG 4.0 Groups* [54]: dry eucalypt forest and woodland (henceforth dry forest), grassland, highland and treeless vegetation (henceforth highland), moorland, sedgeland and rushland (henceforth sedgeland), scrub, heathland and coastal complexes (henceforth heath), and wet eucalypt forest and woodland (henceforth wet forest). The areas thus discriminated were examined on aerial photograph images with contours superimposed to find sites at which unburned and recently burned vegetation of the same type were adjacent in similar topographic situations and which were accessible by vehicle or a short walk. An attempt was made to select potential sites over the main landmass of the island of Tasmania. Some potential sites were excluded because it was not possible to



get permission to access them. Others were excluded because the mapping was not accurate. Twenty-three sites were selected (Figure 4).

Figure 4. Location of study sites in Tasmania (main), dots indicate a paired (burned and unburned) transect, with colours indicating vegetation type. Inserts are (A) mean daily minimum temperature for July (°C), (B) mean daily maximum temperature for January (°C), and (C) mean precipitation for February, the driest month [53].

Sampling strategy

Sites were visited once only, with data collection for all sites spread over 5 months, between March and July 2021. At each site, a 50 m linear transect was laid, starting between 5 and 15 m inside the burned area, running orthogonal to the burn edge, where possible, to reduce possible edge effects. Another transect was similarly placed in an adjacent unburned area of the same vegetation type. At 10 m intervals, including 0 m, a 1 x 1 m quadrat containing a 100-cell grid was placed along the transect, laid on the right-hand side of the tape when facing the burn centre. Each 10 m interval was the centre point of the quadrat edge. This resulted in six quadrats per transect, with elevation recorded at each quadrat using the Garmin GPSMAP 64. In addition, *local* (surrounding 15 m of quadrat) scorch height was recorded to the nearest metre where possible. Slope was also recorded at the local level, categorised into *very gentle* (<1-3°), *gentle* (3-10°), *medium* (10-30°), and *steep* (>30°), then ranked 1 to 4 respectively.

In all quadrats, percentage cover was estimated to the nearest percent with the aid of a 10 x 10 grid, for each of rock, grass, herb, sedge/rush, shrub, pteridophytes, cryptogams, bare ground, coarse woody debris (greater than 5 cm diameter), ground litter and canopy cover. Bare ground cover was only counted if no other cover attributes were above. Within each quadrat, herbivore scats were individually counted and recorded as macropod, wombat, deer, or rabbit. Bennett's wallaby, pademelon, and eastern-grey kangaroo (also known as the forester kangaroo) (*Macropus giganteus*) scats overlap in shape and size, so were merged as 'macropod' to reduce observer error and provide greatest accuracy in overall scat count [55]. No eastern-grey kangaroo sightings were made during fieldwork, nor during any travels between sites, so they may represent little to none of the final macropod scat count.

Soil attributes were collected through in-situ measurement with the Fieldscout (TDR 150). Inside each quadrat, the two 7.6 cm rods were pushed downwards into the ground layer (O and/or A horizon) where possible. Rods were fully inserted as the sampling volume comes from the entire length, and any exposed rod reduces sampling accuracy. If resistance was met, the rods were cleaned and inserted into a different section of quadrat. This was repeated until a reading was made. A reading provided soil moisture as volumetric water content (%), soil conductivity as micro siemens per centimetre (µS/cm), and soil temperature in degrees Celsius (°C).

Statistical analyses

Statistical analyses were performed using the R statistical language program (Version 1.4.1717) unless otherwise stated. A result was regarded as significant if p =/<0.05. One-way Analysis of Variance (ANOVA) was used to determine if scat counts for each species differed between burned and unburned paired sites, or between vegetation types.

The ratio between mean scat numbers per square metre in the recently burned areas and that in the adjacent controls was calculated for each of the four herbivore taxa by each of the six vegetation types. The direction and linear strength of the relationships between the ratios for each taxon and the mean unburned fodder cover was calculated for each of the six vegetation types using the product moment correlation coefficient.

For macropod scat abundance, all combinations of theoretically feasible predictor variables were used to create general linear models using the default procedure in

Minitab16. In these models, site location was used as a random factor. Significant predictors, which formed the best explanatory model, were explored graphically using the *ggplot2* package in R version 1.4.1717 [56].

For wombat, deer and rabbit, quadrat-level observations of scats were dominated by zero-inflation, which was expected from their defecation habits and latrine use. Quadrats were therefore analysed as scat 'presence versus absence', rather than scat abundance used for macropods. All combinations of predictor variables were tried in a logistic regression for best fit. Logistic regression was completed through Minitab 16 Statistical Software (Minitab 2010). Significant predictors, which formed the best model for each group, were explored graphically using the *ggplot2* package and base R version 1.4.1717 [56].

In order to compare the significant predictor of macropod scat abundance in the present study with a similar legacy dataset [10], percentage fodder cover with *site location* as a random factor was used to predict macropod scats in the subset of dry forest, sedgeland and grassland quadrats in the present study and the same model applied to fodder dry weight with all quadrats in the earlier study.

4. Results

Vegetation type was a significant predictor for scat abundance in macropods (p = <0.001), wombats (p = <0.05), deer (p = <0.05), and rabbits (p = <0.05). Macropod scats were the most abundant of the four herbivore groups. The highest quadrat scat number was 101 for deer scats in highland vegetation. Only macropod scats were observed in wet forest, with rabbits also absent from grassland sites, and deer also absent from heath (Figure 5).

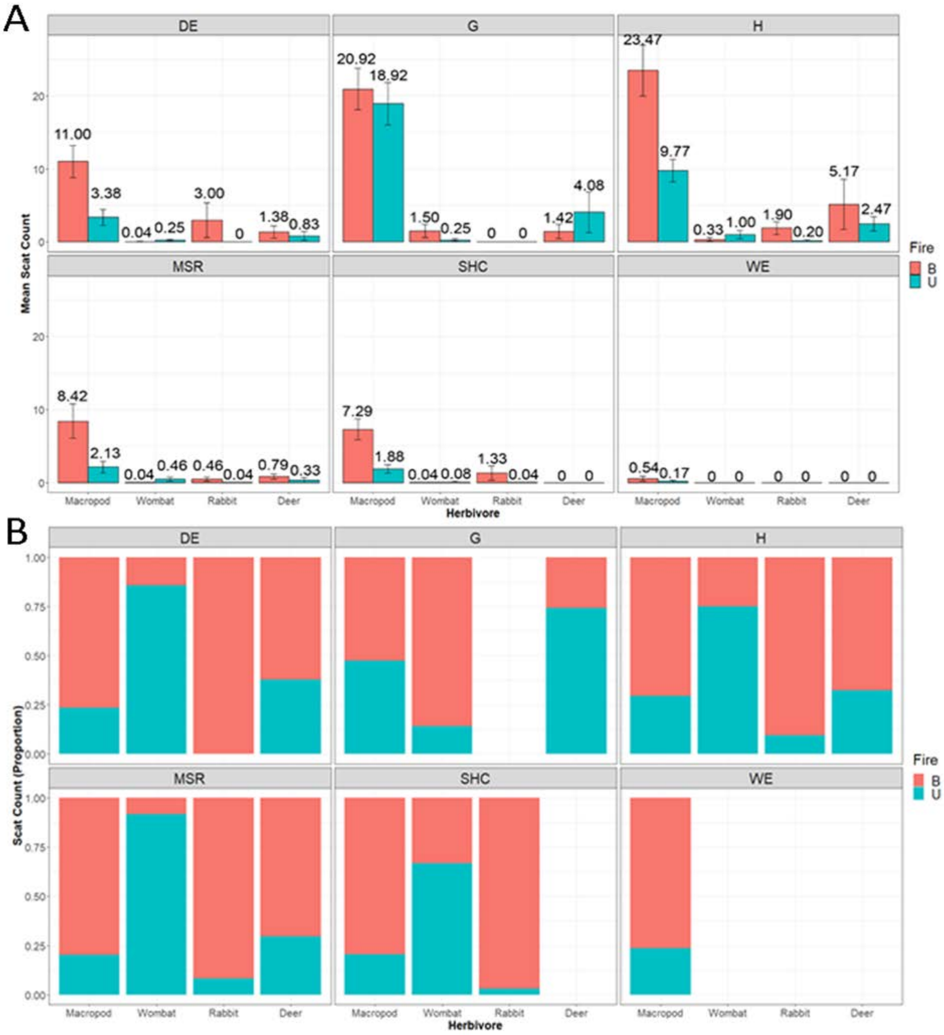


Figure 5. (A - top) Mean scat count with standard error bars for recently burned (B, red) and unburned (U, blue) sites, by vegetation community type and (B - bottom) scat count presented as a proportion of abundance within recently burned (red) and unburned (blue) environments. Dry forest (DE), Grassland (G), Highland (H), Sedgeland (MSR), Heath (SHC), and Wet Forest (WE).

Macropod scat means were higher in burned transects within each vegetation type. In contrast, wombats scat means were only higher in burned grasslands, with greater abundance in the unburned pairs, and complete absence in wet forest. Deer scat means were higher in burned dry forest, highland, and sedgeland, but lower than unburned pairs in grasslands, and absent from scrub and wet forests. Rabbit scat means were higher in burned than unburned plots where present and absent from grasslands and wet forest (Figure 5).

The greater the fodder cover in the unburned area the less was the concentration of scats in the recently burned areas (scats burned/scats unburned) for both macropods (r = -0.864, $d.f.$ = 5, p = 0.023) and rabbits (r = -0.989, $d.f.$ = 3, p = 0.020). The relationship was the reverse for wombats (r = 0.928, $d.f.$ = 4, p = 0.023). There was no relationship for deer (r = -0.038, $d.f.$ = 3, p = 0.962).

Fodder cover and the cover of shrubs were the most explanatory predictors with significant slopes for macropod scat abundance (Regression Equation: Macropod = 0.025 + 0.977 Fodder - 0.0113 Shrub; R^2 = 98.74%) (*df* $_{(2,275)}$; *F* = 8873.08; *p* = <0.001). This regression equation gave the highest r-squared value, but only by 0.02 when compared to the regression equation of fodder alone (R^2 = 98.72%). Shrub cover (*F* = 3.78) contribution to the model may be largely an artifact of fodder (*F* = 8371.66) absence, only contributing 1:2,214.72 or 0.045% to the model. Therefore, fodder presence appeared to be the most significant control on macropod scat count (Figure 6).

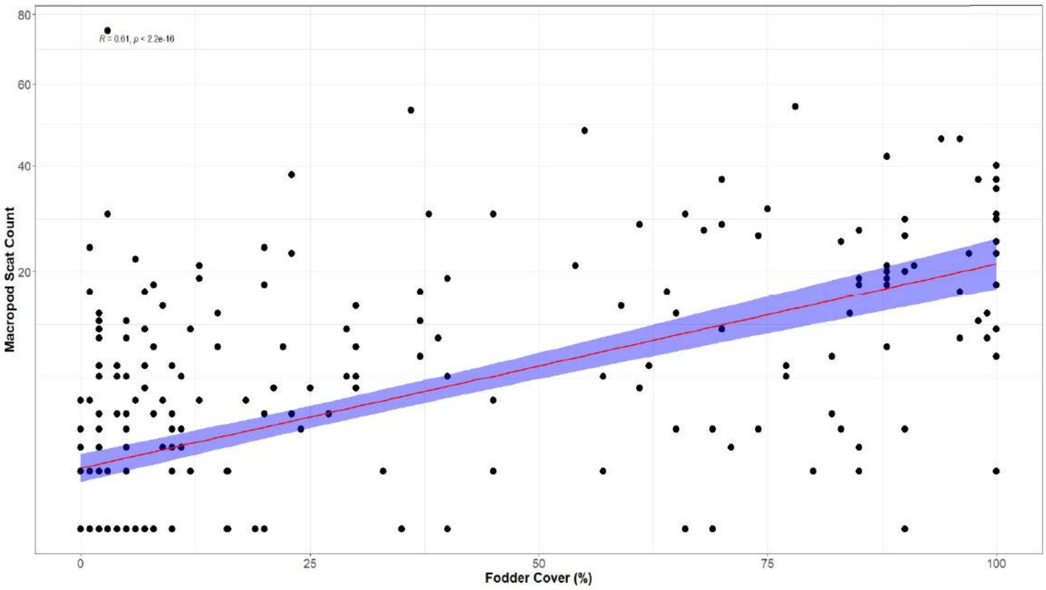


Figure 6. Total scat count (log10) recorded for macropods by percentage fodder cover. Regression line in red, with 95% error bars in blue. Correlation coefficient; R = 0.61, p = <0.001.

Fodder dry weight was a very strong predictor of macropod scats per site in the legacy data set (Regression equation: macropod scats = 110.6 + 703.4 Fodder; R^2 = 83.2%) (*df* $_{(1,6)}$; *F* = 24.77; *p* = <0.005), as in our comparison data set using fodder cover (Regression equation: macropod scats = -0.206 + 0.986 Fodder; R^2 = 98.5%; *df* $_{(1,119)}$; *F* = 8016.94; *p* = <0.001).

Wombat scats were present in 16 locations. Percentage shrub cover (*z* = 3.58; *p* = <0.001) and percentage fodder cover (*z* = 2.83; *p* = 0.005) were the most explanatory predictors in the best wombat scat binary logistic regression model (wombat scats = -3.59639 + 0.0178 Fodder - 0.0290 Shrub) *(Test that all slopes are zero: G = 15.309, DF = 2, P-Value = 0.000)* (Concordant = 74.1%, Discordant = 25.3%).

Deer scats were present in 17 locations. Percentage bare ground cover (*z* = 3.49; *p* = <0.001) and percentage fodder cover (*z* = 3.45; *p* = <0.05) were the most explanatory predictors in the best deer model (deer scats = -2.89593 + 0.0318656 Bare Ground + 0.0169178 Fodder) *(Test that all slopes are zero: G = 18.820, DF = 2, P-Value = 0.000)* (Concordant = 73.8%, Discordant = 25.7%).

Rabbit scats were present in 12 locations. Percentage bare ground cover (*z* = 5.45; *p* = <0.001) and percentage herb cover (*z* = 3.93; *p* = <0.001) were the most explanatory predictors of rabbit scat presence/absence in the best model (rabbit scats = -3.37802 + 0.0553503 Bare Ground + 0.0367967 Herb) *(Test that all slopes are zero: G = 43.018, DF = 2, P-Value = 0.000)* (Concordant = 86.1%, Discordant = 12.8%).

4. Discussion

Our hypothesis that the effects of fire on herbivore abundance would increase with decreasing abundance of food plants in the unburned vegetation was consistent with our data for macropods and rabbits but was inconsistent with our data for wombats and deer. This represents a ‘fodder reversal phenomenon’ not observed previously in the literature, due presumably because our study is one of the first to compare so many species over such a diverse set of environmental variables and vegetation types.

That wombats appeared beneficially affected by fire in grassland relative to macropods or even rabbits may reflect their known preference for the softer herbs and grasses [36,37] that can be maintained by grazing after fire [57]. Conversely, macropods and rabbits have broader food preferences, extending to trees, shrubs, and coarser grasses, which are available in higher volume in unburned grasslands. The lower wombat abundance of burned heath, highland, dry forest and sedgeland vegetation communities relative to their unburned pairs (Table 1) may in fact be explained by behavioural, rather than exclusively food preferences. Wombats prefer sites without palatable vegetation to establish latrine sites, which in this study was a defining characteristic of unburned sections of adjacent burned areas. Therefore, it is evident that post-fire sward composition and cover is beneficial for some native vertebrate herbivores and not others, a fodder reversal phenomenon that occurs across a diverse suite of environmental variables and vegetation communities.

Table 1. Ratio of scats in burned quadrats to those in unburned quadrats and mean fodder cover by vegetation type and herbivore taxa. * = herbivore not present.

Vegetation type	Macropod	Wombat	Deer	Rabbit	Fodder (%)
Dry eucalypt	3.25	0.16	50.00	1.66	34.0
Grassland	1.11	6.00	*	0.35	95.0
Highland	2.40	0.33	9.50	2.09	30.0
Sedgeland	3.95	0.09	11.50	2.39	22.0
Heath	3.88	0.50	33.25	*	4.5
Wet forest	3.18	*	*	*	1.0

Deer scats were abundant in burned environments in this present study, consistent with the results of fallow deer research in mainland Australia [58], Portugal [59], and the United States [60]. Their absence from the grassland in the present study is not typical however, and presumably has occurred because much of the low altitude, low-rainfall Tasmanian Midlands grassland country is fenced to exclude them. Thus, the non-significant relationship between the ratio of scats in burned versus unburned and fodder cover may not well represent the true natural range or activities of the species.

We did however find some communalities between native herbivores, in that the abundances of their scats were best predicted by fodder and shrub cover and some communality between the two exotic species in that the abundances of their scats were both well-predicted by bare ground. However, the hypothesis that the native macropods (Macopodidae) and common wombats (*Vombatus hirsutus*) would respond differently to the environmental effects of fire than the introduced rabbit and fallow deer was not supported by our data, with all species having distinct environmental responses.

Fallow deer produce patches of bare ground during the rutting season in the United States [61], with the same behaviour seen in sambar deer (*Rusa unicolor*) in south-eastern Australia [62]. However, their association with bare ground seems more likely to result from the slow rate of recovery of the highland vegetation in which they were abundant than from their direct effects.

Rabbit scats were associated with greater herb cover, consistent with work in similar temperate regions, where low, herbaceous cover attracts grazing rabbits [63,64]. Overgrazing of herbs can occur in areas of high-density rabbit populations [65,66], which can increase bare ground exposure [67]. Again, the relationship with bare ground is more likely to be a product of the recovery rate of the vegetation types in which they occur than a direct effect of their presence.

5. Conclusions

In a changing climate in which fire is likely to be a more frequent event [68], our data suggest minimal effects on populations of macropods and wombats are likely. Similarly, frequent fire will not be likely to substantially affect populations of rabbits. However, our data do suggest that deer are disproportionately favoured by recent fire.

We have shown that fire can have disproportionate impacts to fodder cover between Tasmanian ecosystems, whereby fire reduced food resources in vegetation rich in them. The present study has demonstrated a complex fire-environment-herbivore matrix, and although currently widespread and abundant, native species are not free from future climate threats, particularly in the post-fire niche. Conservation management in Tasmania must consider multi-species and multi-ecosystem comparisons and the fire and fodder reversal phenomenon in the mitigation of threats to native species to maximise native species' ability to occupy resources in a changing climate.

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Data Availability Statement: Data are available by request to the corresponding author.

Conflicts of Interest: The authors declare no conflict of interest.

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