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A rapid assessment of potential herbivory impacts of a reintroduced mammal in a predator-free woodland sanctuary

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Author contributions

LSO, GB, CW, and RC conceptualised the study. LSO and GB designed the methodology with input from EC, CW, and RC. LSO, GB, and EC collected the data. LSO analysed the data and led the writing of the manuscript. All authors contributed to manuscript drafts and gave final approval for publication.

Data availability

All data and R code used in this study is available from https://github.com/Isoloughlin/MFWS_RapidFloristics_2021

Summary

Fenced sanctuaries that exclude feral predators are critical for threatened species conservation. However, adaptive management of these sanctuaries requires careful consideration of the potential impact herbivore populations free from predation can have on the condition of native vegetation. The Mulligans Flat Woodland Sanctuary (MFWS) in the Australian Capital Territory comprises critically endangered box-gum grassy woodland, threatened orchids, abundant macropods, and a reintroduced population of the eastern bettong (*Bettongia gaimardi*, hereafter “Ngaluda”). To understand how Ngaluda, along with other herbivores, may be potentially impacting vegetation across the MFWS we undertook a rapid assessment of indicator plant species. We monitored 106 plots for 13 target species (10 species with tuberous roots that the burrowing Ngaluda would be preferentially targeting and three non-tuberous species). We found that most floristic indicators we investigated – including richness of target species and the abundance of lilies – were higher in the Goorooyarroo area of the MFWS (where Ngaluda are absent and wallabies are rare) compared to the Mulligans Flat area of the MFWS (where Ngaluda are present and wallabies are abundant), suggesting a negative impact of the overall herbivore assemblage of Mulligans Flat. However, within just Mulligans Flat, some indicators, including the abundance of a common orchid, were significantly lower in areas associated with high Ngaluda activity irrespective of other herbivore densities. We found no instance of Ngaluda presence or higher activity being associated with higher values for any floristic indicator we investigated. These results are consistent with known impacts of abundant herbivores and reintroduced digging mammals in other predator-free sanctuaries in Australia. Our results highlight that Ngaluda herbivory is likely outweighing any positive effect of their diggings on native vegetation, and indicates the need for careful risk mitigation when deciding how critically endangered animals and vegetation communities are managed together in sanctuaries.

Key words

Canberra; Buru; Baray; box gum grassy woodland; Dharaban; digging marsupial; geophytes; orchids; restoration; rewilding; urban ecology

Implications for Managers

- Management of both extant and reintroduced species that are likely to be highly successful in predator-free fenced Sanctuaries needs to consider and monitor for the potential negative ecological effects of those species.
- While the reintroduction of burrowing species like bettongs will promote native forbs and geophytes through their diggings, these benefits can potentially be outweighed by negative effects of their herbivory in a predator-free sanctuary.
- Knowledge of the effects that reintroduced herbivores have on the recipient ecosystem of a sanctuary is critical for effective management for the benefit of both threatened animals and vegetation communities.

Introduction

Conservation management frequently requires decisions to be made despite high uncertainty about the predicted outcome (Halpern *et al.* 2006; Wilson *et al.* 2007). This is particularly true for the management of rare and threatened species where data on their ecological niche, threats and function are likely limited (Scheele *et al.* 2017; Murphy *et al.* 2018; Neeson *et al.* 2018). Taking an adaptive management approach that explicitly recognises important areas of uncertainty and seeks to resolve them through integrated research and management is critical for improving the knowledge-base and conceptual models that underpin decision making (Lindenmayer *et al.* 2008; Chadès *et al.* 2017; Gillson *et al.* 2019). Adaptive management also provides a framework for considering the trade-offs, risks, and potential conflicts between multiple conservation objectives associated with a decision (Driscoll *et al.* 2016; Fraser *et al.* 2017).

Considerations of risk, uncertainty, and balancing multiple conservation objectives are particularly important for the management of fenced wildlife sanctuaries. In Australia, fenced sanctuaries have played a key role in securing populations of critical-weight-range native mammals threatened by predation from the invasive red fox (*Vulpes vulpes*) and feral cat (*Felis catus*) (Dickman 2012; Kanowski *et al.* 2018). However, fenced sanctuaries are prone to ecosystem imbalance due to the absence of predators and competitors and the resulting overabundance of herbivores (Verdon *et al.* 2016; Linley *et al.* 2017; Moseby *et al.* 2018). For example, the successful reintroduction of digging mammals (such as burrowing bettong *Bettongia lesuer* and bilby *Macrotis lagotis*) across multiple sanctuaries in semi-arid Australia has been associated with decreases in floristic values and vegetation condition, including lower plant species diversity, reduced frequency of important functional plant groups, and declines in seedling abundance and survival (Verdon *et al.* 2016; Linley *et al.* 2017; Moseby *et al.* 2018; Kemp *et al.* 2021; Michael *et al.* 2022). Ecologically, this is analogous to the predictable impacts of abundant large herbivores anywhere apex predators have been extirpated (e.g. kangaroos *Macropus* spp. throughout south-eastern Australia; Morgan 2021) and why densities of such species are actively managed in sanctuary settings (Manning *et al.* 2011; Shorthouse *et al.* 2012). However, these examples of reintroduced species represent a management trade-off of accepting some floristic value loss in a widespread vegetation community to prevent the extinction of highly threatened herbivores.

In 2011, the eastern bettong (*Bettongia gaimardi*, hereafter referred to by their traditional Ngunnawal name “Ngaluda”) was successfully reintroduced to a sanctuary dominated by critically-endangered yellow box (*Eucalyptus melliodora*) – Blakely’s red gum (*E. blakelyi*) grassy woodland and derived grassland in the Australian Capital Territory (Manning *et al.* 2019). The aim of the reintroduction was both to secure a species that had been extinct from the Australian mainland for a century and restore lost ecological function to the woodland community (Shorthouse *et al.* 2012; Manning *et al.* 2019). Ngaluda are digging mammals – widely considered ecosystem engineers – whose soil disturbance

benefits the ecosystem by facilitating nutrient cycling and seedling establishment (Rose & Johnson 2008; Eldridge & James 2009; Ross *et al.* 2020). While Ngaluda diggings and their positive effects have been widely acknowledged and researched at the sanctuary (Manning *et al.* 2019; Munro *et al.* 2019; Ross *et al.* 2019, 2020), any potential negative effects that Ngaluda may have on plants from herbivory and soil disturbance remain unknown.

The aim of this study was to rapidly assess some key floristic values from across the sanctuary area where Ngaluda are present and compare to the floristic values of adjoining woodland reserves where Ngaluda are absent. Complicating our inference is that wallabies (swamp wallaby *Wallabia bicolor* and red-necked wallaby *Notamacropus rufogriseus*, hereafter collectively “Baray”) are highly abundant in the sanctuary but rare in the adjoining reserves. However, the need to complete a rapid assessment was motivated by three time-sensitive factors. First, Ngaluda were soon to be translocated into a new predator-free sanctuary comprising the adjoining woodland reserves. Second, there were anecdotal observations suggesting that orchids and other geophytes were very abundant in areas of the new sanctuary compared to the established sanctuary where they appeared rare. Third, no systematic floristic monitoring of either area had been undertaken in the previous 10 years, meaning spring of 2021 was potentially the final opportunity to compare data on the presence and absence of Ngaluda between the two areas. We developed a targeted “indicator” species survey that allowed us to quickly collect spatially extensive and comparative data. To understand the relative influence of different drivers of floristic values we asked three questions: (1) to determine the effects of overall difference in herbivore assemblages on floristic value we asked *does the abundance of lilies, orchids and other indicator groups and species differ among the different sanctuary areas?* (2) to determine the effects of ground cover dominance independent of herbivory we asked *do ground cover and other vegetation attributes strongly influence plant indicator groups or species?* And (3) to determine the Ngaluda effects independent of Baray we asked *within just the sanctuary area where Ngaluda are present, do differences in overall macropod grazing influence plant indicator groups or species?*

Methods

Study site: the Mulligans Flat Woodland Sanctuary

Our study was conducted at the Mulligans Flat Woodland Sanctuary (MFWS), which consists of two adjoining nature reserves on the urban fringe of Canberra, south-eastern Australia. The MFWS primarily contains critically endangered box-gum grassy woodlands and derived grasslands, with small areas of open forest and patches of natural temperate grassland (Lepschi 1993; McIntyre *et al.* 2010). These woodlands, dominated by *E. melliodora* and *E. blakelyi*, have been significantly impacted by land clearing, livestock grazing, invasive pest species, and loss of indigenous management following European occupation (Yates & Hobbs 1997; Lindenmayer *et al.* 2010). The Ngunnawal people are the

Traditional Custodians of the land and waters in the ACT, and for tens of thousands of years actively managed woodlands in the region, shaping the structure and function of these ecosystems.

The MFWS comprises an original 458 ha sanctuary (est. 2009) in the Mulligans Flat Nature Reserve (hereafter “Mulligans Flat”) and an extended 801 ha sanctuary (est. 2018) made up of part of the Goorooyarroo Nature Reserve (hereafter “Goorooyarroo”, ~60% of the extended sanctuary) and three environmental offset areas (hereafter “Offsets”, ~40% of the extended sanctuary) (Figure 1). All areas of the MFWS have similar recent histories of once being leasehold grazing land, with some areas of cropping and pasture improvement before being conserved and managed for their ecological values (McIntyre et al. 2010; Shorthouse et al. 2012). However, the areas differ in total time and intensity of agricultural impacts, the legacy effects of which determine floristic community composition (McIntyre et al. 2010, 2017). In general, Mulligans Flat was less impacted and has been managed for ecological values longer than Goorooyarroo (gazetted reserves in 1994 and 2003 respectively), with agricultural management of the Offsets ceasing in 2017. All areas are now managed for their conservation value with significant restoration efforts focussed on the Offsets to improve their poorer overall condition. Ngaluda were introduced to Mulligans Flat in 2012 and their introduction into the extended sanctuary is planned for 2023. Eastern grey kangaroo (*Macropus giganteus*, hereafter “Buru”) densities are similar across the two areas (ACT Government 2021). However, Baray (swamp wallaby and red-necked wallaby) are abundant in Mulligans Flat, having increased dramatically since fencing, and rare in Goorooyarroo.

The MFWS is also the site of the Mulligans Flat – Goorooyarroo Woodland Experiment: a manipulative field-based experiment that investigates the impact of a set of combined management actions to restore and enhance biodiversity (Manning et al. 2011; Shorthouse et al. 2012). Part of the experiment involves the reduction of grazing by large macropods (specifically established to exclude only Buru because at the time Baray were rare but grazing by both is reduced), achieved through fencing (two levels: Low Grazing (fenced) and High Grazing (unfenced)) (Figure 1). In 2012 a Ngaluda exclusion treatment (smaller exclusion fences that would not exclude large macropods) was applied to a subset of sites in Mulligans Flat. However, they did not effectively exclude Ngaluda (which were able to climb over), and the large macropods almost completely avoid them (Evans et al. 2019). These smaller fenced areas therefore represent a further reduction of large macropod grazing to almost zero, resulting in higher vegetation biomass. Anecdotal observations of diggings and sightings suggest these areas are in fact strongly preferred by Ngaluda (Authors, pers. comm.). In 2018, two of these fenced areas were modified to effectively exclude Ngaluda with the addition of a “floppy top” to prevent them climbing over. We also know that Ngaluda activity is significantly higher in the Low Grazing areas of Mulligans Flat compared to the High Grazing areas, likely because of a preference for more ground cover for foraging and shelter (Munro et al. 2019).

Floristic indicator monitoring

We undertook targeted species surveys at 106 plots across different areas of the MFWS (Mulligans Flat $n = 46$, Goorooyarroo $n = 30$, and Offsets $n = 30$) (Figure 1). We primarily targeted geophytes and species with tuberous root resources (10 species) to capture any effects of Ngaluda, which are known to eat and negatively impact populations of these kinds of species (Ross 2020). We also targeted three control species without tuberous resources which would be responding to the overall herbivory pressure, not targeting by Ngaluda. Most plots ($n = 82$) were associated with the ACT Government's Herbage Mass Monitoring Program which collects vegetation structure and ground cover data to inform Buru and biomass management across the nature reserve network (ACT Government 2021). The other 24 plots were in the smaller-fenced, Ngaluda exclusion areas in Mulligans Flat that either did effectively exclude Ngaluda thanks to the addition of a "floppy top" ($n = 4$ plots in two fenced areas) or did not exclude Ngaluda but instead promoted their presence and activity ($n = 20$ plots in 10 fenced areas) (Figure 1). All plots were grouped in pairs at least 100 m apart in a mapped polygon (or "site") of relatively homogenous woodland vegetation ($n = 53$ polygons).

Surveyed plots were 400 m² circular quadrats (radius = 11.3 m), consistent with floristic plots already being monitored across the Offsets, and by other research in grassy ecosystems that aims to maximise the number of species observed (Armstrong *et al.* 2013). Monitoring at this scale increased our chances of capturing relatively rarer and less abundant species in our surveys. Each plot was searched by one person for a minimum of 35 minutes (or by two people for a minimum of 20 minutes) with the presence or absence of the following targeted indicator species recorded: *Arthropodium* spp., *Bulbine bulbosa*, *Wurmbea dioica*, *Burchardia umbellata*, *Microseris lanceolata* (Dharaban), *Craspedia* spp., *Leptorhynchos squamatus*, *Chrysocephalum apiculatum*, *Stackhousia monogyna* and all members of the Orchidaceae family identified to genus (4 species observed). Abundance was then scored as count of individuals from species grouped together into four "indicator groups". The groups were (i) "lilies" (*Arthropodium*, *Bulbine*, *Wurmbea*, *Burchardia*; in reference to the common-name use of the term), (ii) "orchids", (iii) "tuberous daisies" (Dharaban and *Craspedia*) and (iv) "control species" (*Leptorhynchos*, *Chrysocephalum*, *Stackhousia*; those without tuberous resources). Abundance was scored as either "0" (absent), "1" (1-9 individuals), "2" (10-99 individuals), "3" (100-999 individuals) or "4" (1000 or more individuals). Monitoring was undertaken between 26 October and 16 November 2021.

Vegetation monitoring and other covariates

Ground cover and vegetation structure monitoring was undertaken at all plots that were not in Ngaluda fenced areas ($n = 82$). Within the area of each monitoring plot, a step-point-intercept approach was used where either 75 (Offsets) or 100 (Mulligans Flat and Goorooyarroo) "steps" are taken at random and the ground cover vegetation at the point of

the step recorded as either one of 25 different categories (ACT Government 2020; Snape *et al.* 2021). Those 25 detailed categories were summarised into 10 percent-groundcover variables of interest for our study: native grass, native shrub, other native species, rock, bare ground, leaf litter, dead grass thatch, exotic broadleaf, or exotic grass. These variables were standardised as a proportion of total steps (0-1) and the additional variable of “proportional nativeness of the perennial vegetated ground layer” was calculated (hereafter “proportional nativeness” = native perennial cover / (native perennial cover + exotic perennial cover)). Average grass height was also calculated from 10 measures of grass height (to nearest centimetre) taken randomly around the plot, meaning 12 vegetation variables were considered in total.

Three additional categorical variables were associated with our observations. They were: (1) “Condition State” that was derived from vegetation condition mapping undertaken by ACT Government. Each plot was identified as either a “Woodland” (mature trees present with a native dominated ground layer), “Derived Grassland” (mature trees absent with a native dominated ground layer), or “Exotic Woodland” (mature trees present or absent with an exotic dominated ground layer); (2) “Experimental Grazing Treatment” was identified as either “High Grazing” or “Low Grazing” as per the Buru exclusion areas that exist throughout the MFWS for the restoration experiment (Manning *et al.* 2011). Ngaluda fenced areas were identified as “Ngaluda Fence (High Grazing)”, “Ngaluda Fence (Low Grazing)”, or “Ngaluda Fence (Floppy Top)” depending on their context; and, (3) “Dominant Grass Species” was the most common species across 10 grass height measures in the vegetation monitoring, associated with our observations as being either *Themeda triandra*, *Rytidosperma* spp., *Austrostipa* spp., “Other Native” (mix of less common native grasses), or “Exotic” (combined non-native grasses).

Data analysis

We collected data sufficient to model the abundance of all four indicator groups and the occurrence of seven plant indicator species (*Arthropodium* spp., *Bulbine bulbosa*, *Wurmbea dioica*, *Microtis* spp., *Craspedia* spp., *Leptorhynchos squamatus* and *Chrysocephalum apiculatum*). We also summarised our data to model the response of “indicator group richness” (count of plant indicator groups present (0-4)), “target species richness” (count of plant indicator species present (0-13)), “highest indicator group abundance” (highest count for any of the plant indicator groups present), and “total indicator group abundance” (sum of abundance scores for plant indicator groups present). This provided us with a total of 15 response variables to investigate.

We performed a principal component analysis on the 12 ground cover and vegetation variables to identify potential co-linearity among variables and broad gradients in environmental variation. This analysis reduced our 12 variables to four new axes that accounted for approximately 73% of total variation in those variables. The first axis PC1 (Eigenvalue = 4.1, 37% variance explained) had a high negative loading for average grass

height and exotic grass cover, and a high positive loading for proportional nativeness and native grass cover. The other three axes accounted for 10-15% of additional explained variance each and represented co-linearity between the cover of thatch and the cover of bare ground, leaf litter and shrubs on PC2, thatch cover and exotic broadleaf cover on PC3, and rock cover and exotic broadleaf cover on PC4.

Each response variable was the subject of three Generalised Linear Mixed Models (GLMM) that correspond to the three questions of this study. To address Question 1 (do response variables differ among the different areas of the MFWS?), all observations were included ($n = 106$) with each response fitted with a GLMM that included the additive effects of Sanctuary Area ("Mulligans Flat", "Goorooyaroo", or "Offsets"), condition state, experimental grazing treatment and dominant grass species. To address Question 2 (are response variables influenced by ground cover and vegetation structure?), the subset of observations with vegetation covariate data ($n = 82$) were fitted with a GLMM that included the additive effects of Sanctuary Area and the four principal components. This approach provides a more robust test of the potential contribution of these covariate measures than had they been included in the full model addressing Question 1. To address Question 3, (do response variables differ among grazing treatments where Ngaluda are present?), the subset of observations from Mulligans Flat ($n = 46$) were fitted with a GLMM that included only the effect of experiment grazing treatment.

We used mixed models over linear or generalised linear models for two reasons. First, abundance scores and richness response variables were modelled with Poisson error distributions and log-link functions, while occurrence variables were modelled with binomial error distributions and logit link functions. Second, the random effect of "polygon" was included in all models to account for any spatial autocorrelation associated with the paired nature of our plots. Tests for overdispersion were undertaken to assess whether there was additional variance in the data than assumed by the error distributions and verify homogeneity and expected properties of residuals. If models were overdispersed, a random observation was included as a random effect to correct for the unexplained variance (Zuur *et al.* 2009). For the models used to investigate Questions 1 and 2, we used Akaike's Information Criterion corrected for small sample sizes (AICc) to rank subsets of the full model and determine the best (lowest AICc) and whether there were any supported ($\Delta\text{AICc} < 2$) models. Where multiple models were supported, the model that included "Sanctuary Area" and had the simplest structure was used to make inference. All numerical predictor variables were scaled to a mean of zero and a standard deviation of one, prior to modelling, to allow direct comparison of regression coefficients.

All analyses were performed using R version 4.1.3 (R Core Team 2022). Models were fit using the 'glmmTMB' function in the "glmmTMB" package (Brooks *et al.* 2017), models were compared using the 'dredge' and 'AICc' functions in the "MuMIn" package (Barton 2020), and the explained variance (R^2) of each model was calculated using the 'r2_nakagawa' function in the "performance" package (Lüdtke *et al.* 2021).

Results

We observed at least one target species in 76 of the 106 plots surveyed across the MFWS (72%). *Microtis* (onion orchids) were the most common orchid genera, occurring in 42% of plots, followed by *Thelymitra* (sun orchids) present in 13% of plots. *Arthropodium* spp. and *Wurmbea dioica* were the most common of the target lilies, occurring in 30% and 28% of plots respectively. *Burchardia umbellata*, *Microseris lanceolata* (Dharaban) and *Stackhousia monogyna* were rare in MFWS, each recorded in <5% of plots. The complete absence of any target species was relatively rare within the Mulligans Flat and Goorooyarroo (13% and 26% of plots respectively) compared to the Offsets where most plots recorded zeros (70%).

Average grass height differed between the experimental grazing treatments within Mulligans Flat (Low Grazing = 10.7 cm [9.2 – 12.2 cm 95% CI]; High Grazing = 6.1 cm [5.9 – 6.3 cm]) but not within Goorooyarroo (Low Grazing = 14.9 cm [12.9 – 16.9 cm]; High Grazing = 13.1 cm [12.5 – 13.8 cm]).

Question 1: Does the abundance and occurrence of plant indicators differ among the different areas of the Sanctuary?

Sanctuary Area featured in the top-ranked or a supported model for explaining variation in 10 of the 14 plant indicator responses (Table 1). There was a positive effect of Goorooyarroo on indicator group richness, target species richness, the sum of indicator abundance scores, the abundance of the lilies and daisies (control) indicator groups, and the occurrence of *Arthropodium* spp. and *Wurmbea dioica* compared to Mulligans Flat (Table 1). Of those 10 response models that featured Sanctuary Area, nine also featured one or both of Condition State and Dominant Grass in their top-ranked or supported model (Table 1).

The positive effects of Goorooyarroo on various plant indicators was most evident when Condition State was also considered (Figure 2). Most target species were rarely recorded in Exotic Woodland irrespective of Sanctuary Area (Figure 2). For indicator group richness, target species richness, and lilies indicator abundance score (Figure 2a,b,e), Woodland in Goorooyarroo was associated with significantly higher values than Woodland in Mulligans Flat (Figure 2). For example, an average Woodland plot in Mulligans Flat would include 2.5 target species and count less than 10 lilies compared to an average Woodland plot in Goorooyarroo that would include five target species and count either more than 10 or more than 100 lilies (Figure 2). The average abundance score for the control species indicator group was higher in Goorooyarroo compared to Mulligans Flat irrespective of Condition State (Figure 2f).

Question 2: Do ground cover and vegetation structural attributes strongly influence plant indicator groups or species among areas of the Sanctuary?

Sanctuary Area still featured in the top-ranked or a supported model for explaining the variation observed in 8 of the 13 plant indicator responses that could be modelled from the subset of plots with corresponding covariate data (n = 82) (Table 2). All best models also featured the significant positive effect of PC1 on all plant indicator responses except for *Craspedia* spp. (Table 2). This represents a general response of all indicators being lowest where grass height and exotic cover was high, and highest where proportional nativeness and total native cover was high.

The positive effects associated with PC1 were generally greater in Goorooyarroo compared to Mulligans Flat (Figure 3). Mulligans Flat was predicted to record on average two target species and count less than 10 lilies and control species in plots with the greatest native ground cover, whereas the equivalent values were predicted to occur in Goorooyarroo where proportional nativeness and total native ground cover were much lower (Figure 3). The highest indicator abundance score recorded per plot, and the abundance scores of the orchids and tuberous daisies, were all positively associated with PC1 and were not related to Sanctuary Area at all (Figure 3).

Question 3: Within the Mulligans Flat area where Ngaluda are present, do differences in overall macropod grazing influence plant indicator groups or species?

Indicator group richness, target species richness, and highest indicator abundance score recorded per plot were negatively associated with the Low Grazing treatment compared to High Grazing within Mulligans Flat (Figure 4a-c). Low Grazing plots were characterised by, on average, a single target species with less than 10 individuals, while High Grazing plots were characterised by 2.5 target species with at least one group having 10 to 100 individuals present (Figure 4a-c).

The abundance score of the orchid indicator group – and the occurrence of *Microtis* which was almost exclusively responsible for that score – was significantly lower in Low Grazing plots, Bettong Fence (Low Grazing) and Bettong Fence (High Grazing) plots (which do not exclude Ngaluda) than in High Grazing plots (Figure 4d). Those grazing treatments recorded on average 0-9 individuals compared to an average 10-99 individuals recorded for the unmanipulated High Grazing plots (Figure 4d). Orchid abundance or occurrence in Bettong Fence (Floppy Top) plots (which do exclude Ngaluda) was not different from the High Grazing treatment (Figure 4d).

Discussion

We assessed floristic values from across a woodland sanctuary with areas of different overall herbivory pressures to try and understand any potential effects of a reintroduced digging herbivore – Ngaluda (eastern bettong). We found that most floristic indicators we investigated, including the richness of target species, total abundance score, and the abundance of lilies, were greater in woodland where Ngaluda were absent

(Goorooyarroo) compared to equivalent woodland where Ngaluda were abundant (Mulligans Flat). We also found that within Mulligans Flat the experimental grazing contexts that were associated with higher Ngaluda activity had some lower floristic values, including significantly lower abundance of a common orchid, irrespective of whether the densities of other large macropods were high or low. While the differences observed between Mulligans Flat and Goorooyarroo could be explained by either Ngaluda presence and/or Baray numbers (swamp wallaby and red-necked wallaby that are abundant in Mulligans Flat but rare in Goorooyarroo), the differences observed within Mulligans Flat more clearly suggest a negative effect of Ngaluda. Our rapid assessment highlights the impacts of both Ngaluda in concert with Baray and of Ngaluda on its own, which is consistent with the negative effects of overabundant herbivores generally, and reintroduced digging mammals on native vegetation observed in other Australian sanctuaries specifically (Verdon *et al.* 2016; Linley *et al.* 2017; Moseby *et al.* 2018; Kemp *et al.* 2021; Michael *et al.* 2022).

Evidence of overall higher herbivory pressures in Mulligans Flat impacting floristic values

Goorooyarroo plots contained on average higher richness of our targeted forb species than Mulligans Flat plots. Woodland forb diversity is influenced by multiple interacting processes, including soil nutrification, overgrazing and weed invasion that suppresses native forbs (Prober *et al.* 2002, 2016; McIntyre & Lavorel 2007) and favourable seasonal conditions, cool burning, and a heterogenous native ground layer that promote them (Smallbone *et al.* 2007; Prober *et al.* 2009; McIntyre *et al.* 2017). Past studies of the MFWS when the herbivory pressures were more uniform found no difference in species richness between Mulligans Flat and Goorooyarroo, with native forbs in general increasing consistently in both areas in response to more favourable conditions between 2007 and 2011 (McIntyre *et al.* 2014, 2017). The richness patterns in the targeted species we observed is counter to these results, as we would have expected indicator species richness to be either similar between Mulligans Flat and Goorooyarroo as indicated by previous monitoring, or potentially greater in Mulligans Flat where there are fewer areas of high soil nutrification owing to a less-intense agricultural land-use history.

We found some evidence that the occurrence of four target species (of the seven species with sufficient data) was greater in Goorooyarroo than Mulligans Flat. These include the lilies *Arthropodium* spp. and *Wurmbea dioica* that have below-ground tubers, but also the control species *Leptorhynchus squamatus* and *Chrysocephalum apiculatum* that do not have specific below-ground resources Ngaluda may target. The occurrence of these common species was not significantly different between the more degraded Offsets area and Mulligans Flat, suggesting that soil condition and other factors associated with different land-use histories are not responsible for these occurrence patterns. Instead, these occurrence patterns suggest the greater overall herbivory pressures at Mulligans Flat (due to abundant Ngaluda and Baray) is limiting for these species compared to the overall lower herbivory pressures at Goorooyarroo (where Ngaluda are absent and Baray rare).

The relative abundance of lilies and control species was also significantly higher in Goorooyarroo compared to Mulligans Flat. These results again highlight the impact of the overall higher herbivory pressure of abundant Ngaluda and Baray, but also suggest a synergistic effect of Ngaluda-targeted herbivory. Control species were ~1-order of magnitude less abundant in Mulligans Flat which can be interpreted as the impact of overall general herbivory, whereas the lilies group were ~1-2-orders of magnitude less abundant inferring an amplification of the general herbivory effect (1-order) from likely targeted herbivory. If Ngaluda were not having a specific impact on these tuberous species, as they are known to have on *Wurmbea* specifically (Ross 2020), then we would have expected the same level of impact from general herbivory of Baray and Ngaluda as observed for the control species. While these tuberous plants would be consumed by a broad range of animals, including some birds and insects, it is unlikely the effects of these differ between the two sanctuary areas. For example, beetles are more abundant across MFWS in areas that had previously been fertilised for pasture improvement (Ross *et al.* 2017), meaning if root and tuber consuming beetles were impacting lilies in one area over the other, we would expect to observe that impact in Goorooyarroo that has a greater legacy of pasture improvement (McIntyre *et al.* 2010). Our comparison of floristic values between Mulligans Flat and Goorooyarroo clearly show a negative impact of a predator-free sanctuary with higher herbivory pressures (of Ngaluda and Baray combined) on floristic values, that are not likely the result of some other legacy-effect or ecological process.

Evidence of woodland condition and ground cover impacting floristic values along with herbivory

The ecological condition of the woodland vegetation as measured by the dominance of native species in the ground layer explained much of the variation observed in our floristic indicators. Target species were rare and often completely absent in woodland or derived grassland with a predominantly exotic ground layer, and there was a negative effect of increasing exotic cover and average grass height on indicator richness and the abundance score of all four indicator groups. This is consistent with widely demonstrated impacts that past land-use, soil nutrification, weed invasion, and biomass accumulation have on native species establishment and persistence (Prober *et al.* 2005; Blumenthal 2006; Prober & Wiehl 2012; Bernard-Verdier & Hulme 2019; O'Reilly-Nugent *et al.* 2019). Conversely, we found the highest richness and abundance of all indicator groups were observed in plots that had the most intact native ground layer. Variation in some indicators (e.g. orchid abundance score that was almost exclusively *Microtis*) was best explained by woodland condition and/or ground cover and not Sanctuary Area at all, suggesting overall differences in herbivory between Mulligans Flat and Goorooyarroo at a reserve-scale were not influencing these values more than ground cover processes at the patch-scale. These results highlight the importance of management interventions that decrease weed dominance and biomass accumulation in maintaining opportunities for the native forbs we targeted in our survey.

The ecological condition of the woodland vegetation did not fully explain the differences in floristic values observed between Goorooyarroo and Mulligans Flat. While the negative effect of exotic cover and grass height on floristic indicators was consistent among the MFWS areas, the positive effect of native dominance of the ground layer was amplified in Goorooyarroo relative to Mulligans Flat. This means that any like-for-like comparison of woodland along that continuum of increasing native dominance has Goorooyarroo containing higher floristic values than Mulligans Flat. For each indicator where both Sanctuary Area and PC1 were significant predictors, the response curve of Mulligans Flat was the same as the Offsets area. The Offsets were expected to have lower floristic value even in the areas where native species dominate the ground layer owing to the more recent history of livestock grazing and agricultural management. These results further indicate the impacted floristic values of Mulligans Flat compared to Goorooyarroo are the product of herbivory difference between the two areas, not differences in ground layer condition.

Evidence of Ngaluda impacts on floristic values at Mulligans Flat

The lower floristic values observed at Mulligans Flat compared to Goorooyarroo are driven largely by the overall greater herbivory pressures experienced at Mulligans Flat that contains both abundant Ngaluda and Baray. However, analysis of floristic differences within Mulligans Flat does suggest that specific Ngaluda herbivory impacts are also occurring, based on floristic differences among experimental grazing treatments within Mulligans Flat, and the known responses of Ngaluda to those. Ngaluda activity is similar (low or absent) in High Grazing and the Bettong Fence (Floppy Top) plots (see Munro *et al.* 2019) and it is these two types of plots in which the abundance of the onion orchid *Microtis* spp. was highest, despite the activity of larger macropods being highly dissimilar across them (high vs absent). This indicates grazing by larger macropods is not a major determinant of *Microtis* abundance as the highest values were found under completely different grazing pressures. Low Grazing areas and the other Bettong Fences are the contexts where Ngaluda activity is highest (see Munro *et al.* 2019) and where the abundance of *Microtis* is significantly lower. As our orchid response contrasts exactly to Ngaluda activity (low where high, high where low) but is disconnected from larger macropod activity (high where Buru or Baray activity is either low or high) we conclude that it is herbivory by Ngaluda, not any direct or indirect effect of Buru and Baray, that is most likely responsible for this pattern. While *Microtis* abundance was the clearest result, three other richness and abundance indicators were significantly reduced in Low Grazing areas of decreased Buru and Baray densities and higher Ngaluda activity, further supporting the conclusion that targeted herbivory by Ngaluda has a significant additional impact following general herbivory by all macropods.

The Ngaluda population in Mulligans Flat grew quickly and since autumn 2016 has been at the relatively stable and density-dependent size of between 150-200 individuals (Manning *et al.* 2019). This asymptotic population size is thought to be the carrying capacity of the sanctuary based on available food resources limiting juvenile survival (Manning *et al.* 2019). Whether or not this density-dependent population represents an overabundant

population in terms of having detrimental ecological effects remains untested. At the time of our study Ngaluda had been present in Mulligans Flat for nine years and at an abundant population size for the preceding five years meaning their effects on the woodland community should be evident. For example, a decline in palatable plant cover was observed as soon as the population of reintroduced burrowing bettongs began to grow at Arid Recovery (Moseby *et al.* 2018) and increased plant species richness was evident within two years of excluding reintroduced digging mammals from areas at Scotia Sanctuary (Michael *et al.* 2022). If Ngaluda herbivory was not having a net negative effect on these species we would expect them to be at least be as abundant in Mulligans Flat as in Goorooyarroo, or potentially more abundant if Ngaluda diggings were have a net positive effect of facilitating establishment (as hypothesised in Ross *et al.* 2020).

Study limitations and implications for adaptive management

We are confident that our rapid assessment has identified that a predator-free sanctuary with increased herbivory pressures from the combined herbivore assemblage has clear impacts on the floristic values of an endangered ecological community. Our results also strongly suggest an additional impact of targeted herbivory on specific floristic values by a reintroduced digging herbivore. While Buru densities between Mulligans Flat and Goorooyarroo remain similar (ACT Government 2021), since the establishment of the original sanctuary the densities of Baray (wallabies) and Wilay (brushtail possum *Trichosurus vulpecula*) have increased at Mulligans Flat and therefore limits our inference from reserve-level comparisons of Ngaluda presence or absence. We can largely dismiss Wilay as a key driver of our results as forbs typically are an extremely minor component of their diet (How & Hillcox 2000; Sweetapple *et al.* 2004), but that is not the case for Baray, which are generalist grazers that will preferentially consume forbs (Davis *et al.* 2008; Di Stefano & Newell 2008). Ultimately more research with greater replication and better controls is needed to confidently identify the relative contribution of Baray and Ngaluda to clear overall impacts of herbivory.

The floristic patterns we have observed in the MFWS are consistent with the ecology of the herbivores present, are consistent with the impacts of reintroduced digging mammals in other sanctuaries, and suggest Ngaluda have decreased some floristic values at Mulligans Flat. The adaptive management implications of this rapid assessment are two-fold. First, it highlights that both Ngaluda and these target plant species are values that need active management to ensure they are both enhanced. Second, it demonstrates that there is still uncertainty when it comes to knowing what the balance of Ngaluda effects are in this sanctuary context. Our assessment suggests restoring the ecological function of Ngaluda without any top-down regulation of their population through predation or other methods of population control, means the detrimental effects of their herbivory are likely greater than the beneficial effects of their diggings for key species of this endangered woodland community. Further research is needed to quantify density-impact relationships between Ngaluda and these floristic values to determine at what population size the actions of

Ngaluda would be of net-benefit to native plant diversity. Reintroducing other lost ecological functions to the woodland sanctuary could potentially be used to balance these impacts, including top-order predation (to decrease the effects of Ngaluda) as well as the restoration of traditional indigenous management (to directly enhance floristic value). In the meantime, increasing our knowledge of the effects that reintroduced species have on the recipient woodland ecosystem at the MFWS will help ensure the sanctuary is managed to benefit both critically endangered animals and critically endangered vegetation.

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Tables and Figures

Table 1. Model coefficients (effect sizes) for explanatory variables from the top-ranked Question 1 GLMM for each of 14 plant indicator and species occurrence response variables that could be modelled. Bold values indicate a statistically significant relationship ($P < 0.05$) where 95% confidence intervals do not intercept zero. "Sanctuary Area" refers to Goorooyarroo and Offsets that are compared to Mulligans Flat. "Condition State" refers to Derived Grassland and Exotic Woodland or Grassland that are compared to Woodland. Dominant Grass refers to *Rytidosperma*, *Austrostipa* and Exotic species that are compared to *Themeda*. Marginal R^2 (R^2_m) provides the variance explained only by fixed effects and conditional R^2 (R^2_c) provides the variance explained by the entire model. R^2_c could not be calculated for models that included a random observation effect to correct overdispersion. NA indicates where meaningful effects could not be calculated. "Arthrop." refers to Arthropodium. "Chryso." refers to Chrysocephalum.

	Sanctuary Area		Cond. State		Dominant Grass					
Response	Gooroo	Offsets	Derived Grass.	Exotic Wood.	Rytid.	Stipa	Exotic	AICc	R ² m	R ² c
Indicators										
Indi. Rich.	0.53	-0.18	-0.21	-2.31	-0.16	-1.27	-0.89	321.8	0.66	-
Spp. Rich.	0.73	-0.25	-0.16	-2.41	-0.01	-1.24	-0.95	363.2	0.71	-
High. Score	0.22	-0.72	0.09	-2.47				312.7	0.62	-
Sum Scores	0.69	-0.48	-0.14	-2.49	-0.07	-0.96	-0.93	413.4	0.75	-
Lilies	1.08	-0.46	-0.63	NA	<0.01	-0.75	-1.14	223.3	0.98	1.00
Orchids	<0.01	-0.52	0.26	NA	<0.01	-1.03	-1.07	261.9	0.97	0.98
Daisies (T)					-1.64	NA	-1.05	149.3	0.95	0.96
Daisies (C)	1.34	-1.95						209.3	0.32	0.62
Spp. Occ.										
Arthrop.	1.69	-0.71	-1.30	NA				124.9	0.93	0.94
Bulbine	1.30	-0.54						91.0	0.81	0.86
Wurmbea	2.90	2.56			0.07	-3.77	-5.26	114.9	0.43	0.70
Microtis			0.12	0.00	6.97	-15.92	-16.35	111.4	0.45	0.99
Craspedia			15.80	10.98	NA	NA	-11.63	91.6	0.53	0.99
Chryso.					9.87	-6.73	7.39	90.7	0.05	0.99

Table 2. Model coefficients (effect sizes) for explanatory variables as they feature in the top-ranked Question 2 GLMM for each of 13 plant indicator and species occurrence response variables that could be modelled. Bold values indicate a statistically significant relationship ($P < 0.05$) where 95% confidence intervals do not intercept zero. “Sanctuary Area” refers to Gorooyarroo and Offsets that are compared to Mulligans Flat. Principle Components (PC1, PC2, PC3, PC4) represent multiple broad environmental gradients in ground layer vegetation cover and structure. Marginal R^2 (R^2_m) provides the variance explained only by fixed effects and conditional R^2 (R^2_c) provides the variance explained by the entire model. R^2_c could not be calculated for models that included a random observation effect to correct overdispersion. “Arthrop.” refers to Arthropodium. “Leptoryn.” refers to Leptorhynchus.

	Sanctuary Area		Principle Components					
Response	Gooroo	Offsets	PC1	PC2	PC3	AICc	R ² m	R ² c
Indicators								
Indi. Rich.	0.78	-0.13	0.87		0.27	223.3	0.59	0.60
Spp. Rich.	0.95	-0.09	0.94		0.26	252.4	0.63	0.66
High. Score			1.00	-0.18		213.7	0.60	-
Sum Scores	1.13	0.18	1.13	-0.23	0.37	290.8	0.64	0.76
Lilies	1.12		0.95			168.9	0.47	-
Orchids			1.86	-0.44		157.7	0.73	0.75
Daisies (T)			0.60			124.8	0.12	0.37
Daises (C)	1.65	-0.66	1.18			146.2	0.58	0.64
Spp. Occ.								
Arthrop.	2.65	1.36	1.56			84.5	0.50	-
Microtis			67.24	-16.79		42.1	0.46	1.00
Craspedia				-0.84		74.8	0.12	0.41
Leptoryn.	3.10	-2.12	3.06			58.5	0.97	0.98
Chryso.	1.97	-0.05	0.90			74.5	0.38	-

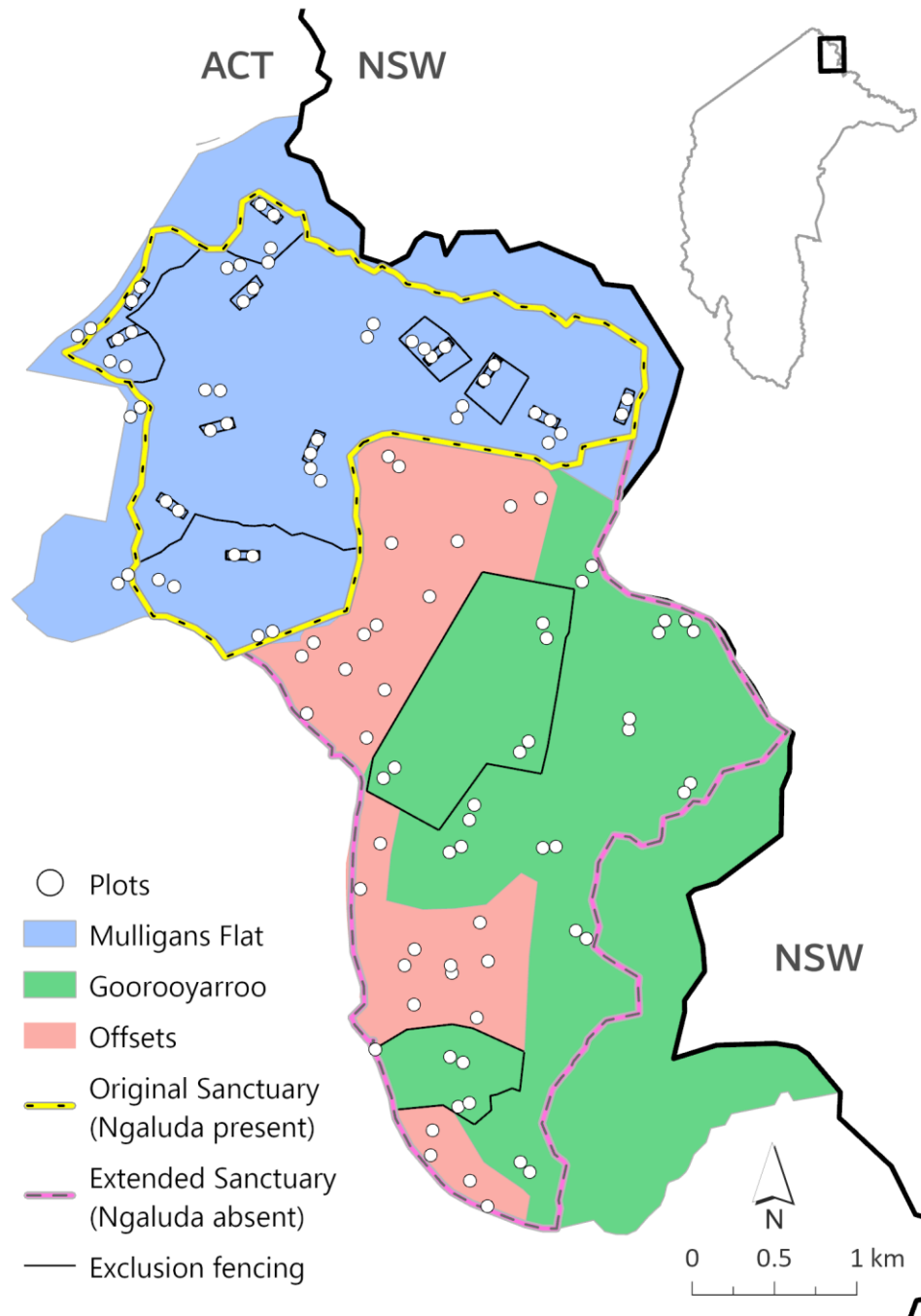


Figure 1. Map of the Mulligans Flat Woodland Sanctuary (MFWS) in the Australian Capital Territory (ACT), south-eastern Australia. Displayed are the locations of the 106 plots monitored for this study, the three different areas that comprise the MFWS (Mulligans Flat, Goorooyarroo and Offsets), the boundaries of the original and extended sanctuaries where Ngaluda are present or absent, and the exclusion fencing that are either “Low Grazing” areas of reduced Buru densities (larger areas) or Bettong Fences (smaller rectangle areas).

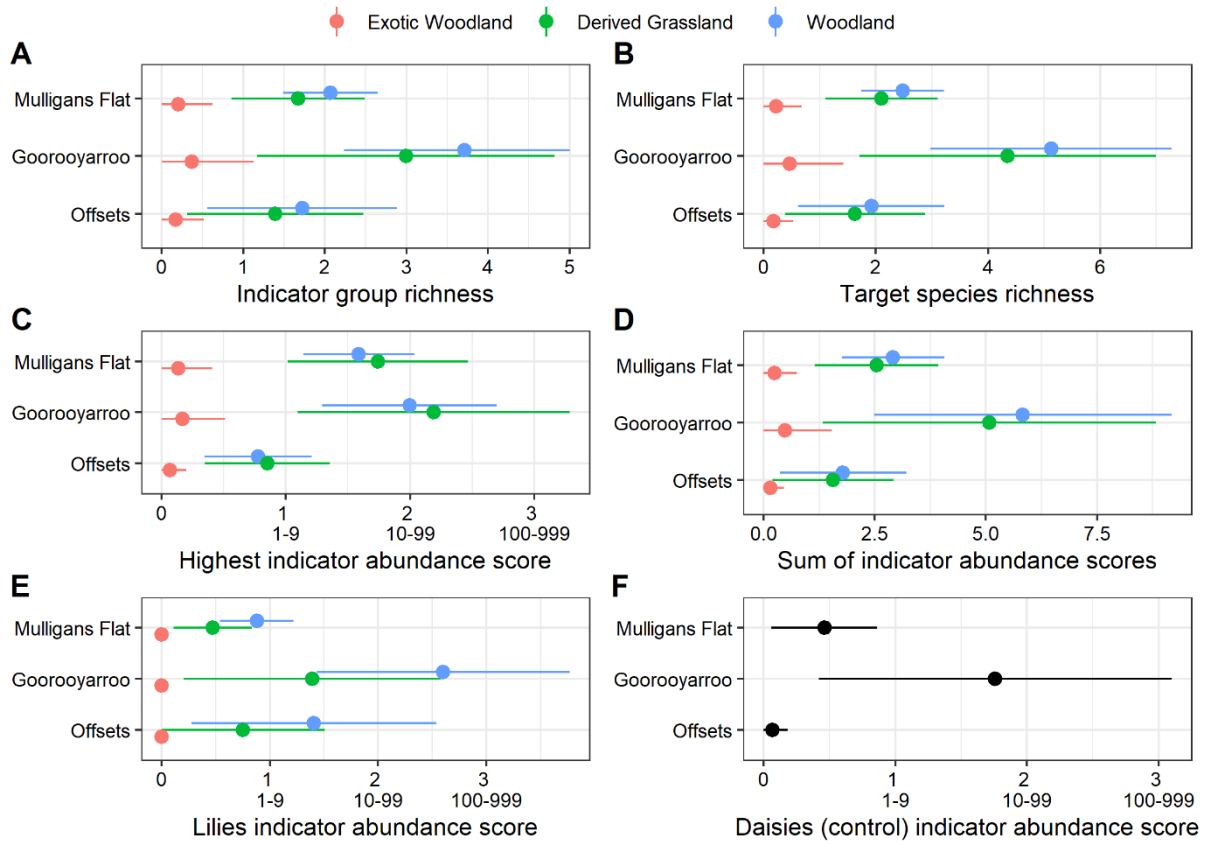
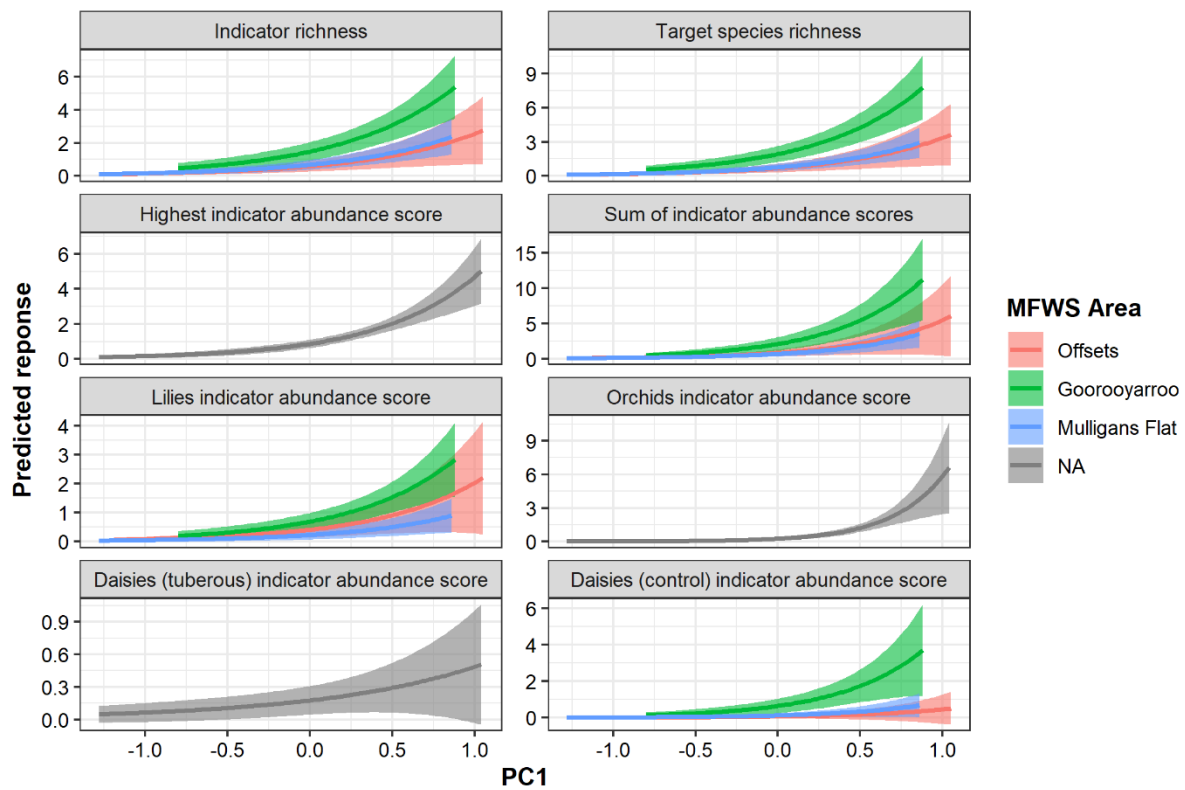


Figure 2. Predicted average (\pm 95% CI) plant indicator responses in different Sanctuary Area (Mulligans Flat, Goorooyarroo or Offsets) and Condition State (Woodland, Derived Grassland, Exotic Woodland) contexts at the MFWS. Predicted values are for the top-ranked Question 1 GLMM where predictions were made by varying both "Sanctuary Area" and "Condition State" and holding "Dominant Grass" as "*Themeda*". The exceptions are highest indicator abundance score (C) which did not include dominant grass in it's top-ranked model, and Daisies (control) indicator abundance score (F) that only included Sanctuary Area. There were significant singular effects of "Sanctuary Area" on each variable that were either a positive effect of Goorooyarroo (A, B, D, E), negative effect of Offsets (C), or both (F) compared to Mulligans Flat (Table 1). All significant effects of "Condition State" were a negative effect of Exotic Woodland compared to the Woodland reference level.

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769 **Figure 3.** Relationships between Principal Component 1 (PC1) and plant indicator responses in
770 different Sanctuary Areas. PC1 is an environmental gradient that broadly represents increasing grass
771 height and non-native cover in the negative direction, and increasing proportional nativeness and
772 native grass cover in the positive direction. Predicted values (solid lines) and 95% confidence
773 intervals (shaded areas) were generated from the top-ranked Question 2 GLMM for each variable
774 where different “Sanctuary Area” and “PC1” combinations were set while holding other variables in
775 the model (PC2, PC3 or PC4) at their average values. Grey predictions are where Sanctuary Area did
776 not feature in the top-ranked model (Sanctuary Area = “NA”). Where Sanctuary Area did feature,
777 there was a consistent positive effect of Goorooyarroo and no effect of Offsets on each indicator
778 compared to the Mulligans Flat reference level.

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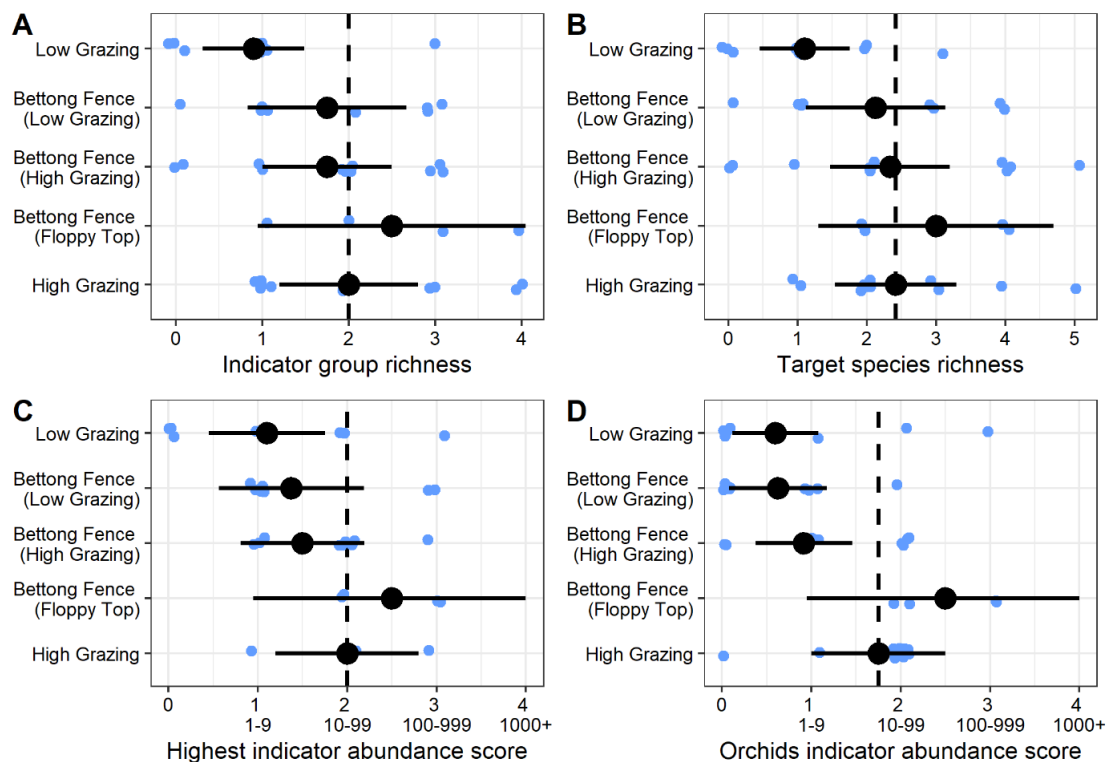


Figure 4. Predicted average (\pm 95% CI) plant indicator responses to different experimental grazing contexts within the Mulligans Flat area of the MFWS. Small blue circles are the jittered raw values from the plot data ($n = 46$). The dashed line represents the model intercept reference condition. Effects of grazing treatments are considered significant where confidence intervals do not intercept the dashed line. High Grazing refers to no manipulation and where Buru and Baray are abundant. Low Grazing refers to large areas that have been fenced where Buru and Baray are less abundant, although Ngaluda activity is higher. Bettong Fences reduce Buru and Baray grazing to effectively none, and either effectively exclude (“Floppy Top”) or amplify (other contexts) Ngaluda presence and activity.