Disentangling chronic regeneration failure in endangered woodland ecosystems

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ABSTRACT

Ecological restoration of degraded ecosystems requires the facilitation of natural regeneration by plants, often augmented by large-scale active revegetation. The success of such projects is highly variable. Risk factors may be readily identifiable in a general sense, but it is rarely clear how they play out individually, or in combination. We addressed this problem with a field experiment on the survival of, and browsing damage to, 1275 hand-planted buloke (*Allocasuarina luehmannii*) seedlings in a nationally endangered, semi-arid woodland community. Buloke seedlings were planted in 17 sites representing four landscape contexts and with three levels of protection from kangaroo and lagomorph browsing. We censused seedlings and measured herbivore activity four times during the first 400 days post-planting, and fitted models of mortality and browse hazard to these data using survival analysis. Increasing lagomorph activity was associated with higher mortality risk, while kangaroo activity was not. Seedling survival was lowest for each treatment within extant buloke woodland, and the highest survival rates for guarded seedlings were in locations favoured by lagomorphs. Damage from browsing was nearly ubiquitous after one year for surviving unguarded seedlings, despite moderate browser activity. On average, unguarded seedlings showed a decline in height, whereas fully guarded seedlings grew 2.3 cm across the survey period. This study demonstrates buloke seedlings should be protected from browsers, even with browsers maintained at moderate to low density, and the location that maximizes survival, and possibly growth rates, is adjacent to dunes. Further work will test this heuristic in an analysis of cost-effective revegetation strategies for this endangered community.

Key words: browsing impact; buloke; herbivore exclusion; mortality; plant guard; revegetation; survival analysis

INTRODUCTION

Ecosystems heavily modified or displaced by agriculture may be at risk of ecological collapse due to the loss of biotic components or ecological functions (Keith et al. 2013; Bland et al. 2018). Ecological restoration of such ecosystems requires facilitation of natural regeneration processes, which is often augmented by large-scale, active revegetation programs (Vesk and MacNally 2006; Molin et al. 2018; Rohr et al. 2018). Ecological interventions are expensive, have high uncertainty and conservation budgets are typically small (Curtis and Lockwood 2000; McLeod 2004; Cooke et al. 2010), so an understanding of the processes underpinning success and failure is critical.

Risk factors that may impede seedling survival are often readily identifiable in a general sense, such as water stress, interspecific competition and herbivory (e.g. Close et. al. 2005). However, it is rarely clear how these risk factors might play out individually, or in combination across spatially heterogeneous landscapes. Such understandings are required to plan and manage cost effective restoration of ecosystems (Dorrough et al. 2008; McBride et al. 2010). For example, hazards of water stress may be independent of, or weakly correlated with, herbivore pressure and the two hazards may differ widely in their consequences for seedlings. Further, mere survival is not enough when exposed to strong grazing or browsing pressure. To attain the population-sustaining characteristics of mature individuals, seedlings and saplings must grow well enough to ‘escape’ their prospective grazers and browsers (Vesk and Dorrough 2006).

Here we examine the complex interaction of risk factors that potentially contribute to regeneration failure for an endangered woodland ecosystem in south-east Australia. The role of herbivores in limiting plant regeneration is a primary management concern in the ecosystem, an entity circumscribed as *Buloke Woodlands of the Riverina and Murray-*

Darling Depression Bioregions (Department of the Environment and Energy 2008). This semi-arid woodland ecosystem was extensively cut from the 1850's to promote pasture growth for cattle and sheep, and most was later cleared for cereal cropping (Cheal et al. 2011). For remnant vegetation, this regime resulted in the extirpation of indigenous fauna and flora, and the introduction of alien species including annual weeds and herbivores, most notably the European rabbit (*Oryctolagus cuniculus*). Concerns about the influence of browsing and grazing herbivores on the species diversity and regeneration of dominant woody species in this area date back at least 50 years (e.g., Cochrane and McDonald 1966). Since then, the largest remnants were incorporated into protected areas (Cheal, et al. 2011) and livestock grazing concessions were phased out in the 1970–90s to facilitate natural regeneration (Cheal 1986; Land Conservation Council 1989; Durham 2001). However, no signal of adequate recruitment or regeneration to replace the ageing stock of remaining mature trees has emerged.

Since the removal of livestock from protected areas, there has been increasing emphasis on the threat that introduced rabbits and the native western grey kangaroo (*Macropus fuliginosus*) pose to restoration. These two herbivores can impede seedling regeneration across a broad swathe of Australian ecosystems (Cheal 1986; Coulson et al. 1989; Bird et al. 2012; Taylor and Pegler 2016; Dillon et al. 2018). Both species preferentially feed on grasses and herbs but they will browse shrubs and seedlings when preferred options become scarce (Coulson and Norbury 1988; Bird et al. 2012; Mutze et al. 2016b).

Previous studies from temperate Australia have demonstrated that rabbits are capable of significant browsing damage and mortality even at low densities <1 ha^{-1} (Lange and Graham 1983; Bird et al. 2012; Mutze et al. 2014; Forsyth et al. 2015). The degrading impact of kangaroos at high densities is clear (Cheal 1986; Coulson et al. 1989; Sluiter et al. 1997), and their population is subject to annual monitoring and control (Morris et al. 2019), but the impacts kangaroos may have on woody perennial species at low–moderate densities are unclear. Kangaroos are typically presented as a subordinate browsing threat in studies of both rabbits and kangaroos (e.g., Bird et al. 2012; Mutze et al. 2016a) with several studies explicitly separating these effects (Cooke 1988; Allcock and Hik 2004; Denham and Auld 2004; Bird et al. 2012).

We conducted a survival experiment on hand-planted buloke (*Allocasuarina luehmannii* R. T. Baker (L. A. S. Johnson)) seedlings using exclosures designed to distinguish the browsing impacts of kangaroos and rabbits. We planted seedlings in distinct spatial contexts representing variation in habitat favourability for kangaroos or rabbits. We expected that seedlings in habitats favoured by rabbits would suffer high mortality, but the likely impact of kangaroos was uncertain. Buloke was selected as the target species because it presents the most persistent regeneration failure amongst the structurally dominant species of the endangered buloke woodland ecological community (Gowans et al. 2010). We examined the variation in seedling browsing and mortality risk with exclosure treatment, herbivore abundance, habitat features and site over time. These data can immediately inform future planting strategies and can also feed into cost-effectiveness analyses with varying levels of protection and herbivore control.

METHODS

Study system and sites

Our experiment was located in the Pine Plains management area of Wyperfeld National Park in north west Victoria, Australia (Appendix 1: Fig. S1). The region typically experiences hot summers and mild to cool winters, with highly variable rainfall throughout the year, which typically occurs as sporadic, localised and often intense rain events. The long term mean annual rainfall of 332 mm (± 109 SD, Bureau of Meteorology Walpeup Research Station No.

76064) was exceeded in 2016 and 2017 when this study took place, with 394 mm and 355 mm recorded respectively (Appendix 1: Fig. S2).

Pine Plains contains the largest (~ 700 ha), albeit highly degraded, remnant of the endangered buloke woodland (Cheal et al. 2011). These woodlands are dominated by buloke and slender cypress-pine (*Callitris gracilis*). The understorey is highly simplified, with an occasional shrub layer and a ground layer dominated by native and introduced herbs and grasses (Gowans and Gibson 2005).

Reproductive biology and regeneration niche of buloke

Buloke is a long-lived tree in the Casuarinaceae family. Although listed as vulnerable in Victoria, it occurs over a wide latitudinal range of Australia (~16–37° S) inland of the Great Dividing Range (Atlas of Living Australia 2019). Buloke is dioecious or sub-dioecious (Conomikes et al. 2011). It is wind pollinated; males may produce copious pollen and females prodigious quantities of cones (Raymond 1990). It can reproduce sexually, and suckers readily following root zone disturbance (Murdoch 2005). As a nitrogen fixer, buloke seedlings are presumed to be highly palatable (Mutze et al. 2016b).

Herbivore species

The European rabbit has become a major pest over much of Australia (Kearney et al. 2018). They consume grasses and forbs but will also feed on seedlings, saplings, shrubs, bark and tubers (Bird et al. 2012; Mutze et al. 2016a; Mutze et al. 2016b), and can browse foliage up to 60 cm in height.

Rabbits have been monitored and controlled (fumigation and warren ripping) at Wyperfeld NP since the 1970s. Since numbers crashed by an order of magnitude following the introduction of a biological control agent (myxoma virus), they have largely been maintained at or below target levels of <1 rabbit/transect km (Sandell 2002; Parks Victoria 2016). European hare (*Lepus europaeus*) occurs at lower densities, have less irruptive population dynamics and potentially a lower capacity for ecological impact than rabbits. We included them here because we could not reliably distinguish the faecal pellets of each species, which we used as our measure of herbivore activity.

The western grey kangaroo is a large, social macropodid marsupial (17–72 kg; Coulson 2008) with a preference for heterogeneous habitats that provide both food and shelter (Arnold et al. 1989; Coulson 1993; Garnick et al. 2016). The western grey kangaroo is generally considered a grazer, but will also browse on shrubs and tree species, particularly if grass availability is low (Coulson and Norbury 1988; Morgan and Pegler 2010). Kangaroo population control has been undertaken by ground-shooting at Wyperfeld NP since the 1980s (Morris et al. 2019).

While feral goats (*Capra hircus*) were present and were recorded on camera traps, so few goat faecal pellets were recorded that goats were excluded from our analyses. Similarly, red kangaroos (*Osphranter rufus*) were present in the park but none was observed within 4 km of the study sites, so this species was not considered further.

Site establishment

A total of 17 locations were randomly selected within areas identified as the former distribution of the buloke woodland community (Gowans and Gibson 2005). We accepted points as suitable buloke habitat if a live or dead buloke tree was located within 200 m. We discarded points if they were located where buloke trees were deemed unlikely to have been present, such as on a dune crest or former lakebed (Cheal et al. 2011), or where there was evidence of a potentially confounding factor, for example recent fire.

Six sites were located within extant open woodland structure still dominated by mature buloke trees, hereafter ‘buloke woodland’. Five sites were located in open grassy areas 198–

331 m from continuous canopy cover, and six were located in open grassy areas adjacent to cover (3–33 m). Three of these latter sites sat adjacent to low *Eucalyptus* mallee woodland and three adjacent to dune ridges dominated by *Acacia* shrubs. These different contexts were selected to capture variation in herbivore activity, as informed by park rangers: kangaroos often use mallee vegetation for shelter and shade and feed in adjacent grasslands, and rabbits favour dune habitats for the formation of warrens, while acacias provide good cover from both aerial and terrestrial predators. Although open grasslands may provide good forage, the lack of nearby shelter suggests a lower herbivory risk for planted seedlings.

We established the 17 (50m x 50 m) sites over 6 weeks in Spring (22 October–1 December) 2016. In each site, we randomly selected 75, 2-m^2 squares from a 25×25 grid (Appendix 1). We randomly assigned one of three herbivore access treatments ($n = 25$, Appendix 1: Fig. S3) to each of the selected cells. Treatments were Open, providing access to all herbivores; Partial, excluding large herbivores (goats and kangaroos) but allowing access to lagomorphs; and Total, excluding all herbivores. Seedlings were planted using a 'Hamilton' forestry tube tree planter (Noble 1993) into loosened soil, to a depth of 2 cm below the surface, then 1L of water was applied. Pre-treatment of the buloke seedlings is described in Appendix 1.

Site variation

Four north–south orientated transects were set up at 10-m intervals across each site for quantifying site variation. To provide an index of herbivore activity at each site, we established 16 faecal pellet accumulation plots (Putman 1984) of 15.75 m^2 ($r = 2.24$ m) at 10-m intervals along each transect (accounting for 10% of site area; Appendix 1). Along the same transects we estimated cover abundance of vegetation strata and ground cover attributes using point intercept method; obtained distance to tree cover from GIS; and measured soil textural characteristics (Appendix 1). We then used principal components analysis on scaled data (Appendix 1: Fig. S4) to evaluate the influential component axes as alternative predictors of mortality and browsing. We tested these component axes against site context (as a categorical variable) and the individual site characteristic variables, and the results are presented in Appendix 1.

Seedling survey

Seedlings were surveyed on four occasions; December 2016 (10–47 days post planting), February 2017, April 2017, and December 2017 (364–406 days post planting). Whenever a dead seedling was encountered (no green plant tissue visible; Bird et al. 2012), we assigned a cause of death (Appendix 1: Table S1) and recorded the final height. During the last survey, we measured the height and stem diameter for all seedlings, recorded the status of all seedlings as live or dead, and categorized the level of damage consistent with browsing (Appendix 1: Table S1). We adopted a conservative approach to herbivore damage, modelling hazard based only on the moderate to extreme cases with damage to the apical (main) stem.

Statistical model

We modelled two aspects of the fate of buloke seedlings using survival analysis (Cox and Oakes 1984; Muenchow 1986; Mills 2011; Austin 2017): the hazard of being browsed by vertebrate herbivores, and the hazard of seedling mortality. The hazard of seedling mortality includes any other factors such as physiological stress from water deficit, pathogen attack, physical damage during planting or trampling by wildlife post-establishment.

The response variable in survival analysis is the instantaneous rate of occurrence of the event (baseline hazard), in our case seedling mortality or seedling browsing. The baseline hazard function was derived from the binary response variable (dead = 1 / alive = 0; browsed = 1 /

not browsed = 0), and time (number of elapsed days since planting), which was supplied to the model as a log-transformed offset to represent degree of exposure to browsing.

Mortality was modelled as a pseudo-Poisson process using a complementary log link (cloglog). The predicted response was a linear function of site context, treatment type, and browser activity (site mean deposition rate of lagomorph and kangaroo pellets) plus the interaction of context with treatment type. Continuous covariates were centred and rescaled by two standard deviations following Gelman (2008). Site was coded as a random effect.

The model described above imposes a constant baseline hazard. For example, in the case of mortality, it assumes that a seedling has a constant instantaneous risk of mortality throughout the experiment. In principle, and with trends in the data, that assumption seemed too simple. We included a quadratic polynomial term on the log of elapsed days, to allow for the cumulative mortality probability to increase more slowly as seedlings became established. No additional smooth term was required to fit the model of browse hazard.

We fit the models in a Bayesian framework using the package *greta* (Golding 2018) for *R* (R Core Team 2018). We ran four MCMC chains, sampling 10 000 iterations after discarding 2000 samples as burn-in. Initial parameter values except for the intercept were drawn from a random Normal distribution centred on 0 (± 0.4 SD). For the intercept, we drew initial values randomly from a Normal distribution with mean of -5, informed by preliminary modelling. The model was evaluated on Gelman Rubin statistics, complete mixing of posterior chains, and by inspecting prediction plots.

The list of variables included in exploratory models are presented in Appendix 1: Table 2, data and code are available via https://github.com/dhduncan/buloke_survival.

RESULTS

The herbivore activity index confirmed our assumptions regarding the different contexts (Fig. 1); wattle dunes and mallee vegetation were most favoured by lagomorphs and kangaroos (respectively) and open grassland sites are least favoured by both species.

We converted the herbivore activity indices to densities following Mutze et al. (2014) for lagomorphs, and Coulson and Rainer (1985) for kangaroos. These conversions suggest that 0–2 lagomorphs and <0.1 kangaroos were present per ha respectively (Appendix 2).

Seedling mortality

Overall, 60% of the 1275 planted seedlings survived the experimental period of just over 400 days. Survival averaged 30% in the open treatment cohort, 75% in the partial exclusion treatment, and 77% in the total exclusion cohort. Of seedlings that survived the year in the open treatment, only 2.5% had escaped browsing damage, compared with 45% of the partial exclusion cohort and virtually all the total exclusion cohort (Fig. 2).

Across all treatments, up to 30% of seedlings died without browsing. Most of those occurred in the first few months following planting. The most common cause of mortality for seedlings was browsing only in the open treatment (73%), while in the partial treatment only 6.5% of dead seedlings had been browsed (Fig. 2). So few seedlings in the total exclusion treatment appeared browsed that we excluded them from the statistical model of browse hazard.

Our observation period of 406 days coincided with favourable environmental conditions compared with long term averages. Twice the average monthly rainfall fell in the second month post planting, and monthly rainfall was around or above the long-term average for 10 of the 12 months (Appendix 1: Fig. S2).

The modelled baseline daily mortality hazard for a seedling in a buloke woodland context, with no protection from browsing (open treatment) was 0.005 (-5.33 on the complementary log-log scale, which translates to an expected cumulative probability of survival over a 365-day period of around 0.2 under median herbivore activity (Fig. 3).

Seedlings planted in the open treatment in buloke woodland (the base case) proved to have the highest mortality risk (Fig. 3). Guards excluding all herbivores (Total) or those that would allow access by small herbivores (Partial) resulted in a 50% reduction of mortality after one year. Guarded treatments located adjacent to wattle dunes were particularly effective, where mean mortality after one year was predicted to be only around 20%, compared to around 65% without guards (Fig. 3).

Kangaroo activity did not predict mortality, with a mean effect centred near zero with high uncertainty (Fig. 4). By contrast, higher lagomorph activity tended to increase the mortality risk, though the 95 % credible interval still included 0 (Fig. 4). For a seedling planted in Buloke woodland (base case) if lagomorph pellets were set to the 90% quartile (0.05 pellets per plot per day, estimated to be equivalent to 1 rabbit/ha; Mutze et al. 2014), the expected probability of survival decreased to 0.07.

Browsing risk

At the end of one year most unguarded planted seedlings were damaged consistent with browsing on the apical stem, from 70% of seedlings in open grassy contexts to 93% of those adjacent to mallee woodlands (Fig. 2), where the hazard in open treatments was significantly higher (Fig. 5). Our model predicts that 100% of seedlings would be damaged inside the first 6 months adjacent to mallee woodlands (Fig. 6), though for other contexts it seems a matter of when, rather than if, unguarded seedlings will suffer browsing damage.

Seedling guards greatly reduced browse hazard. Negligible browse damage occurred in total exclusion guards and, overall, partial exclusion guards reduced the browse damage hazard to around 30–60% (Figs. 5 & 6). However where lagomorph activity was higher (Fig. 5), the browse hazard doubled as lagomorph activity moved from 5th to 95th quantiles of the observed range (Fig. 7).

Our model identified a negative interaction between kangaroo activity and the browsing hazard for that same cohort of partially guarded seedlings (Fig. 5). Although lagomorph activity in open grassy sites was negligible according to our activity index, around one in four seedlings in partial exclusion treatments was damaged by browsing (Fig. 2).

Seedling growth

Growth, measured by change in height (cm) and stem diameter (mm), was consistent with the pattern of mortality and browsing damage. Seedling diameters more than doubled on average (125% increase) across all treatments over the course of the experiment, but seedlings in the open treatment increased less than those in partial and total treatments (Table 1). Mean height change was negative overall (-20%) and only positive (+6.4%, or 2.3 cm) in the total exclusion cohort. Seedlings in the open treatment lost on average two-thirds of their height by the end of the experiment, or at death (whichever came first).

DISCUSSION

Factors that may impede the success of efforts to restore degraded ecosystems are usually identifiable in the generic sense, but the influence of these factors individually and in combination vary between and within heterogeneous sites. This study demonstrates the complex interplay of biotic and abiotic factors that contributed to seedling browsing and survival, and ultimately the success of revegetation efforts to improve ecosystem function.

In a period of above-average rainfall and moderate herbivore activity, 70% of seedlings planted without guards died, the average net change in height was a reduction of more than 50% of starting size, and only 2.5% of remaining seedlings were alive and without browsing damage to the apical stem. These figures help explain why regeneration has been so difficult to achieve in this highly modified ecological community. Average survival varied spatially from near 0% after a year for unguarded seedlings in buloke woodland context to better than 80% for fully protected seedlings adjacent to dunes.

Early mortality was similar among treatments and, given most of those individuals were largely intact at the first census, failure of these seedlings was likely due to moisture stress as has been reported elsewhere (Denham and Auld 2004; Bird et al. 2012). While the annual rainfall was above average, rain events are sporadic and the availability of soil moisture appears to have been insufficient to sustain these individuals. Failure to establish was common to all contexts but was particularly severe in buloke stands, which could indicate greater competition for soil moisture with established adult trees in that environment. Buloke seedlings have been shown to suffer when planted in close proximity to adult trees (Morgan et al. 2013) and for that reason we did not place seedlings within 13 m of a live adult. Nonetheless, differences in resource availability due to root zone competition might make it more difficult for seedlings to grow roots and survive moisture deficit in woodland contexts.

Survival patterns diverged as expected, and as abundantly demonstrated in the literature (e.g. Dillon et al. 2018), survival was far better when seedlings were guarded. However, we found no difference in survival between the types of protective guard—seedlings protected from both lagomorphs and kangaroos, or only kangaroos. While it could be inferred that kangaroos are a more damaging browser of buloke seedlings than rabbits, such a finding would strongly contradict the considerable body of work demonstrating that in semi-arid ecosystems rabbits are the more destructive browsers (e.g., Bird et al. 2012; Mutze et al. 2016a; although see

Kirkpatrick and Bridle 2013 for a different ecosystem). Converting pellet accumulation data to a density estimate suggested that kangaroos were below target densities, which is in accordance with data collected by the park management agency (see Morris et al. 2018). Like Bird et al. (2012), our model suggested that kangaroo activity across the range observed here did not explain mortality hazard. However, kangaroos may have impacts at higher densities, as demonstrated elsewhere (e.g., Cheal 1986, Sluiter et al. 1997).

Mortality tended to be higher in sites with greater lagomorph activity, which accords with numerous past studies. Partial treatments were also less effective in reducing browse hazard where lagomorph activity was relatively high. These observations suggest lagomorphs were the more damaging of the two browser groups. We suspect that lagomorphs may not have been strongly motivated to access the seedlings in partial guards, given the availability of alternative forage outside guards. Indeed, Cooke (1988) encountered a similar pattern and with additional trials was able to show that rabbits were not accessing all tree guards designed to exclude only kangaroos.

Our study location Pine Plains is considered a relatively homogenous semi-arid woodland landscape for management purposes, but our results show how variation in habitat type, and planting site context influence browsing and mortality hazard in important ways, mostly as a function of soil characteristics and availability of shelter from adult trees and shrubs. We exploited these differences to observe variation in survival under different levels of exposure to herbivores. It follows that the most cost-effective restoration options may similarly exploit that heterogeneity to guard less or differently where those hazards are reduced. We also recognise the need for caution in interpreting these results. While we gained insight about herbivore impacts from exploiting habitat variation, experimental manipulation of herbivore density would provide stronger inference.

Survival of a buloke seedling through a year in a natural setting is a remarkable event, as evidenced by the chronic lack of regeneration in this landscape. Even so, survival for one year does not equate to restoration success. Seedlings need to attain an escape height or bulk such that they are no longer vulnerable to browsing damage under all but the most extreme scarcity of forage. Previous work with buloke suggested that severely browsed seedlings are extremely slow to recover, even if protected from further browsing (Murdoch 2007). Seedlings remain susceptible to browsing damage by herbivores until they are at least seven years of age and are not considered ‘safe’ from browsers until over nine years of age (>60 mm basal stem diameter; Murdoch 2007) due to the low presentation of foliage. The poor height growth increment in our study reflected a high frequency of damage to apical stems. Damage to apical stems consistent with vertebrate herbivore browsing (due to the bite pattern or ancillary evidence of lateral browsing on branchlets) was evident in around two-thirds of all seedlings in open treatments, and up to half of those in the partial treatments. Even our total protected seedlings only showed average net increase of around 2.3 cm height and 0.27 cm basal diameter over one year, so the recovery period from browsing damage could be substantial. What constitutes escape size is also a function of available resources, as in times of extreme forage scarcity, vertebrate herbivores may damage or kill mature trees and shrubs: Rabbits can ring bark trees and shrubs (Tiver and Andrew 1997), and kangaroos can consume woody plant material including root tissue (Morgan and Pegler 2010).

In practical terms, hand-planted seedlings and saplings will require protection from browsers for a decade and guards will need to be maintained and potentially replaced as plants become larger. Guarding groups of plants rather than individuals may be a viable option. These possibilities could all be examined in an analysis of cost-effective restoration options using growth and survival parameters from our study.

Soil moisture relations may play an important role in the observed growth pattern, and further analysis emphasizing growth response data might benefit from substitution of our categorical site context variable for sand (or clay) percentage. In model testing, sand (or clay) percentage proved a viable alternative continuous predictor in place of site context, with survival higher in sandier sites. A spatial model of cost-effective planting for optimal canopy replacement may also benefit from the use of soil predictors in place of site context.

Conclusions

Our case study demonstrates how empirical studies can untangle the influence of a range of factors that limit ecosystem recovery. To achieve cost-effective restoration of degraded woodland ecosystems under an adaptive management framework, management agencies need quantitative links between herbivore densities, their impacts and interactions, and the effectiveness of management interventions in the system. Our study cannot satisfy all those requirements, but it does yield an immediately actionable heuristic model of where and how to revegetate endangered buloke woodlands. Seedlings must be protected from vertebrate browsing in all contexts, particularly given that they may need a decade or more of growth to reach escape height. Although habitats near dunes are favoured by lagomorphs, and particularly rabbits, if seedlings are given robust protection, the best results may be achieved planting near dunes. These insights could be incorporated into a spatially explicit restoration strategy via cost-effectiveness analyses including plant growth and survival data under varying rainfall and soil moisture conditions together with fluctuations in herbivore density and control scenarios.

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DATA ACCESSIBILITY

Data and code are available at https://github.com/dhduncan/buloke_survival.

TABLES

TABLE 1 Growth summary (mean with standard deviation in parenthesis) for 1275 hand-planted buloke (*Allocasuarina luehmannii*) seedlings. Growth calculations were made at the end of the experiment (max 406 days), or during the census when individuals were first recorded as dead. Bold values highlight negative net change.

	Exclusion treatment (*n*=425 per cohort)		
Seedling growth	Open	Partial	Total
Height (cm)	**-22.2** (12.2)	**-1.5** (12.5)	+2.3 (10.9)
Stem Ø (mm)	+0.9 (1.1)	+2.7 (1.6)	+2.7 (1.6)

FIGURE LEGENDS

FIGURE 1 Average rate of pellet accumulation per plot per day for each context, relative to the observed maxima for kangaroos (open circles) and lagomorphs (filled circles); 1 = ca. 0.12 and 0.1 pellets 15.75 m^2 day^{-1} respectively.

FIGURE 2 Final status of 1275 hand-planted buloke (*Allocasuarina luehmannii*) seedlings, across three treatments in each of four contexts: buloke woodland (BW; *n* = 150); adjacent to wattle dune (WD; *n* = 75); adjacent to mallee woodland (MW; *n* = 75); and open grassland (OG; *n* = 125). Final status was assigned after a maximum of 406 days, December 2017. Dead (no trace) are shaded the same as Dead + extreme damage, as that was their most plausible fate.

FIGURE 3 Predicted survival of hand-planted buloke (*Allocasuarina luehmannii*) seedlings (mean ± 95% credible interval) over 365 days for combinations of planting context and browser exclusion treatment with median levels of kangaroo and lagomorph activity. Random site variation was excluded from the prediction.

FIGURE 4 Standardized model coefficient estimates (median ± 50% and 95% posterior intervals) for the instantaneous mortality hazard of hand-planted buloke (*Allocasuarina luehmannii*) seedlings. Values are expressed on the complementary log-log scale. Positive values imply greater hazard and thus lower survivorship. The model intercept (-5.33, not shown) referred to an unguarded seedling planted into the buloke woodland context with average levels of kangaroo and lagomorph pellets. The standard deviation for the random effect of site (not shown) was 0.75 (0.19 SD). Grey line and fill indicate where 0 is included within the 95% credible interval, and grey open symbol indicates where 0 is included within the 50% credible interval.

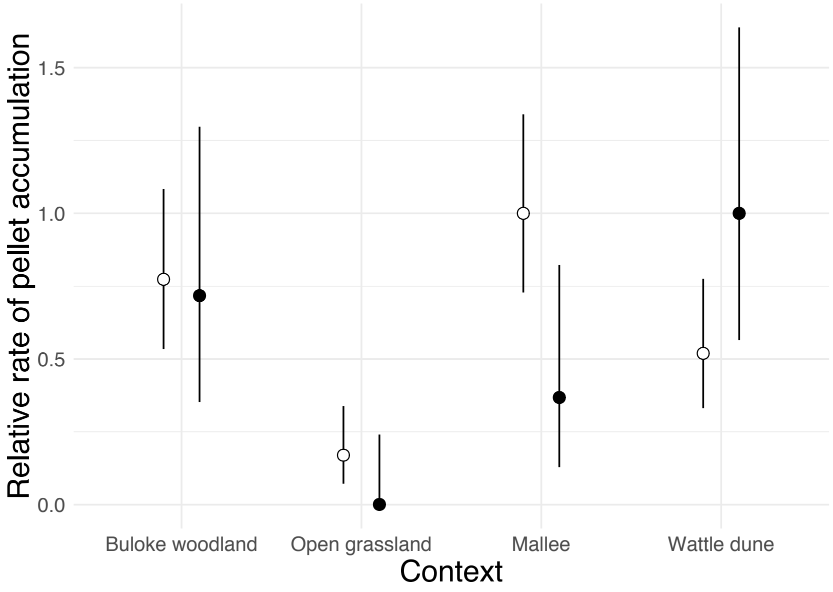
FIGURE 5 Standardized model coefficients (median ± 50% and 95% posterior intervals) for the instantaneous hazard of browsing for hand-planted buloke (*Allocasuarina luehmannii*) seedlings. Values are expressed on the complementary log-log scale. Positive values imply greater browse hazard. The model intercept was -4.32 (0.013) and refers to an unguarded seedling planted into the buloke woodland context and subject to average herbivore activity levels. Grey lines and fill indicate where a 95% credible interval includes 0, and grey open symbol where 0 is included within the 50% credible interval.

FIGURE 6 Adjusted accumulated risk of browse damage (mean ± 95% credible interval) for hand-planted buloke (*Allocasuarina luehmannii*) seedlings over 365 days as a function of planting context and browser exclusion treatment. The prediction does not include random site variation.

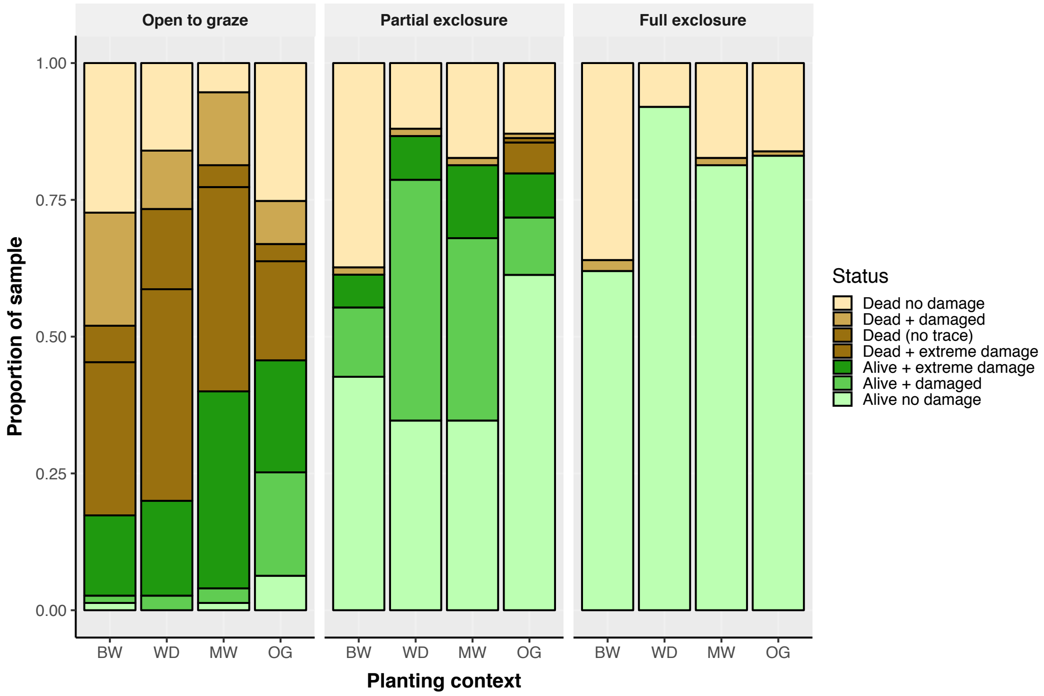
FIGURE 7 Predicted cumulative effect at 365 days of lagomorph activity (± 95% CI) on the browse hazard for hand-planted buloke (*Allocasuarina luehmannii*) seedlings at each of the three landscape contexts where lagomorph activity was recorded.

FIGURES

Figure 1

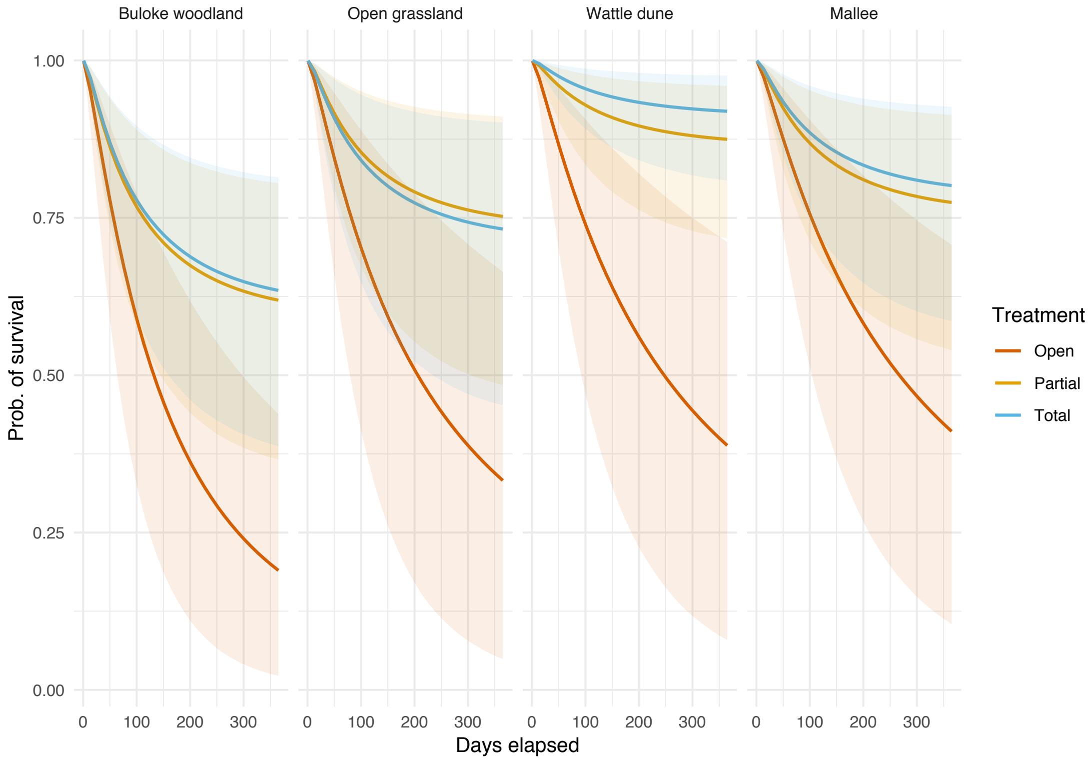


618 **Figure 2**



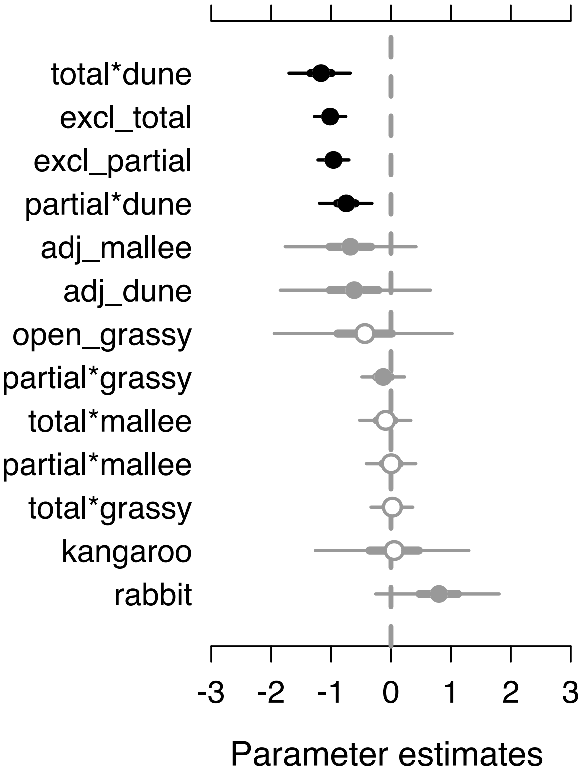
619

620 **Figure 3**

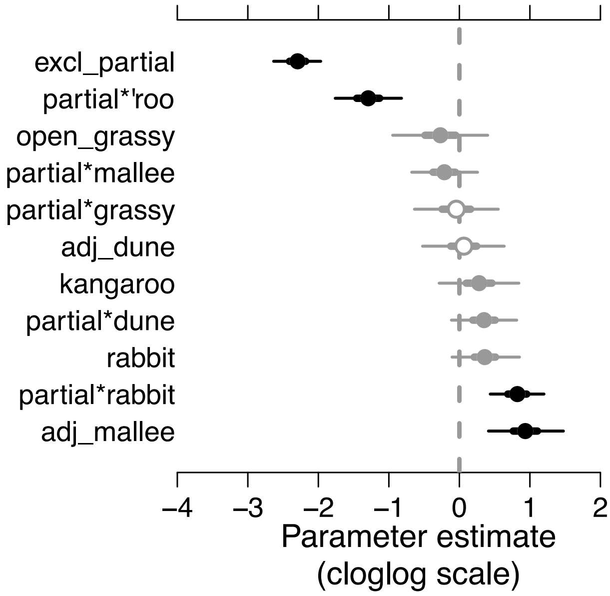


621

Figure 4

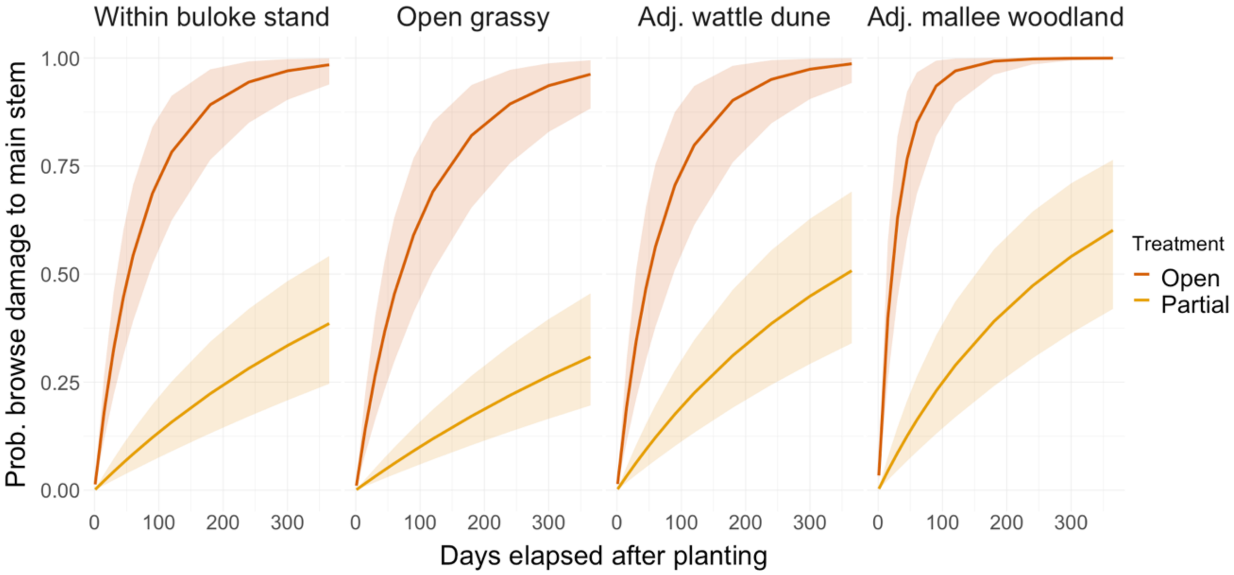

total*dune
excl_total
excl_partial
partial*dune
adj_mallee
adj_dune
open_grassy
partial*grassy
total*mallee
partial*mallee
total*grassy
kangaroo
rabbit
-3
-2
-1
0
1
2
3
Parameter estimates

624 **Figure 5**

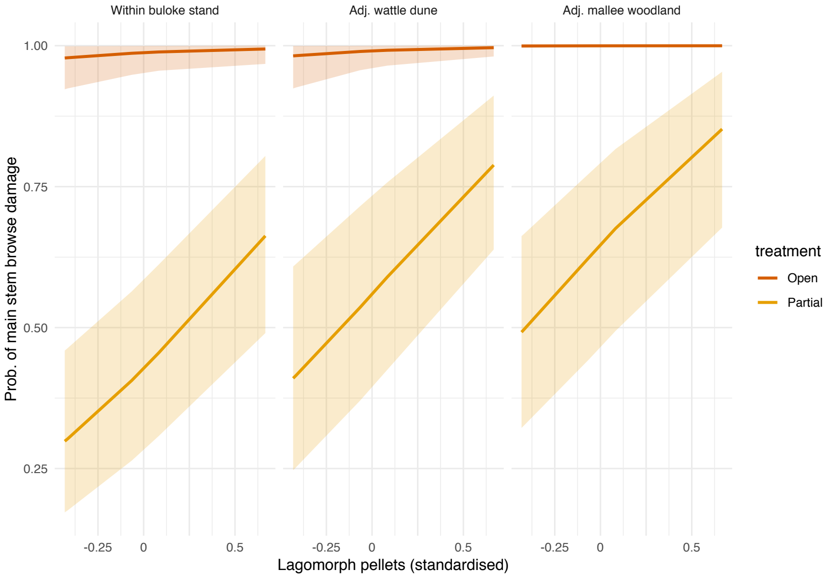


625

Figure 6


Within buloke stand
Open grassy
Adj. wattle dune
Adj. mallee woodland
Prob. browse damage to main stem
1.00
0.75
0.50
0.25
0.00
0
100
200
300
Days elapsed after planting
Treatment
Open
Partial

628 **Figure 7**



629