

Non-target impacts of weed control on birds, mammals, and reptiles

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Abstract. The impacts of invasive plant control on native animals are rarely evaluated. Using data from an eight-year study in southeastern Australia, we quantified the effects on native bird, mammal, and reptile species of (1) the abundance of the invasive Bitou Bush, *Chrysanthemoides monilifera* ssp. *rotundata*, and (2) a Bitou Bush control program, which involved repeated herbicide spraying interspersed with prescribed burning. We found that overall species richness of birds, mammals, and reptiles and the majority of individual vertebrate species were unresponsive to Bitou Bush cover and the number of plants. Two species including the nationally endangered Eastern Bristlebird (*Dasyurus brachypterus*) responded positively to measures of native vegetation cover following the control of Bitou Bush. Analyses of the effects of different components of the treatment protocol employed to control Bitou Bush revealed (1) no negative effects of spraying on vertebrate species richness; (2) negative effects of spraying on only one individual species (Scarlet Honeyeater); and (3) lower bird species richness but higher reptile species richness after fire. The occupancy of most individual vertebrates species was unaffected by burning; four species responded negatively and one positively to fire. Our study indicated that actions to remove Bitou Bush generally have few negative impacts on native vertebrates. We therefore suggest that controlling this highly invasive exotic plant species has only very limited negative impacts on vertebrate biota.

Key words: animal response to weed control; Bitou Bush; fire management; herbicide impact on animals; indirect impacts; invasive alien plant management; non-target impacts; off-target impacts; secondary effects; weed control; weed management impacts.

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INTRODUCTION

Invasive plants are a major threat to biodiversity worldwide (Sala et al. 2000), and there is considerable annual expenditure on their control

(e.g., McNeely et al. 2003, Simberloff 2013). For example, in the USA, environmental impacts of alien species are estimated to cost approximately US\$120 billion per year (Pimentel et al. 2005). In Australia, an estimated ~AUD 110 million dollars

was spent directly on controlling invasive alien plants in 2004, although the annual economic costs of such plants was estimated to be AUD 3.5–4.5 billion (Sinden et al. 2004). Despite a desire for vegetation dominated by native plants, there are often complex issues associated with alien species control, including the cost vs. efficacy of control (Lindenmayer et al. 2015b) and non-target impacts on other species. Invasive plants can provide food or habitat for a wide range of native species (Low 1999, Zavaleta et al. 2001, Davis et al. 2011), including endangered taxa (Lampert et al. 2014), so their removal can negatively affect native biodiversity (Rinella et al. 2009, Lampert et al. 2014). Furthermore, the effects of the weed control procedure itself can directly harm native species (Matarczyk et al. 2002, Crone et al. 2009, Firm et al. 2010), such as herbicide impacts on pollinators (e.g., herbicide effects on pollinators; Potts et al. 2010).

Although there is considerable understanding of invasive species ecology, control efforts are often evaluated in terms of their positive or negative impacts on (non-target) biota (Hulme 2006, Reid et al. 2009, Martin and Murray 2013, Shackelford et al. 2013, Buckley and Han 2014) (but see Brooke et al. 2013, Lee et al. 2013, Douglas et al. 2014, Lampert et al. 2014, Oppel et al. 2016), with the exception of introduced biological control agents (Louda et al. 2003).

In this study, we used an eight-year quasi-experiment (*sensu* Manly 1992, Cunningham and Lindenmayer 2016) in southeastern Australia to quantify the effects of weed control of the invasive shrub, Bitou Bush, *Chrysanthemoides monilifera* ssp. *rotundata*, on native birds, mammals, and reptiles. Bitou Bush was introduced to Australia in 1852 to stabilize coastal sand dunes after sand mining, livestock grazing, and other human disturbances (French et al. 2008, Downey et al. 2009). It is one of Australia's top 32 worst environmental weeds and can have substantial impacts on invaded ecosystems (Vranjic et al. 2012) including altering habitat suitability for wildlife (French and Zubovic 1997), excluding native plants (French et al. 2008), and altering ecological processes such as decomposition and nutrient cycling (Lindsay and French 2005, French et al. 2008).

A series of sub-treatments involving herbicide spraying, burning, and repeat spraying is a widely employed method to control Bitou Bush

(Lindenmayer et al. 2015b). Herbicide (and especially glyphosate, the herbicide used here) and fire are commonly used weed control techniques, although not routinely together (Kettenring and Adams 2011). Recent work has revealed that the spray–burn–spray treatment sequence is both the most cost-effective and ecologically effective approach for controlling Bitou Bush and promoting the recovery of native plant species richness and cover (Lindenmayer et al. 2015b). However, the effects on native animal biota of the spray–burn–spray approach to Bitou Bush control remain poorly understood. Given this knowledge gap, our study aimed to answer the following four questions.

Question 1. Do native birds, mammals, and reptiles respond negatively to infestations of Bitou Bush? We postulated that native vertebrates would be negatively affected by the occurrence and abundance of Bitou Bush. This was because other authors have found that it alters habitat suitability for a range of animal taxa (e.g., French and Zubovic 1997, reviewed by French et al. 2008, Downey et al. 2009, Adair et al. 2012).

Question 2. What is the impact of the Bitou Bush control protocols on birds, mammals, and reptiles? That is, “Do vertebrate species richness and the occurrence of individual species increase or decrease following Bitou Bush removal?” Native vertebrates may increase in richness and occurrence because of previously documented (Lindenmayer et al. 2015b), positive effects of Bitou Bush removal on native vegetation (Fig. 1b). Recovery of native vegetation may restore the historical conditions to which native vertebrates are adapted, including habitat structure and composition (Mason and French 2007), microclimatic conditions (Lindsay and French 2005), and prey populations such as invertebrates (French and Eardley 1997, Lindsay and French 2004b). Conversely, there may be negative effects of Bitou Bush removal because Bitou Bush provides cover and/or foraging habitat for some vertebrates (Fig. 1a; French et al. 2008, Schirmel et al. 2016) or because the weed control method directly reduces the survival or reproduction of native animals (Fig. 1c), as has been observed with glyphosate and amphibians (Relyea 2005). There may be neutral or no discernible impacts of Bitou Bush removal if animals are insensitive to changes in vegetation structure and cover created by Bitou Bush.

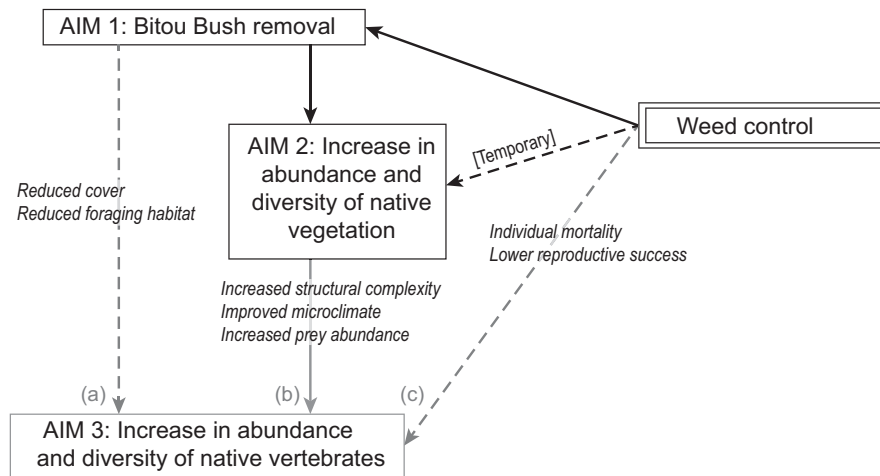


Fig. 1. Hypothesized way in which invasive plant species control, Bitou Bush removal, and native vegetation recovery affect vertebrate animal populations. Boxes with single-line border show management aims; box with double-line border shows management action. Black lines represent demonstrated relationships (Lindenmayer et al. 2015b). Gray lines (a–c) represent relationships examined in this paper, overlain with hypothesized mechanisms. Solid lines are intended (positive) effects; dashed lines are unintended (negative) effects. The figure relates to Questions 2 and 3 in the text.

Question 3. Does spraying, fire, or a combination of the two have the greatest (positive or negative) effect on vertebrate biota, whether direct (Fig. 1c) or indirect (Fig. 1a, b)? It was possible to address this question because there are data from areas where the normal treatment sequence protocol is incomplete (see *Study design*). Spraying is obviously a novel form of human disturbance in our study area, but its application via ultra-low-volume (ULV) herbicide might have relatively benign direct effects on vertebrates (Martin and Murray 2013). Conversely, the application of fire following herbicide application (which can be both severe and intense; sensu Keeley 2009) may have more pronounced direct effects of fauna.

Question 4. Does the control of Bitou Bush affect particular kinds of species, as reflected by their key life history attributes? An increasing number of studies are showing that the response of biodiversity to disturbance can be predicted on the basis of functional characteristics (Tilman 2001, Schleuter et al. 2010) such as taxa with particular life history attributes (Hidasi-Neto et al. 2012, Lindenmayer et al. 2015a). We could only examine Question 4 relative to birds in our study, because species numbers and functional diversity were too low for mammals and reptiles. At the outset of this study, we postulated that small-bodied

bird species that nest and/or forage in understory vegetation would exhibit strong responses to Bitou Bush control as treatment protocols can result in the short-term removal of the shrub layer (Lindenmayer et al. 2015b).

Answering the four key questions outlined above generates new insights into the effects of invasive plant species control on non-target native vertebrate biota. While our work is a detailed case study of a single weed species, our general (quasi)-experimental approach, and associated analyses in which the impacts of subsets of the overall treatment protocol are disaggregated, is useful for informing studies of non-target effects of other invasive plant control programs. Importantly, unlike most studies that examine impacts of weed control (Kettenring and Adams 2011), our investigation was conducted at spatial scales that managers act and over timeframes where longer-term effects of invasive species control can be observed.

METHODS

Study area

Our study area was the Bherwerre Peninsula within Booderee National Park (BNP), 200 km south of Sydney, southeastern Australia (midpoint

is 35°10' S, 150°40' E). The region has a temperate climate with an average rainfall of approximately 1250 mm per annum spread relatively evenly over the year. Average minimum and maximum air temperatures for February (summer) are 18–24°C and for July (winter) 9.2–15°C.

Bitou Bush is widespread on Bherwerre Peninsula where it was extensively planted to stabilize stand dunes following vegetation clearing and cattle grazing that occurred before BNP was established as a national park (see Lindenmayer et al. 2014, 2015b). Intensive disturbances such as sand mining have never occurred on the Bherwerre Peninsula, nor in other parts of BNP (Lindenmayer et al. 2014).

The treatment protocol employed in Bitou Bush control

The full-treatment regime for Bitou Bush control in BNP is a combination of sequential sub-treatments. A key sub-treatment is targeted spraying of ULV glyphosate by helicopter using a concentration of 15% glyphosate. Spraying takes place in winter when native plants are relatively inactive but Bitou Bush remains metabolically active (Toth et al. 1993). Hence, this spraying method attempts to minimize the mortality of native flora (Lindenmayer et al. 2015b).

After the first application of herbicide, dead Bitou Bush plants “cure” for >1 yr before being burned in a prescribed fire which typically occurs in winter or early spring in any given year. The fire triggers germination of Bitou Bush seed in the soil, and a year later, a follow-up spray of ULV glyphosate kills fire-triggered seedlings. Treatment burns are applied to 15- to 85-ha areas of vegetation where Bitou Bush has been sprayed in any given year. These areas are currently not subject to additional prescribed burning programs for fire hazard reduction or the protection of human infrastructure.

Unlike many other invasive plant species control programs, there is no replanting or seeding of native plants in BNP as it is assumed that native vegetation will recover by seeds dispersing from nearby vegetation (Lindenmayer et al. 2015b).

Study design

Our study comprised 44 sites on which we completed repeated surveys of vegetation cover,

birds, mammals, and reptiles. All sites were located in the same broad area (with similar climatic conditions). We targeted two vegetation types where Bitou Bush invasion is a particular problem: Swamp Oak (*Casuarina glauca*) (six sites) and forest dominated by Bangalay (*Eucalyptus botryoides*; 38 sites). Previous vegetation surveys have indicated that there is generally only limited difference in the structural and understorey composition of the vegetation between Swamp Oak and Bangalay forest (Lindenmayer et al. 2016a). The sample size for Swamp Oak was limited but it was not possible to add further locations to the study because this rare vegetation type does not exist elsewhere in our study area (or more widely within BNP). However, it is listed as an endangered ecological community in New South Wales (DECC 2007), in part because of land clearing. Therefore, understanding the impacts of Bitou Bush occurrence and treatment on the fauna inhabiting Swamp Oak vegetation is important.

Of the 44 sites in our study, 24 were in an area initially infested with Bitou Bush which we term the “Bitou Bush zone.” To these, we added a matched set of 20 reference sites where Bitou Bush was absent (and always had been, to the best of our knowledge). Data from reference sites provided information on fauna from areas free from both Bitou Bush and Bitou Bush control. Previous dune stabilization programs on the Bherwerre Peninsula meant that the reference sites tended to be ~500 m further from the coast than area supporting sites characterized by major infestations. Sites were a minimum of 200 m apart (and typically 500 m apart) to minimize the risk that fire or spraying inadvertently affected neighboring sites. These site separation distances also were employed to minimize spatial dependence, with trap recapture and radio-tracking results from previous studies of mammals and reptiles, indicating very few individuals from the majority of species move in excess of such distances.

The recommended spray–fire–spray treatment regime requires several years to be fully implemented, and each of our 24 sites infested with Bitou Bush was surveyed on a number of occasions at different stages of the treatment sequence. This enabled comparisons of no treatment, a partial sequence of treatments, and a full

sequence to be made from repeated observations at the same site. Thus, as a given site was surveyed many times throughout the duration of our study, it could appear under different treatment sequences according to the progression of particular treatments over time (see Tables 1–3). Notably, because of logistical issues, to date some areas have not received the complete spray–fire–spray regime and others have been subject to only parts of it. In some cases, unplanned fires disrupted the desired treatment sequence.

We are acutely aware of some of the limitations of our study’s experimental design. Indeed, working with a Weed of National Significance (see AWC 2012) in a National Park presents some practical and logistical constraints for the design of a large-scale field study. Because of the legal requirement for managers to actively control some invasive species (including Bitou Bush), it can be impossible to establish a “perfect experiment” with a fully randomized and fully factorial design (*sensu* Fisher 1935, Cunningham and Lindenmayer 2016) comprising different treatment regimes. For example, under the management plan for BNP, areas invaded by Bitou Bush must be subject to some kind of treatment (even if the recommended protocol cannot be fully implemented; see Lindenmayer et al. 2013). This

precluded the establishment of permanent “control” sites where Bitou Bush occurred but remained untreated. In addition, the large area of Bitou Bush infestation on Bherwerre Peninsula meant that it was not possible to spray all affected areas at the same time. Furthermore, there were insufficient resources to burn all treated areas simultaneously. Notwithstanding these challenges for experimental design, high levels of replication and appropriate inferential statistics can help to offset some of the effects of logistical and other constraints, yielding useful results (Manly 1992, Cunningham and Lindenmayer 2016). Although integrating research with management can present challenges for experimental design, stronger links between invasive species research and management can allow research to be conducted over longer periods of time and over larger spatial scales, and for weed control to be fully costed (Kettenring and Adams 2011).

Field surveys of vegetation cover

We completed detailed surveys of vegetation structure and plant species composition at each of our field sites every second year between 2007 and 2014 (more details are provided in Lindenmayer et al. 2015*b*). A single observer (CM) completed all vegetation surveys. To facilitate these

Table 1. Levels of replication for bird surveys for each of the disturbance sequences in each year.

Disturbance sequence	Year								Count
	2006	2007	2009	2010	2011	2012	2013	2014	
FFS	0	0	2	1	0	0	0	0	3
FSS	0	0	0	1	0	0	0	0	1
SFS	0	2	1	3	2	2	0	0	10
SSF	0	1	3	0	0	0	0	0	4
SSS	0	0	0	5	7	6	5	2	25
XFS	0	0	1	2	4	1	0	0	8
XSF	0	2	5	2	1	0	0	1	11
XSS	1	2	1	1	0	1	3	2	11
XXF	0	0	0	2	3	2	0	0	7
XXX	2	2	1	1	5	7	11	15	44
XXS	0	8	9	5	1	4	4	3	34
XXFc	13	13	1	1	1	0	0	0	29
XXXc	8	8	20	20	20	21	21	21	139
Count	24	38	44	44	44	44	44	44	326

Notes: Where there were less than three such sub-treatments in the four years prior to a survey, we use the letter X to show the missing treatment. Thus, the sequence spray–fire–spray is denoted as SFS, but where only a single spray event was conducted the code is XSS, and in the absence of any part of the treatment sequence, the code is XXX. Reference sites without Bitou Bush were denoted XXFc or XXXc depending on whether or not they had been burned in the previous four years. In the codes for disturbance sequence, S denotes spray and F denotes fire.

Table 2. Levels of replication for mammal trapping surveys for each of the treatment sequences in each year.

Disturbance sequence	Season									Total
	2006	2007	2008	2009	2010	2011	2012	2013	2014	
FFS	0	0	0	2	1	0	0	0	0	3
FSF	0	1	1	0	0	0	0	0	0	2
FSS	0	0	0	2	3	0	0	0	0	5
SFF	0	0	2	0	0	0	0	0	0	2
SFS	1	1	4	2	3	3	0	0	0	14
SSF	0	1	1	2	0	0	0	0	0	4
SSS	1	1	2	2	6	7	7	3	0	29
XFS	0	0	0	0	1	1	4	0	0	6
XSF	2	2	1	3	1	0	0	0	1	10
XSS	3	4	2	3	0	2	2	5	1	22
XXF	0	0	0	0	2	1	1	0	0	4
XXFc	13	6	1	1	0	0	0	0	0	21
XXX	4	1	1	1	1	7	7	10	14	46
XXS	4	10	9	5	5	2	2	5	6	48
XXXc	8	13	20	20	9	13	9	21	9	120
Count	36	40	44	43	32	36	32	44	31	336

Notes: Where there were less than three such sub-treatments in the four years prior to a survey, we use the letter X to show the missing treatment. Thus, the sequence spray–fire–spray is denoted as SFS, but where only a single spray event was conducted the code is XXS, and in the absence of any treatment, the code is XXX. For the sites that were not part of the Bitou Bush-infested area, we added “c” to the sequence code. Reference sites without Bitou Bush were denoted XXFc or XXXc depending on whether or not they had been burned in the previous four years. “Season” refers to the year in which the trapping season began. In the codes for disturbance sequence, S denotes spray and F denotes fire.

surveys, we established a permanent 100 m long transect at each of our 44 study sites. The choice of transect length was influenced by the substantial heterogeneity in vegetation cover at BNP where major changes in vegetation type often occur over a short distance (Lindenmayer et al.

2016a, b). Transect lengths in excess of 100 m would have resulted in many transects spanning two vegetation types.

Each of the 44 sites in our study consisted of star picket markers set at 0-m, 20-m, 40-m, 60-m, 80-m, and 100-m points along the permanently

Table 3. Levels of replication for reptile surveys for each of the disturbance sequences in each season.

Disturbance sequence	Year and season								Total
	2011 Summer	2011 Winter	2012 Summer	2012 Winter	2013 Spring	2013 Summer	2014 Spring	2014 Summer	
FFS	0	0	1	0	0	0	0	0	1
SFS	2	2	0	2	0	0	0	0	6
SSS	3	4	1	2	1	1	1	1	14
XFS	1	5	1	1	0	0	0	0	8
XSF	1	1	0	0	0	0	1	1	4
XSS	1	1	1	2	2	6	2	2	17
XXF	1	3	0	2	0	0	0	0	6
XXX	8	5	4	7	12	11	16	15	78
XXS	6	1	6	5	8	5	3	3	37
XXXc	13	21	9	19	19	21	20	9	131
Count	36	43	23	40	42	44	43	31	302

Notes: Where there were less than three such sub-treatments in the four years prior to a survey, we use the letter X to show the missing treatment. Thus, the sequence spray–fire–spray is denoted as SFS, but where only a single spray event was conducted the code is XXS, and in the absence of any disturbance, the code is XXX. For the sites that were not part of the Bitou Bush-infested area, we added “c” to the sequence code. Reference sites without Bitou Bush were denoted XXFc or XXXc depending on whether or not they had been burned in the previous four years. In the codes for disturbance sequence, S denotes spray and F denotes fire.

established transect. We recorded the co-ordinates of each transect using a global positioning system. We established four 10 × 10 m permanent survey plots set at least 20 m apart along the 100-m transect on each of our 44 sites within which percentage cover measurements were completed using on-the-ground estimation for live Bitou Bush, dead Bitou Bush, other plant species, and crown cover of overstory and understorey woody species. We derived a list of species in each 10 × 10 m survey plot.

We completed counts of the number of individual live Bitou Bush plants, dead Bitou Bush plants, other exotic plant species, and native plant species within a 1 × 1 m survey plot that was located in the middle of the 10 × 10 m plots.

Field surveys of vertebrates

Birds.—We used the “point interval count” (Lindenmayer et al. 2009b) method to survey birds in spring (September) each year between 2007 and 2014. This entailed an observer recording the numbers of all species of birds that are seen or heard within 5 min and within 50 m of a permanent marker point at 20 m and 80 m along the permanent transect on each of our sites. All sites were surveyed at least twice in a given one-week-long survey period. Different observers completed the two surveys on different days to reduce observer and day effects on the data (see Cunningham et al. 1999, Lindenmayer et al. 2009b). To further ensure the quality of the field data, (1) we surveyed birds at the same time in spring each year; (2) we avoided surveying birds when it was raining, foggy or windy as such conditions can influence the ability to record birds; and (3) only highly experienced observers (with more than 10 yr of field experience) conducted surveys of birds. We did not assume that our data from counts at the 20- and 80-m points were independent. Rather, our survey protocols yielded detection frequency data, that is, the number of plots out of four at a site (*viz.*: two plots at a site × two surveys at a site in a given year) where a given species was detected. Hence, the maximum value for detection frequency was four.

Bird life history attributes.—We collated data on bird species traits to address Question 4 (see *Introduction*) on links between temporal changes in species’ occurrence within areas subject to

Bitou Bush treatment and particular kinds of life history attributes. We summarized data on life history (habitat, diet, foraging substrate, movement, social system, nesting and mating behavior, and reproductive output) and morphological (body mass and relative wing length) traits (see HANZB 1990–2007, BirdLife Australia 2014). These traits are thought to reflect the ability of species to respond to environmental changes such as changes in vegetation structure and cover (Luck et al. 2012, Lindenmayer et al. 2015a).

Mammals.—Our data for terrestrial mammals were based on trapping conducted each December from 2007 to 2014. The infrastructure we established at each of our 44 sites encompassed three kinds of trap arrays that typically catch different kinds of mammal species in our study area (Lindenmayer et al. 2008a, 2016a): (1) An Elliott aluminum box trap (10 × 10 × 30 cm (Elliott Scientific Equipment, Upwey, Victoria, Australia) was placed at 10-m intervals along each transect (with the 100-m point untrapped, giving 10 traps per transect); (2) a small wire cage trap (20 × 20 × 50 cm) was placed at the 20-m, 40-m, 60-m, and 80-m points along each transect; and (3) a large wire cage trap (30 × 30 × 60 cm) was placed at the 0-m and 100-m points along each transect.

Trapping protocols at each site involved opening Elliott traps and cage traps for three consecutive days. Traps were baited with a mixture of peanut butter and rolled oats. Elliott traps and cage traps in which an animal had been captured were wiped clean, re-baited, and re-positioned where the initial capture had taken place. All captured mammals were marked with rapidly drying white corrector fluid, which has been shown to remain on the marked animal for at least a week (Cunningham et al. 2005), a sufficient period of time to complete surveys in any given year. The focus of our study was on native vertebrate species. Exotic vertebrates, such as the Red Fox (*Vulpes vulpes*), Feral Cat (*Felis catus*), Black Rat (*Rattus rattus*), House Mouse (*Mus musculus*), and European Rabbit (*Oryctolagus cuniculus*), are rare in BNP, including Bherwerre Peninsula (Lindenmayer et al. 2014, 2016a).

Reptiles.—We surveyed reptiles in December each year between 2007 and 2014 by establishing three kinds of artificial substrates at the 20-m and 80-m points along the permanent transect at

each site. These were two sheets of corrugated iron (each of 1×1 m), four standard size roofing tiles, and large (1-m^3) wooden sleepers (i.e., wooden railroad ties). These substrates are crude surrogates that approximate the kinds of natural sheltering habitats used by different species of reptiles, and they typically result in the detection of a range of different species on a given site (Michael et al. 2012).

Statistical analysis

We used hierarchical generalized linear modeling (HGLMs; Lee et al. 2006) to quantify the impacts of Bitou Bush control measures on the species richness of birds, mammals, and reptiles. For species richness data, we assumed a quasi-Poisson distribution with a log-link function and a gamma distribution with a log-link function for the random component of the model.

We used HGLMs to analyze detection frequency data for the more common individual species of birds and capture data for the more common individual species of mammals and reptiles. We modeled those species for which there were sufficient data to facilitate rigorous statistical analyses and construct robust statistical models; hence, we targeted those taxa for which there were more than 75 detections across all sites and treatments in the study. This resulted in models for 28 individual species of birds, four species of mammals, and two species of reptiles. For these analyses, we assumed a quasi-Poisson distribution with a log-link function and a gamma distribution with a log-link function for the random component of the model.

To ensure that relationships between vegetation cover and animal response were valid, we included data from vertebrate surveys in our analysis only if there was a vegetation survey within one year of the trapping survey, with no fire between the trapping survey and the vegetation survey. Levels of replication from surveys of each vertebrate group and as a function of the various Bitou Bush treatment sequences are shown in Tables 1–3.

In all models reported, we included site as a random term to account for between-site differences not related to the treatments. We checked the fitted models using visual inspection of histograms of residuals, plots of residual against fitted values, and plots of residuals against corresponding

expected normal quantiles. Because many treatments were applied after surveys had commenced, comparison of treatment sequences was possible for individual sites, and estimates of treatment effects were based on the combination of both observed within-site differences and observed between-site differences. Thus, each treatment site was surveyed on a repeated basis after different sub-components of the treatment sequence.

We divided candidate predictors into four groups (Table 4). The first group comprised measures of Bitou Bush infestation; the second was related to the sequence of treatments applied to control Bitou Bush; the third group comprised native vegetation type and time; and the fourth group comprised measures of vegetation other than Bitou Bush. We quantified levels of correlation between candidate predictors. For example, the correlation between the percentage of live Bitou Bush cover and the total number of Bitou Bush plants had a value for Pearson's r of 0.53. Correlations between other candidate predictors (e.g., live and dead Bitou Bush cover) were generally negligible ($r < 0.1$). Initially, we ignored the random structure and fitted a number of subsets of the predictors. Initially, our candidate set comprised vegetation type and time as well as the measures related to the treatments to control Bitou Bush. This was because our primary aim was to establish whether or not the measures to control Bitou Bush had an effect, either direct or indirect, on the fauna. We fitted all possible subsets of these predictors, and ranked these models using the Schwarz Information Criterion (BIC). We then fitted the best model for the fixed effects with site random effects included in the model. We used Wald tests to identify the terms that still had significant effects. We then tried adding all possible combinations of the measures of Bitou Bush infestation to the chosen model, and again chose a preferred model in a similar way to that described above. Finally, we finally repeated this process adding measures of vegetation other than the various measures of Bitou Bush. We dropped terms that were non-significant at the 5% level from the final models reported.

To investigate the structure of the bird community and bird life history attributes, we applied correspondence analysis (Greenacre 2007) to the number of detections of bird species for each site–survey combination in the Bangalay forest.

Table 4. Groups of candidate predictors used in statistical modeling of vertebrate response to Bitou Bush control (see *Statistical analysis*).

Group of candidate predictors	Description of group	List of predictors
1	Measures of Bitou Bush infestation	Whether or not site was in the Bitou Bush-infested area Percentage of live Bitou Bush cover Percentage of dead Bitou Bush cover Total number of Bitou Bush plants
2	Measures relating to the sequence of Bitou Bush treatments	Burned in previous year Burned in previous two years Sprayed in previous year Sprayed in previous two years Spraying followed by fire in previous two years
3	Vegetation type and time measures	Forest vegetation type Number of years elapsed since study commencement
4†	Measures of vegetation other than those associated with Bitou Bush	Number of native plant seedlings Number of grass plants Number of bracken fern stems Percentage cover of native plant species Percentage crown cover

† Available only for the 24 sites of the Bitou Bush vegetation study; our analyses were completed with and without these predictors.

Because of the relatively small number of observations for Swamp Oak, we were not able to accurately adjust for differences in species composition between the two vegetation types. We excluded all species with less than 10 detections. We fitted linear models to relate site–survey components to site and vegetation attributes using restricted maximum likelihood (McCulloch et al. 2008). We fitted linear models to relate bird species components from the correspondence analysis to bird life history attributes, fitting a separate model for each attribute.

We used GenStat Release 17.1 to fit the HGLMs and for the correspondence analysis, and we used R version 3.2.1 to produce graphics (Payne et al. 2007, R Core Team 2015).

RESULTS

Relationships between the occurrence of Bitou Bush and vertebrates

We identified no significant relationships between any measure of Bitou Bush cover or abundance and the species richness of birds, mammals, or reptiles (Appendix S1: Tables S1 and S2). At the individual species level, we found a significant negative relationship between the number of Bitou Bush plants and the occurrence of the Eastern Bristlebird (*Dasyurus brachypterus*;

$\chi^2 = 6.6$, $P = 0.010$) and the Eastern Yellow Robin (*Eopsaltria australis*; $\chi^2 = 4.3$, $P = 0.039$; Appendix S1: Table S1; Fig. 2). The abundance of the Long-nosed Bandicoot (*Perameles nasuta*) was significantly positively related to the amount of live Bitou Bush ($\chi^2 = 10.9$, $P < 0.001$; Appendix S1: Table S2; Fig. 3). For the amount of dead Bitou Bush, there was a positive response for the detection frequency of Lewin's Honeyeater (*Meliphaga lewinii*; $\chi^2 = 4.9$, $P = 0.026$), Little Wattlebird (*Anthochaera chrysoptera*; $\chi^2 = 10.8$, $P = 0.001$), and Rufous Whistler (*Pachycephala rufiventris*; $\chi^2 = 7.5$, $P = 0.006$; Fig. 4) and for the abundance of the Bush Rat (*Rattus fuscipes*; $\chi^2 = 4.4$, $P = 0.035$; Fig. 5).

The Brown Gerygone (*Gerygone mouki*) was significantly less likely ($\chi^2 = 5.9$, $P = 0.015$) to be found within the area of our study encompassing sites initially infested by Bitou Bush than within area supporting reference sites where Bitou Bush has never occurred. The reverse effect was identified for the Delicate Skink (*Lampropholis delicata*; $\chi^2 = 22.1$, $P < 0.001$) and two species of birds, Noisy Friarbird (*Philemon corniculatus*; $\chi^2 = 5.7$, $P = 0.017$) and Scarlet Honeyeater (*Myzomela sanguinolenta*; $\chi^2 = 8.7$, $P = 0.003$), all of which were significantly more likely to be found in the area encompassing sites initially infested by Bitou Bush (Appendix S1: Tables S1 and S2; Fig. 6).

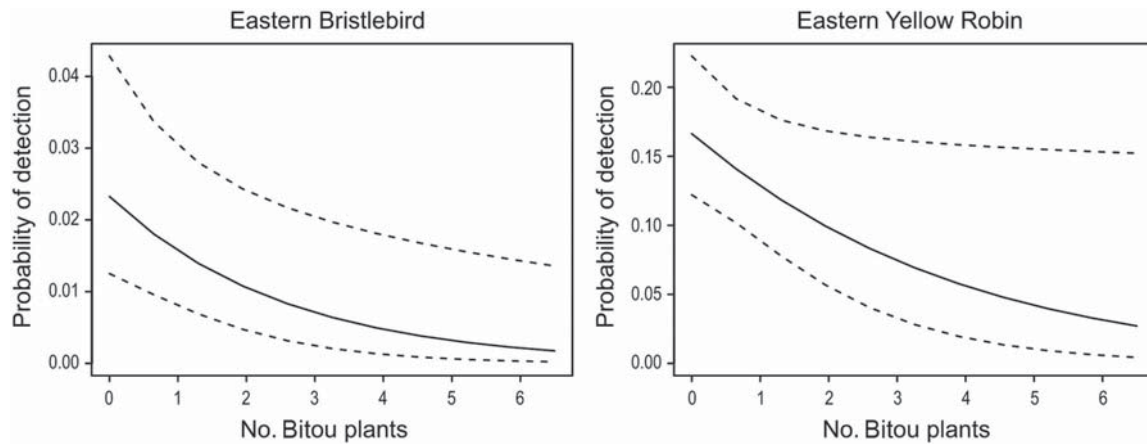


Fig. 2. Relationships between the number of Bitou Bush plants per square meter and the probability of detection of the Eastern Bristlebird and the Eastern Yellow Robin. The solid line corresponds to the mean effect in the model, and the dashed lines are the 95% confidence intervals.

The effects of fire and spraying on vertebrates

We examined the effects of Bitou Bush control treatments on vertebrates in the first and second years after fire, the first and second years after spraying, and after a combination of spraying and fire in the previous two years. There was a significant negative relationship ($\chi^2 = 4.6$, $P = 0.032$) between bird species richness and fire in the previous year (Fig. 7; Appendix S1: Table S1). In contrast, there was a significant positive relationship between reptile species richness and fire

in the previous two years ($\chi^2 = 24.3$, $P < 0.001$; Fig. 7; Appendix S1: Table S2). The Eastern Whipbird (*Psophodes olivaceus*; $\chi^2 = 5.9$, $P = 0.015$), Golden Whistler (*Pachycephala pectoralis*; $\chi^2 = 6.0$, $P = 0.014$), Brown Antechinus (*Antechinus stuartii*; $\chi^2 = 20.8$, $P < 0.001$), and the Long-nosed Bandicoot ($\chi^2 = 7.6$, $P = 0.006$) responded negatively to fire in the previous two years (Fig. 8). In contrast, the Common Brushtail Possum (*Trichosurus vulpecula*) responded positively to fire in the previous two years ($\chi^2 = 7.2$, $P = 0.007$; Appendix S1: Table S2; Fig. 8). The Brown Thornbill (*Acanthiza pusilla*) was more likely to occur ($\chi^2 = 7.9$, $P = 0.005$), whereas the Scarlet Honeyeater was less likely to occur ($\chi^2 = 8.4$, $P = 0.004$) on sites that had been sprayed in the previous two years (Appendix S1: Table S1; Fig. 9).

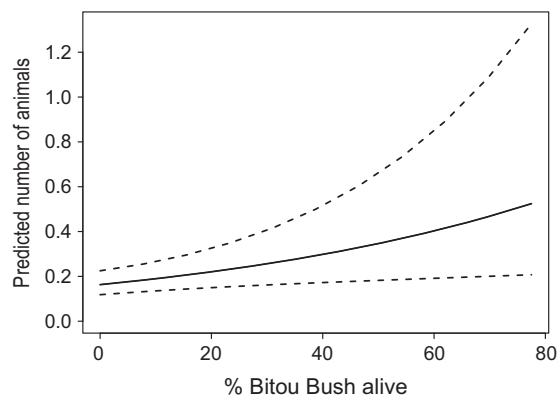


Fig. 3. Effect of percentage of live Bitou Bush cover on abundance per site of the Long-nosed Bandicoot. The solid line corresponds to the mean effect in the model, and the dashed lines are the 95% confidence intervals.

Effects of native vegetation recovery following Bitou Bush control

There were significant relationships between the detection frequency of three bird species and measures of native vegetation cover following Bitou Bush control. The Eastern Bristlebird and the New Holland Honeyeater (*Phylidonyris novaehollandiae*) responded positively to increased native vegetation cover following Bitou Bush removal ($\chi^2 = 19.6$, $P < 0.001$; $\chi^2 = 4.3$, $P = 0.039$, respectively). The estimated proportion of sites with detections for no native vegetation cover

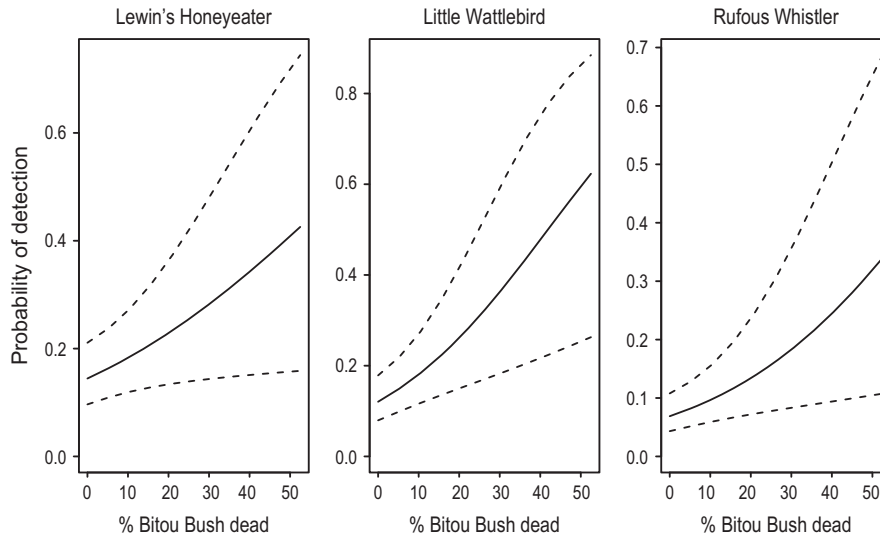


Fig. 4. Effect of percentage cover of dead Bitou Bush per site on the probability of detecting the Lewin's Honeyeater, the Little Wattlebird, and the Rufous Whistler. The solid line corresponds to the mean effect in the model, and the dashed lines are the 95% confidence intervals.

and for 100% native vegetation cover for the Eastern Bristlebird were 1% and 16%, respectively. Corresponding figures for the New Holland Honeyeater were 8% and 22%, respectively.

Bird community structure, bird life history attributes, and Bitou Bush control

The first three components from the correspondence analysis accounted for 7.3%, 6.2%, and

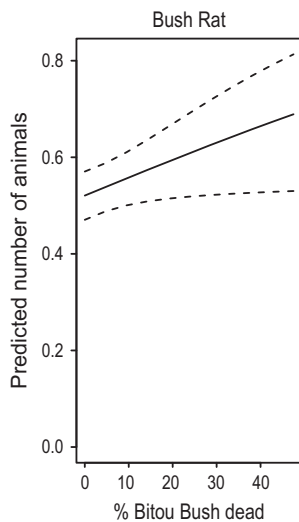


Fig. 5. Effect of percentage cover of dead Bitou Bush per site on the abundance of the Bush Rat. The solid line corresponds to the mean effect in the model, and the dashed lines are the 95% confidence intervals.

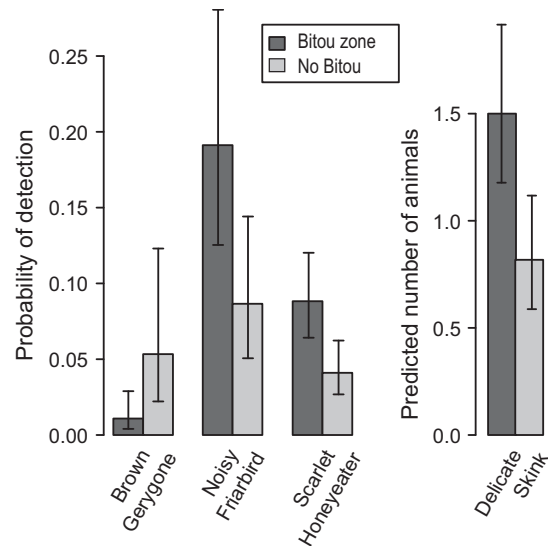


Fig. 6. Estimated probabilities of detection of three bird species and abundance of the Delicate Skink per site on Bitou Bush experimental sites (the Bitou zone) and in similar sites from main study (denoted no bitou). The diagrams show standard errors.

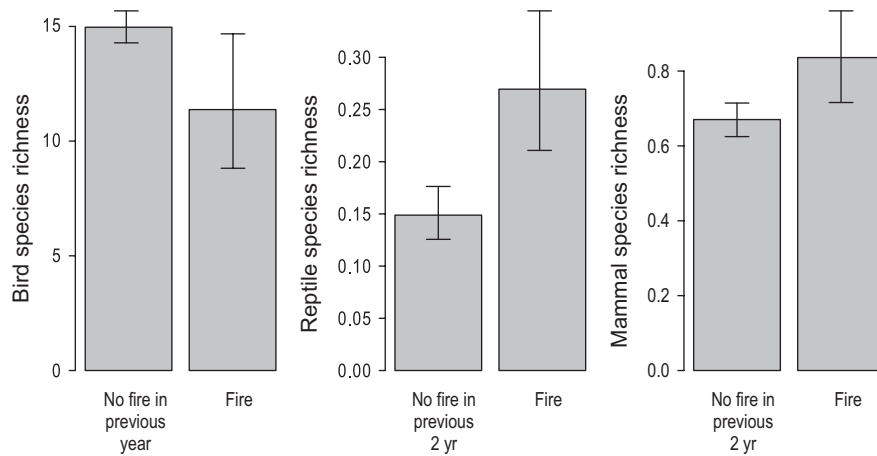


Fig. 7. Relationships between fire and the species richness of birds, reptiles, and mammals. The diagrams show standard errors.

5.7% of the variation, respectively, indicating that species composition was determined by a large number of factors and that within Bangalay forest, bird community structure was largely independent of the Bitou Bush control measures and the observed changes in vegetation. However, the third component of the correspondence analysis was significantly ($F_{1,36} = 27.7$, $P < 0.001$) related to whether or not a site was located within the

area infested by Bitou Bush. For some life history attributes, we uncovered evidence of a highly significant relationship to the scores from the correspondence analysis. For example, for the third component, there was a negative relationship with the cube root of body weight ($F_{1,42} = 9.4$, $P = 0.004$). Larger birds tended to be in the area where Bitou Bush was absent. A weaker effect was uncovered for nest height ($F_{1,42} = 4.4$,

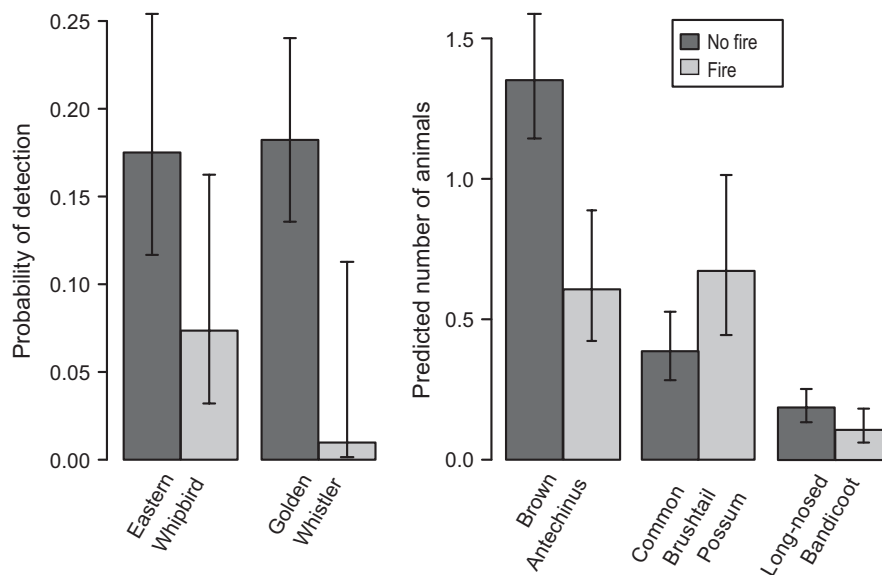


Fig. 8. Effect of fire on the estimated detection frequency of two bird species and abundance of three mammal species. The diagrams show standard errors.

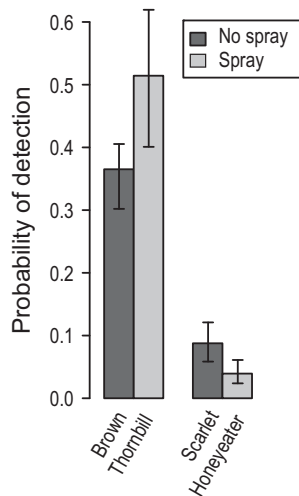


Fig. 9. Effect of spraying in the previous two years on the estimated detection frequency of two bird species. The diagrams show standard errors.

$P = 0.04$): Birds nesting at greater heights were more likely to occur in the area that remained free from infestation by Bitou Bush. Notably, these life history relationships were broadly consistent with the results identified for individual bird species (see Appendix S1: Table S1).

Other effects

We found significant positive year effects for the detection frequency of the Brown Gerygone ($\chi^2 = 25.9$, $P < 0.001$), Rufous Whistler ($\chi^2 = 13.4$, $P < 0.001$), and the number of captures of the Common Brushtail Possum ($\chi^2 = 24.7$, $P < 0.001$; Appendix S1: Tables S1 and S2). In contrast, there was evidence of negative year effects for mammal species richness ($\chi^2 = 39.1$, $P < 0.001$), reptile species richness ($\chi^2 = 74.0$, $P < 0.001$), and the detection frequency or number of captures of the Crimson Rosella ($\chi^2 = 14.9$, $P < 0.001$), Eastern Whipbird ($\chi^2 = 23.0$, $P < 0.001$), Red Wattlebird ($\chi^2 = 8.4$, $P = 0.004$), White-throated Treecreeper ($\chi^2 = 7.9$, $P < 0.005$), Brown Antechinus ($\chi^2 = 87.0$, $P < 0.001$), Long-nosed Bandicoot ($P < 0.001$), Bush Rat ($\chi^2 = 56.1$, $P < 0.001$), and Delicate Skink ($\chi^2 = 41.9$, $P < 0.001$).

Vegetation-type effects were uncommon; mammal species richness was significantly greater in Swamp Oak ($\chi^2 = 7.3$, $P = 0.007$) than in Bangalay forest (Appendix S1: Tables S1 and S2). At the individual species level, the detection

frequency of the Eastern Bristlebird was significantly greater ($\chi^2 = 6.1$, $P < 0.014$) in Swamp Oak woodland than in Bangalay forest.

DISCUSSION

Our examination of the impacts of invasive Bitou Bush and Bitou Bush control on vertebrates indicated overall species richness, and the majority of individual species were unresponsive to a range of measures of Bitou Bush abundance over the eight-year duration of our study. However, two species, including one that is endangered (the Eastern Bristlebird), responded positively to increases in native vegetation cover following the control of Bitou Bush. In terms of the impacts of different components of the treatment protocol, we found (1) no negative effects of spraying on species richness of various groups of vertebrates and on only one individual species and (2) lower bird species richness but higher reptile species richness after fire. Fire effects at the individual species level also were relatively uncommon (four species responded negatively and one positively; Appendix S1: Tables S1 and S2).

There is increasing recognition that weed control measures must result in net benefits to the associated biotic communities. However, comparatively few studies assess non-target impacts (but see Brooke et al. 2013, Lee et al. 2013, Lampert et al. 2014, Oppel et al. 2016), or determine the efficacy and impacts of weed control at spatial and temporal scales in which managers act (Reid et al. 2009, Kettenring and Adams 2011). Indeed, Kettenring and Adams (2011) found that of 355 studies documenting invasive plant control research, over 60% examined weed control that was administered for less than a year, 52% of studies monitored biotic responses for up to a year afterward, and the area sampled for treatment effects was usually less than 1 m². They concluded that many of these limitations could be addressed by integrating research and management (Kettenring and Adams 2011). Working with managers of BNP and within their management framework, our study necessarily examined the effects of invasive plant control at meaningful spatial and temporal scales. The approach we have taken in this study assisted in identifying which parts of an invasive plant species control program might have positive or

negative effects on non-target vertebrate biota and whether, for example, such impacts are due to habitat removal or due to the direct effects of spraying or fire. We discuss these key findings further in the remainder of this section and conclude with some implications for management.

Question 1. Do native birds, mammals, and reptiles respond negatively to infestations of Bitou Bush?

Most individual vertebrate species and overall species richness for birds, reptiles, and mammals were unresponsive to the presence of Bitou Bush. This result contrasts the overall findings of a recent meta-analysis that examined impacts of invasive plant impacts on animal abundance, fitness, and diversity (Schirmel et al. 2016). However, it is consistent with the seemingly neutral effects of invasive plants on animal diversity in scrubland and forest (Schirmel et al. 2016), the ecosystem types most similar to the ones we examined. Two species of birds, including the endangered Eastern Bristlebird, responded negatively to the number of Bitou Bush plants. The reason for this relationship for the Eastern Bristlebird remains unclear, but other work has indicated that the species is strongly associated with native vegetation cover (Baker 2000, Lindenmayer et al. 2009a). A predominance of Bitou Bush may erode habitat suitability for the species, thereby accounting for the species' apparent aversion to areas with many individual invasive plants. This conclusion appears to be supported by other findings in this study suggesting that the Eastern Bristlebird responds in a significant positive way to increasing native vegetation cover following Bitou Bush removal; a result that indicates replacement of exotic vegetation with native vegetation is a management intervention is beneficial to this endangered species. Notably, other authors have expressed concern about the sensitivity of the Eastern Bristlebird to fire (e.g., Baker 2000, although see Lindenmayer et al. 2016c), but we found no evidence of such effects in this investigation. Therefore, the potential impacts of the fire sub-component of Bitou Bush removal appear to be outweighed by the positive impacts of removing this invasive plant species and transforming the type of cover to one dominated by native vegetation.

We identified a significant positive response to the amount of live Bitou Bush for only one

mammal species, the Long-nosed Bandicoot. It is possible that Bitou Bush was providing cover for diurnal nest sites and protection from introduced predators such as the Red Fox.

Question 2. What is the impact of Bitou Bush control efforts on birds, reptiles, and terrestrial mammals? And Question 3. Is it the spraying, the fire, or a combination of both that has the biggest (positive or negative) effects on native biodiversity?

Several studies have highlighted the negative effects of invasive plant species control on non-target biota (e.g., Lampert et al. 2014); this includes work on Bitou Bush in eastern Australia (Matarczyk et al. 2002). However, we found no negative effects of spraying on vertebrate species richness and on only one individual species (the Scarlet Honeyeater). One species—the Brown Gerygone—responded positively to spraying. Herbicide use in Bitou Bush control is generally via ULV aerial application, which may explain why it had a benign direct effect on vertebrates. An earlier study found little or no impact of glyphosate herbicide spraying on reptiles (Martin and Murray 2013). Similarly, litter invertebrates (which are prey for a range of vertebrate species in this study) also appear to be relatively unaffected by herbicide spraying (Lindsay and French 2004a). It remains unclear why the Scarlet Honeyeater exhibited a negative response to spraying. Detailed additional studies (possibly eco-toxicological investigations; e.g., Dowding et al. 1999, Brooke et al. 2013) would be required to uncover the mechanisms driving the responses observed for this species. There has been increasing removal of glyphosate from general sale, but the effects on biodiversity of alternative herbicides would need to be subject to rigorous testing similar to that employed in the study reported here.

Bird species richness was lower but reptile species richness was higher on sites that had burned in either the previous year (birds; Appendix S1: Table S1) or both of the previous two years (reptiles; Appendix S1: Table S2). Vegetation structure and cover are important habitat components for many species (MacArthur and MacArthur 1961, Morrison et al. 2006), and fire can substantially alter habitat suitability for them, including in vegetation types in our study area (Lindenmayer et al. 2016b). However, only

two individual bird species and two mammal species responded either negatively or positively to fire either one or two years previously (Appendix S1: Table S1)—an unexpected result given the substantial effects of fire in other studies of this group of vertebrates in BNP (Lindenmayer et al. 2008*b*, 2016*b*). In the case of birds in our study, it is possible that the paucity of fire effects was associated with the mobility of some species and the relatively small scale over which areas of treated Bitou Bush were burned. However, mobility does not explain the paucity of effects for other groups such as mammals and reptiles which tend to be more movement-limited than birds.

The removal of vegetation cover may promote habitat suitability for reptiles by changing ground-level light and temperature regimes (Whelan 1995, Lindenmayer et al. 2008*c*). However, we found no negative or positive effects of fire in either the previous year or previous two years on any individual reptile species (Appendix S1: Table S2). Coastal vegetation types in eastern Australia can be highly fire prone (Bradstock et al. 2012), and it is likely that populations of most species are capable of persisting in environments subject to repeated fire events, although major changes to fire regimes (*sensu* Gill 1975) can have profound negative effects on biota (e.g., Woinarski et al. 2015).

Lewin's Honeyeater, Little Wattlebird, and the Rufous Whistler were more likely to occur on sites characterized by high levels of dead Bitou Bush. This suggests that these birds were benefiting from the spraying of Bitou Bush but subsequent burning of dead Bitou Bush may result in treated areas becoming less suitable for these three bird species. The reasons for these findings remain unclear.

Question 4. Does the control of Bitou Bush affect particular kinds of species as reflected by their key life history attributes?

Our results based on correspondence analysis contained evidence of a difference in the composition of the bird assemblage between areas infested with Bitou Bush and matched reference sites where Bitou Bush has never occurred. The reasons for these differences remain unclear, especially as the two areas in which the sites were located were characterized by similar climatic conditions and

were matched for vegetation types and other attributes. Aligned with these differences was evidence of differences in the life history attributes of birds within the area infested by Bitou Bush and those occurring primarily outside the infested area. Smaller-bodied bird species were more often recorded in the zone infested with Bitou Bush. It is possible that the dense structure generated by this invasive weed species provided cover for small-bodied birds, consistent with theories such as the landscape texture hypothesis (Fischer et al. 2008).

Ecological effectiveness

Results obtained from addressing Questions 1 and 2 in this study suggest that actions to remove Bitou Bush have few negative impacts on native vertebrates. Thus, the benefits of Bitou Bush control on native animals outweigh the costs (i.e., in Fig. 1a, c, responses are minor compared with the response in Fig. 1b). Our analyses also suggest that control efforts for Bitou Bush can have positive effects on species such as the endangered Eastern Bristlebird through promoting the recovery of native vegetation cover (Fig. 1b, response). This is an important finding as BNP is a stronghold for the few remaining populations of this species (Lindenmayer et al. 2009*a*, 2014). In addition, the spraying and fire sub-components of the treatment protocols appear to have limited effects on vertebrates (i.e., direct and indirect negative impacts of weed control on animals are negligible within two years following control (Fig. 1a, c, responses).

CONCLUSION

Invasive species control programs can sometimes have unexpected perverse effects (Zavaleta et al. 2001, Caut et al. 2009). This includes invasive plant control programs which can have negative non-target impacts on native biota, including those that are endangered (Lampert et al. 2014). Despite the ubiquity of invasive plant control programs (Hulme 2006), comprehensive assessments of the positive and negative impacts of weed control are rare, yet are essential for guiding successful and cost-effective interventions (Sinden et al. 2008, 2013). Our case study illustrates the importance of considering not only the direct effects of control measures on

the target organism itself, but also potential effects on other organisms in that ecosystem. The goal of invasive plant management is often simply the removal of the invasive plant; however, this goal needs to be placed in the context of broader goals relating to biodiversity conservation and ecosystem restoration. Assessing the impacts of control on the broader ecological community can either bolster the case for control where benefits to other species are apparent or indicate that control is inappropriate where strong negative effects are observed. Regardless, analyses such as those reported in this study can also point to ways in which control measures can be made more effective in achieving broad conservation goals.

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