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2 Title: Effects of a short fire-return-interval on resources and assemblage structure of
3 birds in a tropical savanna

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17 Running title: Short fire-return-intervals and birds

18

19

1 **Summary**

2 Fire frequency is a key land management issue, particularly in tropical savannas
3 where fire is widely used and fire recurrence times are often short. We used an
4 extended BACI (Before-After-Control-Impact) design to examine the impacts of
5 repeated wet-season burning for weed control on bird assemblages in a tropical savanna
6 in north Queensland, Australia. Experimentally replicated fire treatments (unburnt,
7 singularly burnt, twice burnt), in two habitats (riparian and adjacent open woodland),
8 were surveyed over three years (1 year before 2nd burn, 1 year post 2nd burn, 2 years
9 post 2nd burn) to examine responses of birds to a rapid recurrence of fire. Following the
10 second burn, species richness and overall bird abundance were lower in the twice burnt
11 sites than either the unburnt or singularly burnt sites. Feeding group composition varied
12 across year of survey, but within each year, feeding guilds grouped according to fire
13 treatment. In particular, abundance of frugivores and insectivores was lower in twice
14 burnt sites, probably due to the decline of a native shrub that produces fleshy fruits,
15 *Carissa ovata*. Although broader climatic variability may ultimately determine overall
16 bird assemblages, our results show that a short fire-return-interval will substantially
17 influence bird responses at a local scale. Considering that fire is frequently used as a
18 land management tool, our results emphasise the importance of determining appropriate
19 fire-free intervals.

20

21 *Key words:* alien plant species, BACI, birds, feeding guild, fire, fire frequency, tropical
22 savanna, riparian habitat, rubber vine.

23

1 **Introduction**

2 Fire is a widespread influence on ecosystems, and is one of the most powerful
3 tools available for extensive management of vegetation. The human-mediated use of
4 fire has important ramifications for the environment, and fire frequency has emerged as
5 a key attribute of fire regime (Williams *et al.* 2003), particularly because it is often
6 manipulated for land management practices. Australia is the most fire-prone continent
7 on Earth (Bowman 2003), and human-mediated fire has influenced the Australian
8 landscapes for at least 5,000 years (Johnson 2006). In particular, the extensive tracts of
9 tropical savannas in northern Australia are subjected to a high prevalence of fire. The
10 characteristic seasonality of tropical savannas, with a distinct wet season followed by an
11 extended dry season, ensures that low-intensity fires are frequent (Russell-Smith *et al.*
12 1997). Indeed, most savanna habitat in Australia receives fire at least once every five to
13 ten years (Lacey *et al.* 1982) and large areas are burnt annually (Russell-Smith *et al.*
14 1997).

15 Although tropical savannas and associated biota are often considered resilient to
16 the effects of fire (Andersen *et al.* 2005), certain elements, such as riparian or monsoon
17 forests, may be adversely affected by high fire frequencies (Andersen *et al.* 2005;
18 Russell-Smith and Bowman 1992) and there is evidence that inappropriate fire regimes
19 are linked to the decline of several bird and mammal species (Franklin 1999; Franklin *et*
20 *al.* 2005; Pardon *et al.* 2003). Thus, understanding the ecological impacts of frequent
21 fire is critical for land managers, particularly in landscapes where fire is often used for
22 landscape management.

23 A practical land management application of fire in northern Australia is for the
24 control of invasive alien plants (Emery and Gross 2005; Grice 1997). Rubber vine

1 (*Cryptostegia grandiflora*) is one of Australia's most significant invasive species, due to
2 its deleterious affect on native ecosystems (Commonwealth of Australia 1999). This
3 globally distributed woody weed smothers native vegetation and threatens native
4 biodiversity values of tropical savannas, especially within the riparian zones (Tomley
5 1998; Valentine 2006; Valentine *et al.* 2007a). Fire can reduce rubber vine survival,
6 and therefore burning may be a useful tool to control rubber vine infestations (Bebawi
7 and Campbell 2000, 2002; Grice 1997). Burning an area twice, with a short fire-return-
8 interval is often required to control woody weeds (Vitelli and Pitt 2006), including
9 rubber vine (Radford *et al.* 2008). However, little is known about the potential impacts
10 of repeated management burning on native fauna over short time frames.

11 The effects of fire frequency on communities is often ascertained by comparing
12 sites with different fire histories (e.g. high versus low: Andersen *et al.* 2005; Govender
13 *et al.* 2006; Parr *et al.* 2004; Woinarski 1990; Woinarski *et al.* 1999) and generating
14 correlative evidence on the biotic responses. Here, we use an experimental approach to
15 understand the mechanisms of effects of regular fires in a tropical savanna. Using an
16 experimental framework in which some sites were burnt, while others were not, to
17 measure the effects of fire (Radford *et al.* 2008; Valentine *et al.* 2007b), we then
18 reburned some of the burnt plots as soon as possible following the first fire (i.e. after
19 two years) to measure the effects of a short fire-return-interval on bird assemblages.
20 This design allows us to examine the impact of a repeat burn using a before-
21 after/control-impact (BACI; Stewart-Oaten *et al.* 1986) design, a technique few fire
22 studies allow (but see Smucker *et al.* 2005). Here, we experimentally examine the
23 response of bird assemblages to a short fire-return-interval in grazed tropical savannas.

1 **Methods**

2 *Study Site and Experimental Design*

3 The study took place in open eucalypt woodlands of the Einasleigh Uplands
4 bioregion (Sattler and Williams 1999), 110 km south of Townsville in north-eastern
5 Queensland, Australia. The experimental design was initially established by the
6 Commonwealth Scientific and Industry Research Organisation – Sustainable
7 Ecosystems (CSIRO-SE) and Tropical Savannas Cooperative Research Centre (TS-
8 CRC) in 1999 for investigating the effectiveness of fire regimes to control rubber vine
9 (Radford *et al.* 2008) Sites were located along three seasonally dry watercourses: Bend
10 Creek (20°16'07"S, 146°37'48"E), One Mile Creek (20°14'10"S, 146°40'35"E) and
11 Cornishman Creek (20°12'18"S, 146°27'15"E), all tributaries of the Burdekin River on
12 commercial lease-hold grazing properties (Figure 1). Along each watercourse
13 approximately three km was divided into landscape size experimental plots that were
14 randomly assigned to a prescribed burning treatment and encompassed both riparian and
15 adjacent non-riparian woodland habitat (see Radford *et al.* 2008 for habitat description;
16 Valentine *et al.* 2007b), henceforth referred to as woodland. Rubber vine occurred in
17 low to moderate infestations in both habitats, but was more prolific in riparian habitat.

18 Each plot was approximately 20 ha in size (encompassing both habitats) and
19 separated from other plots by double fire breaks, spaced at least 50 m apart. On each
20 creek, the same experimental treatments were randomly imposed upon plots and
21 included: *i*) an unburnt control plot; *ii*) a plot that was burnt once, in December 1999,
22 and *iii*) a twice-burnt plot, initial fire imposed December 1999 and second fire imposed
23 December 2001 (Fig. 1). Fire treatments examined in this paper were imposed during
24 the early tropical wet season, following the first substantial rains. In lands used for cattle

1 grazing, managers often burn at the beginning of the wet season to maximize the pasture
2 growth response to fire (Crowley and Garnett 2000). Previous research has also
3 indicated that wet season fires have less effect on bird assemblages than mid-dry season
4 fires (Valentine *et al.* 2007b). A detailed account of the implementation of prescribed
5 burning action undertaken is provided in Radford *et al.* (2008). Here, site refers to
6 either the woodland or riparian habitat of each fire treatment, providing a total of six
7 sites along each water course (one site per habitat of each fire treatment).

8 ***Sampling Strategy***

9 Data were collected during the tropical wet season between January and March
10 2001, 2003 & 2004. Sampling at these times allowed data collection one year after the
11 first burn, one year after the second burn, and two years after the second burn (Table 1).
12 Plots were surveyed in random order within each creek. Bird assemblages were
13 surveyed using two, thirty-minute timed surveys along 250 m line transects running
14 through the middle of each site (habitat/treatment replicate) using the methodology
15 described in Valentine *et al.* (2007b). The abundance of all individual birds observed
16 per transect within a site was averaged. The number of species observed was summed
17 to estimate total species richness for each site. Data on vegetation variables were
18 collected using four large quadrats (20 m x 10 m) in each site. In each quadrat, the
19 number and species of trees and shrubs were recorded. The proportion of rubber vine
20 cover in the understorey was estimated to the nearest 10% in each quadrat. In the last
21 two years of surveys, several plants were observed fruiting, particularly the commonly
22 occurring native shrub currant bush (*Carissa ovata*). Several birds were observed
23 feeding upon this shrub (e.g. noisy friarbirds *Philemon corniculatus* and great
24 bowerbirds *Chlamydera nuchalis*). To examine the potential change in food resources

1 provided by this shrub, we estimated the area (m²) of currant bush within each quadrat
2 in the last two years of surveys. All vegetation data were averaged among the four
3 quadrats to provide an estimate of average vegetation structure within each site.

4 *Analysis*

5 *Species richness and bird abundance*

6 The experiment had a randomized block design and provided the opportunity to
7 use a Before-After-Control-Impact (BACI; Stewart-Oaten *et al.* 1986) approach to
8 examine the impact of the second fire on mean bird abundance and species richness.
9 The BACI ANOVA (Analysis of Variance; conducted in SPSS, version 12) included
10 time (1 year before 2nd fire, 1 year after 2nd fire and 2 years after 2nd fire), fire treatment
11 (unburnt, singularly burnt and twice burnt) and habitat (riparian and woodland) as main
12 effects terms, and creek as a blocking factor. Interaction terms for time*fire treatment
13 and time*fire treatment*habitat were also included to examine the impact of the second
14 burn. If a significant interaction was detected, indicating a significant impact of the
15 second burn, post-hoc ANOVAs were used to further explore sources of variation
16 among factors within each year of survey. Post-hoc ANOVA used fire treatment and
17 habitat as main effects terms (including an interaction term) and creek as a blocking
18 factor. To identify species that may be driving patterns within each year of survey, the
19 responses of 24 commonly occurring bird species (i.e. species observed in at least 20 of
20 the possible 54 time*fire treatment*habitat sites) were examined using ANOVA.

21 *Feeding group assemblage*

22 Bird species were assigned to one of five feeding groups (carnivore, granivore,
23 frugivore, insectivore and nectarivore) based on their dominant source of food, using

1 dietary information from the literature (Catterall and Woinarski 2003; Higgins 1999;
2 Higgins and Davies 1996; Higgins and Peter 2002; Higgins *et al.* 2005; Higgins *et al.*
3 2001; Marchant and Higgins 1990a, b 1993). Feeding group assemblage was examined
4 by comparing the average number of carnivores, granivores, frugivores, insectivores
5 and nectarivores at each site using a MANOVA (SPSS, version 12) with the BACI
6 design (described above). A Canonical Discriminant Analysis (CDA) was used to
7 interpret significant interaction terms and to examine the influence of time and fire
8 treatments on feeding group assemblage. Abundance of each feeding group was
9 subsequently examined independently, using the BACI ANOVA described above (with
10 time, fire treatment, habitat and creek as factors). If a significant time*fire treatment
11 interaction term was detected, post-hoc ANOVA was used to further explore sources of
12 variation within each year of survey (described above).

13 *Vegetation structure and birds*

14 Vegetation structure was examined by comparing the average number of trees,
15 shrubs and the proportion of rubber vine per quadrat in each site using a MANOVA
16 (SPSS, version 12), with the BACI design (described above). The area of currant bush
17 was compared each year surveyed using ANOVA (described above). Species richness,
18 bird abundance and feeding group abundance and the abundance of species that
19 responded significantly to the second fire were compared with vegetation variables
20 within each year of survey using Pearson's correlation coefficients.

21 *Data transformations*

22 Data on rubber vine percentage were adjusted by arcsine square-root
23 transformation (Zar 1999). Species richness, abundance counts (birds, feeding groups,

1 trees and shrubs) and amount of currant bush (m^2) were examined for normality and
2 heteroscedasticity using box plots, Q-Q plots and residual plots. Multivariate linearity
3 was determined by examination of scatterplots of variables used in MANOVA. Species
4 richness and abundance of birds, trees and shrubs, and the amount of currant bush were
5 square-root transformed and individual species abundances and feeding group
6 abundances were $\log_{10}(x + 1)$ transformed to meet assumptions of ANOVA and
7 Pearson's correlation. To aid interpretation, graphs depict the untransformed data.

8 **Results**

9 *Species richness and bird abundance*

10 A total of 67 bird species were identified during the three years of surveys. An
11 additional three species were observed once each during surveys but not positively
12 identified. The unknown species were included in abundance analyses but were
13 excluded from species richness and feeding group analyses. BACI analysis on the
14 square-root transformed species richness detected a significant interaction among time,
15 fire treatment and habitat (Table 2; Fig 2.). This interaction showed that the number of
16 species in the twice-burnt sites was lower than the single-burnt or unburnt sites one year
17 after fire in both habitat types and two years after the second fire in the riparian habitat,
18 but not the woodland habitat. A significant difference in species richness was also
19 observed among creeks. Cornishman creek contained the least number of species
20 compared to either Bend Creek or One Mile Creek (species richness mean [$\pm 95\%$ CI]:
21 Cornishman Creek = 17.05 [1.33]; Bend Creek = 21.94 [2.35]; One Mile Creek = 20.66
22 [2.09]).

1 One year before the second fire, post-hoc ANOVA revealed similar number of
2 species in all fire treatments (Fig. 2), although species richness differed among creeks
3 (ANOVA: $F_{2,10} = 7.722$, $P = 0.009$). One year after the second fire, species richness in
4 the twice burnt sites was lower than in unburnt and singularly burnt sites (ANOVA:
5 $F_{2,10} = 11.459$, $P = 0.003$; Fig. 2) and varied among creeks (ANOVA: $F_{2,10} = 5.032$, $P =$
6 0.031). Two years following the second fire, species richness was still lower in twice
7 burnt sites compared to unburnt and singularly burnt sites (ANOVA: $F_{2,10} = 9.127$, $P =$
8 0.006 ; Fig. 2). Species richness was also lower in the woodland habitat than in the
9 riparian habitat (ANOVA: $F_{1,10} = 9.444$, $P = 0.010$). It is in this year that the difference
10 between habitats became apparent with regards to fire treatment. The single burnt sites
11 in riparian habitat had higher species richness compared to the twice burnt sites, while
12 the single burnt sites in woodland habitat did not differ to the twice burnt sites (Fig 2).
13 At least six species, including great bowerbird (*Chlamydera nuchalis*), red-backed
14 fairy-wren (*Malurus melanocephalus*), yellow honeyeater (*Lichenostomus flavus*),
15 Lewin's honeyeater (*Meliphaga lewinii*), noisy friarbird (*Philemon corniculatus*) and
16 rainbow lorikeet (*Trichoglossus haematodus*), that were regularly observed in the
17 unburnt and singularly burnt sites were absent from the twice-burnt sites in at least one
18 of the years following the second fire.

19 We detected a significant interaction between time and fire treatment on the
20 square-root transformed bird abundance (ANOVA: $F_{4,34} = 7.310$, $P < 0.001$; Fig. 3,
21 Table 2), such that the total abundance of birds decreased following the second fire.
22 Post-hoc ANOVA conducted in each year of survey initially showed higher abundance
23 of birds in the burnt sites compared to the unburnt sites (ANOVA: $F_{2,10} = 6.224$, $P =$
24 0.018 ; Fig. 3). However, one year following the second fire, abundances of birds in the

1 twice burnt sites were lower than the unburnt (ANOVA: $F_{2,10} = 5.463$, $P = 0.025$; Fig.
2 3) and by two years following the second fire, abundances were lower than both unburnt
3 and singularly burnt sites (ANOVA: $F_{2,10} = 8.422$, $P = 0.007$; Fig. 3). In the final year
4 of survey, abundances of birds differed between habitat types, with lower abundances of
5 birds observed in the woodland habitat (ANOVA: $F_{1,10} = 13.988$, $P = 0.004$).

6 *Responses of individual species*

7 A number of species ($n = 16$) showed differences in abundances among fire
8 treatments and/or between habitats (Appendix 1). Before the second fire, striated
9 pardalotes (*Pardalotus striatus*) were more abundant in burnt sites. An interaction was
10 detected between habitat and fire treatment for pied butcherbirds (*Cracticus*
11 *nigrogularis*) and black-faced cuckoo-shrikes (*Coracina novaehollandiae*), graphical
12 interpretation indicated that birds were more abundant in the woodland habitat of burnt
13 sites. In contrast, the red-backed fairy-wren (*Malurus melanocephalus*) showed a trend
14 for lower abundances in the burnt sites. In the two years following the second fire, a
15 few species, including the frugivore mistletoebird (*Dicaeum hirundinaceum*), the
16 granivore red-winged parrot (*Aprosmictus erythropterus*), the insectivore white-throated
17 honeyeater (*Melithreptus albogularis*), and the nectarivores noisy friarbird (*Philemon*
18 *corniculatus*) and rainbow lorikeet (*Trichoglossus haematodus*), had lower abundance
19 in the twice burnt sites compared to either the singularly burnt sites, unburnt sites, or
20 both (Appendix 1). In addition, an interaction between habitat and fire treatment was
21 detected for great bowerbirds (*Chlamydera nuchalis*), graphical interpretation indicated
22 that abundance of this species was lower in the woodland habitat of singularly burnt
23 sites and both habitats of the twice-burnt sites, compared to unburnt sites or the riparian
24 habitat of singularly burnt sites. Five bird species were detected at some point during

1 the surveys with higher abundances in the riparian habitat, and five different bird
2 species were detected with higher abundances in the woodland habitat (Appendix 1).

3 *Feeding group assemblage*

4 We detected an interaction between time and fire treatment in the abundances of
5 feeding groups (MANOVA Wilks' Lambda: $F_{20,100.5} = 1.857$, $P = 0.024$) and significant
6 variation in feeding group abundance among creeks (MANOVA Wilks' Lambda: $F_{10,60}$
7 $= 13.674$, $P < 0.001$) and habitats (MANOVA Wilks' Lambda: $F_{5,30} = 2.568$, $P =$
8 0.048). A Canonical Discriminant Analysis (CDA) was used to examine the influence
9 of the time*fire treatment interaction on feeding group assemblage (Fig. 4). Time
10 separated along the first discriminate axis while fire treatments separated along the
11 second (Fig. 4). Before the second fire, burnt sites grouped together and were
12 influenced by the abundance of granivores and carnivores at these sites (Fig. 4b and 4e).
13 However, following the second fire, unburnt sites grouped away from the twice burnt
14 sites, a grouping that was influenced by the abundance of frugivores, insectivores and
15 nectarivores. During this year of sample the singularly burnt sites were scattered
16 throughout, reflecting the variability in the abundance of the different feeding groups at
17 these sites (Fig. 4a and 4e). The pattern of separation between unburnt and twice burnt
18 sites continued two years following the second fire, with unburnt sites grouping together
19 influenced by the abundance of frugivores. Singularly burnt sites clustered between the
20 two fire treatments (Fig. 4c).

21 The abundance of each feeding group was examined individually, and we
22 detected a significant interaction in the abundance of frugivores between time and fire
23 treatment (ANOVA: $F_{4,34} = 3.299$, $P = 0.022$; Fig. 5a). Frugivore abundance was
24 consistently low during the first year of survey, before the second fire. However,

1 following the second fire, frugivores were least abundant in twice burnt sites (Fig. 5a).
2 The abundance of frugivores also varied among creeks (ANOVA: $F_{2,34} = 3.546$, $P =$
3 0.040), with lower abundance of frugivores observed at One Mile creek compared to
4 Bend creek (Tukey HSD: $P = 0.035$; untransformed means [\pm 95% CI]: One Mile = 0.9
5 [0.4], Bend = 1.8[0.8]). A significant interaction between time and fire treatment was
6 also detected for insectivores (ANOVA: $F_{4,34} = 3.608$, $P = 0.015$). Twelve months
7 following the second burn, twice burnt sites contained lower abundances of insectivores
8 than unburnt sites (Fig. 5b). Similarly, a significant interaction between time and
9 treatment was detected for nectarivores (ANOVA: $F_{4,34} = 3.010$, $P = 0.031$; Fig. 5c)
10 which showed similar patterns to insectivores. Nectarivore abundance was also highest
11 in the riparian habitat (ANOVA: $F_{1,34} = 11.173$, $P = 0.002$; untransformed means
12 [95% CI]: riparian = 7.2 [1.1], woodland = 5.2 [1.1]) and varied among creeks
13 (ANOVA: $F_{2,34} = 4.967$, $P = 0.013$). Nectarivores were observed in higher abundances
14 at Bend creek compared with Cornishman creek (Tukey HSD: $P = 0.014$;
15 untransformed means [95% CI]: Bend = 7.8 [1.8], Cornishman = 5.2 [1.2]). There was
16 no significant interaction term for either granivores or carnivores (Fig. 5d and 5e).
17 Granivore abundance showed a marked decline over time (ANOVA: $F_{2,34} = 18.218$, $P <$
18 0.001) and was particularly low in the final year of surveys (Fig. 5d). The abundance of
19 carnivores similarly varied over time (ANOVA: $F_{2,34} = 11.175$, $P < 0.001$) and was
20 greatest in the first year of surveys (Fig. 5e). There was also some variation in the
21 abundance of carnivores among creeks (ANOVA: $F_{2,34} = 3.378$, $P = 0.046$), with the
22 abundance of carnivores higher at One Mile creek compared to Bend creek (TukeyHSD:
23 $P = 0.037$; untransformed means [95% CI]: One Mile = 3.4 [0.6], Bend = 2.6 [0.9]).

1 *Vegetation structure*

2 We detected a significant difference in vegetation structure between habitats
3 (MANOVA Wilks' Lambda: $F_{3,32} = 51.589$, $P < 0.001$), and among treatments
4 (MANOVA Wilks' Lambda: $F_{6,64} = 4.499$, $P < 0.001$) and creeks (MANOVA Wilks'
5 Lambda: $F_{6,64} = 2.756$, $P = 0.019$), but no significant interaction between time and fire
6 treatment. The abundance of trees was higher in the riparian habitat and varied among
7 creeks (Table 3). Shrub abundance was lower in the burnt sites compared to the unburnt
8 sites and also varied among creeks (Table 3). The proportion of rubber vine was lower
9 in the woodland habitat and in the burnt sites (Table 3).

10 During the first year of survey, few plants were observed fruiting. However, in
11 the remaining two sample years, surveys coincided with fruiting plants, one of the most
12 common of which was the low native shrub currant bush (*Carissa ovata*). One year
13 following the second burn, the amount of currant bush (*Carissa ovata*) was lower in the
14 twice burnt sites compared to the unburnt (ANOVA: $F_{2,10} = 7.472$, $P = 0.010$; mean
15 square-root m^2 per quadrat \pm 95%CI: unburnt = 2.5 ± 1.0 , singularly burnt = 1.4 ± 1.3 ,
16 twice burnt = 0.5 ± 0.5) and varied among creeks (ANOVA: $F_{2,10} = 9.596$, $P = 0.005$).
17 Similarly, the amount of currant bush was lower in the twice burnt sites two years
18 following the second fire (ANOVA: $F_{2,10} = 5.720$, $P = 0.022$; mean square-root m^2 per
19 quadrat [95%CI]: unburnt = $2.9[1.3]$, singularly burnt = $1.1 [1.0]$, twice burnt = 0.7
20 $[0.5]$).

21 *Birds and vegetation*

22 Prior to the second fire, the abundances of both frugivores and insectivores were
23 negatively correlated with the number of trees and the proportion of rubber vine in the
24 understorey (Table 4), indicating that frugivores and insectivores were associated with

1 woodland habitat, and insectivores may also have selected burnt sites. However,
2 following the second fire, the abundance of birds, frugivores and nectarivores, as well as
3 species richness were positively associated with trees, rubber vine or currant bush
4 (Table 4), indicating that several birds were associated with unburnt or riparian habitat.
5 In particular, a positive correlative relationship was observed between the abundance of
6 frugivores and the amount of currant bush (Table 4, Fig. 6). Several great bowerbirds
7 (*Chlamydera nuchalis*) were observed feeding on the berries of currant bush, and the
8 abundances of great bowerbirds and mistletoebirds (*Dicaeum hirundinaceum*) were
9 positively associated with the amount of currant bush (Table 4). The abundance of
10 nectarivores, including noisy friarbirds (*Philemon corniculatus*), was also strongly
11 associated with currant bush.

12 **Discussion**

13 *The impact of a short fire-return-interval*

14 Repeat fires, occurring within short-time frames, substantially altered bird
15 assemblages in grazed tropical savannas. Prior to the second fire, both singularly burnt
16 fire treatments contained higher overall abundance of birds. Increased abundance or
17 species richness of birds in recently burnt sites has been observed in a variety of studies
18 (Braithwaite and Estbergs 1987; Hutto 1995; Valentine *et al.* 2007b; Woinarski 1990),
19 and is attributed to a temporary change in resource availability that benefits some
20 species (Brawn *et al.* 2001; Saab and Powell 2005; Woinarski and Recher 1997).

21 In contrast, following the second fire, there was a reduction in species richness,
22 total bird abundance, the abundance of some feeding groups, and particular species.
23 This suggests that burning for a second time within two years of a fire alters habitat in a

1 manner unfavourable to many birds. As the responses of birds to disturbances are often
2 associated with changes in the availability of resources and vegetation structure (Brawn
3 *et al.* 2001; Davis *et al.* 2000; Kutt and Woinarski 2006; Woinarski and Recher 1997), it
4 is likely that the second fire reduced the quantity or quality of resources important for
5 some species. Interestingly, the abundance of birds and species richness tended to
6 increase in the unburnt sites the first year after the 2nd fire. Given the proximity of the
7 fire treatments, it is possible that birds were moving into the unburnt sites to forage,
8 although we have no supporting data. Dissimilarity in bird assemblages between areas
9 with high versus low burning frequency has been observed in oak savannas (Davis *et al.*
10 2000) and Brazilian rainforests (Barlow and Peres 2004; Barlow *et al.* 2006) where
11 differences were attributed to changes in vegetation structure and resource availability.
12 Similarly, previous studies in tropical savannas have identified fire frequency as an
13 important influence on bird feeding groups (Woinarski 1990; Woinarski *et al.* 1999).

14 ***Changes in food availability – the response of bird feeding groups***

15 Feeding group assemblages varied among year of survey and fire treatments. In
16 particular, the assemblages of feeding groups were strongly separated by year of survey,
17 and probably reflect differences in conditions (e.g. mean annual rainfall). Year-to-year
18 variability in bird assemblages is fairly common in tropical savannas (Woinarski and
19 Tidemann 1991) and is best explained by changes in resource availability that relate to
20 the extremes of within-year seasonality (Woinarski and Tidemann 1991), or differences
21 in the wet season characteristics among years (Taylor and Tulloch 1985). However,
22 within each year of survey, fire treatments showed distinct feeding group assemblages.
23 Although burnt sites initially grouped together, in the two years following the second

1 fire, feeding group assemblages of twice burnt sites diverged increasingly from unburnt
2 and singularly burnt sites.

3 Frugivore abundance was initially low in all fire treatments when few plants
4 were observed fruiting. However, in later years, fruiting shrubs coincided with bird
5 surveys and the abundance of frugivores was lowest in the twice burnt sites. Frequent
6 fires can reduce the abundance and structure of understorey shrubs (Fox and Fox 1986)
7 and burning may also reduce the number of fruiting species (Sanaiotti and Magnusson
8 1995) or fruit production (Setterfield 1997) in the post-fire environment. Berries of the
9 currant bush provide a food resource for frugivores like great bowerbirds (*Chlamydera*
10 *nuchalis*), and may also provide foraging opportunities or shelter for other species. As
11 the amount of currant bush was reduced in twice burnt sites, frugivores may have been
12 affected by the loss of food resources.

13 Following the second fire, the overall abundance of insectivores was lower in
14 twice burnt sites. This pattern was probably driven by reduced abundance of white-
15 throated honeyeaters (*Melithreptus albogularis*). Frequent low intensity-fires can
16 reduce invertebrate abundance and species richness in subtropical eucalypt forests
17 (York 1999, 2000). Although tropical savanna arthropod communities tend to be
18 resilient to fire (Andersen *et al.* 2005; Parr *et al.* 2004), burning does disadvantage
19 certain arthropods and alter the overall composition of arthropod communities
20 (Andersen and Muller 2000; Parr *et al.* 2004), potentially to the disadvantage of
21 insectivorous species. Further, the change in invertebrate communities caused by
22 repeated burning may be amplified in environments with additional disturbances, such
23 as introduced species (Valentine *et al.* 2007a) and grazing (Abensperg-Traun *et al.*
24 1996). A reduction in preferred arthropod abundance may also influence the response

1 of some nectarivores that include arthropods in their diet, such as noisy friarbirds
2 (*Philemon corniculatus*) (Higgins *et al.* 2001).

3 *Changes in habitat structure*

4 Our study examined the effects of a single short fire-return-interval, and both
5 singularly and twice burnt sites had a lower vegetation complexity than unburnt sites.
6 In addition, the twice burnt sites contained lower amounts of currant bush than the
7 unburnt sites. Given that currant bush creates a dense shrubby understorey, the removal
8 of this plant may reduce both available shelter and foraging opportunities for birds. In
9 other parts of northern Australia, where short fire-return-intervals result in frequent fires
10 in tropical savannas, the seedling establishment in shrub and tree species may be
11 reduced (Andersen *et al.* 2005). Frequent fires may also reduce plant species richness
12 (Fensham 1990), particularly of obligate seeding species (Russell-Smith *et al.* 1998).
13 Further, frequent fire in tropical savannas typically leads to reduced vegetation
14 complexity (Bowman *et al.* 1988; Christensen *et al.* 1981) and may disadvantage bird
15 species by removing important nesting or foraging resources (Artman *et al.* 2001).

16 Habitat differences between creeks are likely to be driving some of the
17 differences in bird assemblages and abundance that were also observed. The creeks
18 examined in our study were typical of the region, but they did display variability in
19 terms of the width of creek line, distance to the Burdekin River and underlying cattle
20 management practices. Bend creek had the largest creek width, while One Mile creek
21 had the smallest. Both Bend and One Mile creeks were located on one grazing station,
22 while Cornishman creek was located on an adjacent property and may have experienced
23 different cattle grazing management practices.

1 *Conservation and Management Implications*

2 Given the deleterious impacts of rubber vine on the biodiversity values of native
3 ecosystems (Commonwealth of Australia 1999), its control is of vital importance for
4 land managers. Fire is by far the most economical and effective tool for reducing
5 rubber vine infestations (Grice 1997; Tomley 1998). In our study, burning reduced the
6 amount of rubber vine, and elements of rubber vine vegetation (e.g. rubber vine towers)
7 were visibly less in the twice burnt sites. Prescribed burning to control rubber vine
8 during the early wet season is more effective at reducing rubber vine infestation when
9 the fire is repeated within a short-time frame (Radford *et al.* 2008). However, our results
10 show that two fires in quick succession may have unwanted effects on native birds
11 within the short-term. The longer-term consequences of burning for weed control using
12 a short fire-return interval on birds needs to be examined. The long-term bird
13 assemblage structure is likely to be shaped by subsequent management actions at these
14 sites (including no follow-up management).

15 Fire is clearly a strong influence on the structure of bird assemblages (Woinarski
16 & Recher, Valentine 2007, Davis et al 2000). In this study, we showed that re-burning
17 riparian habitat within two years of a fire reduces species richness and the abundance of
18 some bird species. Frequent burning in tropical savannas can simplify habitat structure
19 (Bowman *et al.* 1988), especially in the riparian zones which tend to have high
20 structural complexity, reducing resources for birds. In areas subject to a range of
21 disturbances, including grazing and introduced plant species, frequent fires may further
22 simplify habitats. The current burning paradigm is variable throughout tropical
23 savannas, but there is a tendency for managers to set fires in the mid-dry or wet seasons
24 to reduce the likelihood of destructive, late dry season fire (Crowley and Garnett 2000;

1 Russell-Smith *et al.* 2003). We recommend that managers exercise caution with respect
2 to the frequency with which they burn. Specifically, burning within a short fire-free-
3 interval will have negative effects on bird diversity in riparian habitats of tropical
4 savannas. Further work is needed to determine appropriate fire-free intervals that meet
5 both land management and conservation objectives.

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2

3 Table 1. The experimental design showing the recent fire history (year since last fire) of
 4 sites for each combination of fire treatment and time. The columns highlighted indicate
 5 the years that bird surveys were conducted.

Fire treatment	Year of survey (as of January)			
	2001 (before 2 nd fire)	2002 (<1 month after 2 nd fire)	2003 (1 year after 2 nd fire)	2004 (2 years after 2 nd fire)
Unburnt	≥ 10 years	> 10 years	> 10 years	> 10 years
Singularly burnt	1 year	2 years	3 years	4 years
Twice burnt	1 year	0 years	1 year	2 years

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2 Table 2. ANOVA F-values for species richness and abundance of birds using BACI.

3 Significant values are in bold (* $P < 0.5$, ** $P < 0.01$, *** $P < 0.001$).

	Time _{df=2,34}	Fire treatment _{df=2,34}	Habitat _{df=1,34}	Creek _{df=2,34}	Time* Fire treatment _{df=4,34}	Time * Fire treatment * Habitat _{df=8,34}
Species richness	9.954***	14.791***	2.898***	14.033***	2.927*	2.610*
Bird abundance	22.991***	3.737*	2.457	1.867	7.336***	1.839

4

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1 Table 3. BACI ANOVA F-values for the number of trees and shrubs per quadrat and
 2 the proportion of rubber vine in the understorey. No significant interaction terms were
 3 detected. Significant values are highlighted in bold (* $P < 0.05$, ** $P < 0.01$, *** $P <$
 4 0.001). Untransformed means (\pm 95%CI) for fire treatments and habitat are shown.
 5 Letters next to fire treatment means indicate differences or similarities of means based
 6 on post hoc Tukey HSD tests ($\alpha < 0.05$).

Vegetation	F-values <small>Error df = 34</small>				Fire treatment means			Habitat means	
	Time <small>df = 2</small>	Fire treatment <small>df = 2</small>	Habitat <small>df = 1</small>	Creek <small>df = 2</small>	Unburnt	Single	Twice	Riparian	Woodland
Trees / quadrat	0.437	2.292	6.577*	3.848*	4.8 ± 0.8^a	4.3 ± 0.6^a	3.9 ± 0.7^a	4.8 ± 0.5	3.8 ± 0.5
Shrubs / quadrat	0.188	6.839**	3.164	5.501**	2.3 ± 0.6^a	1.1 ± 0.5^b	1.3 ± 0.5^b	1.7 ± 0.5	1.4 ± 0.5
Rubber vine %	0.751	7.101**	146.944***	0.588	36.4 ± 5.5^a	25.0 ± 6.3^b	20.4 ± 5.0^b	48.6 ± 6.2	5.9 ± 3.5

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1 Table 4. Pearson correlations (r) of mean bird abundance, species richness, abundance
 2 of feeding groups and abundance of species that responded significantly to the second
 3 fire with the mean number of trees, shrubs, proportion of rubber vine and area of currant
 4 bush per quadrat. Significant values are highlighted in bold (* $P < 0.5$, ** $P < 0.01$, ***
 5 $P < 0.001$). Analyses used squared-root transformations for bird abundance, species
 6 richness, number of trees, shrubs and area of currant bush, $\log_{10}(x + 1)$ transformation
 7 for abundance of feeding groups and individual species and arcsine transformation of
 8 the proportion of rubber vine.

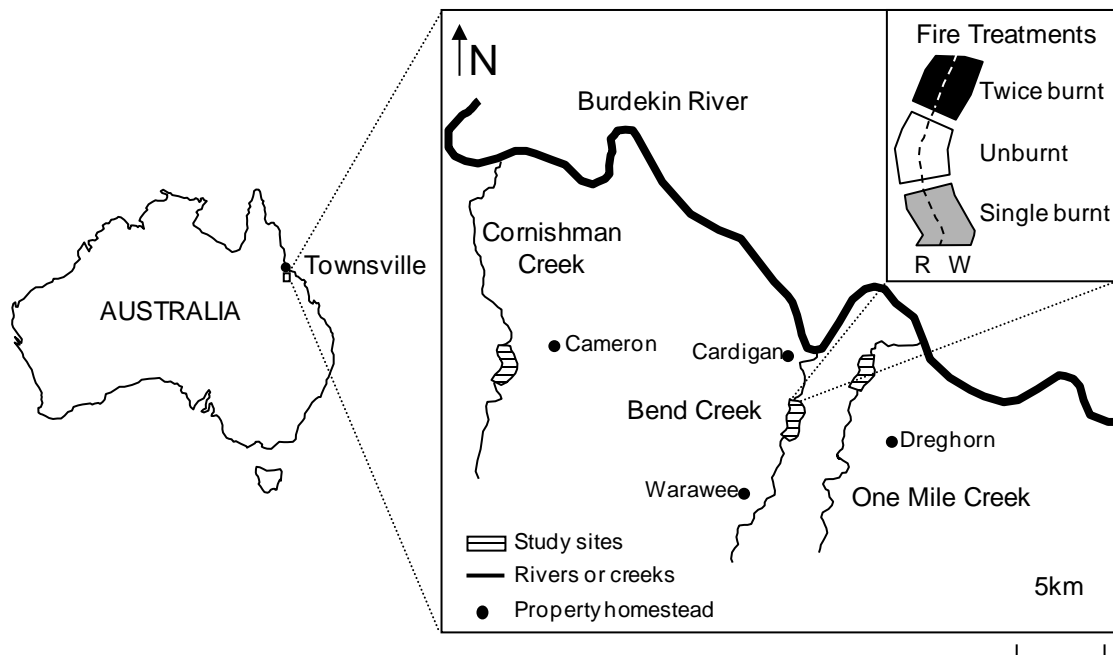
	Before 2 nd fire			1 year after 2 nd fire				2 years after 2 nd fire			
	Tree	Shrub	Rubber	Tree	Shrub	Rubber	Currant	Tree	Shrub	Rubber	Currant
Abundance	-0.202	-0.402	-0.418	0.576*	0.441	0.507*	0.623**	0.022	0.189	0.645**	0.364
Species richness	-0.280	-0.380	-0.320	0.374	0.126	0.433	0.184	0.115	0.188	0.650**	0.417
Carnivores	0.040	-0.466 [^]	-0.350	0.215	0.366	0.170	0.224	-0.328	0.182	0.231	-0.112
Frugivores	-0.587*	0.351	-0.381	0.529*	0.285	0.367	0.763***	0.242	0.083	0.361	0.728**
Great Bowerbird	0.105	-0.335	0.037	0.406	0.483*	0.343	0.537*	0.012	-0.170	0.153	0.504*
Mistletoebird	-0.382	0.080	-0.050	0.466 [^]	0.156	0.279	0.754***	0.365	0.064	0.279	0.748***
Granivores	0.110	0.015	-0.211	0.200	0.040	0.301	0.110	0.244	0.290	0.388	0.183
Red-winged Parrot	0.031	-0.123	-0.077	0.255	0.020	0.340	0.144	-0.159	0.386	0.151	-0.213
Insectivores	-0.279	-0.329	-0.494*	0.394	0.401	0.241	0.365	-0.052	0.152	0.387	0.079
White-throated HE	-0.078	-0.266	0.209	0.154	0.068	0.267	0.248	0.105	0.133	0.315	0.406
Nectarivores	0.041	-0.122	0.242	0.562*	0.407	0.540*	0.600**	-0.002	0.062	0.492*	0.241
Noisy Friarbird	0.443 [^]	0.001	-0.148	0.280	0.105	0.022	0.571*	-0.056	-0.040	-0.104	0.087
Rainbow Lorikeet	-0.168	-0.118	0.124	0.468 [^]	0.038	0.366	0.346	-0.046	-0.255	0.298	-0.032

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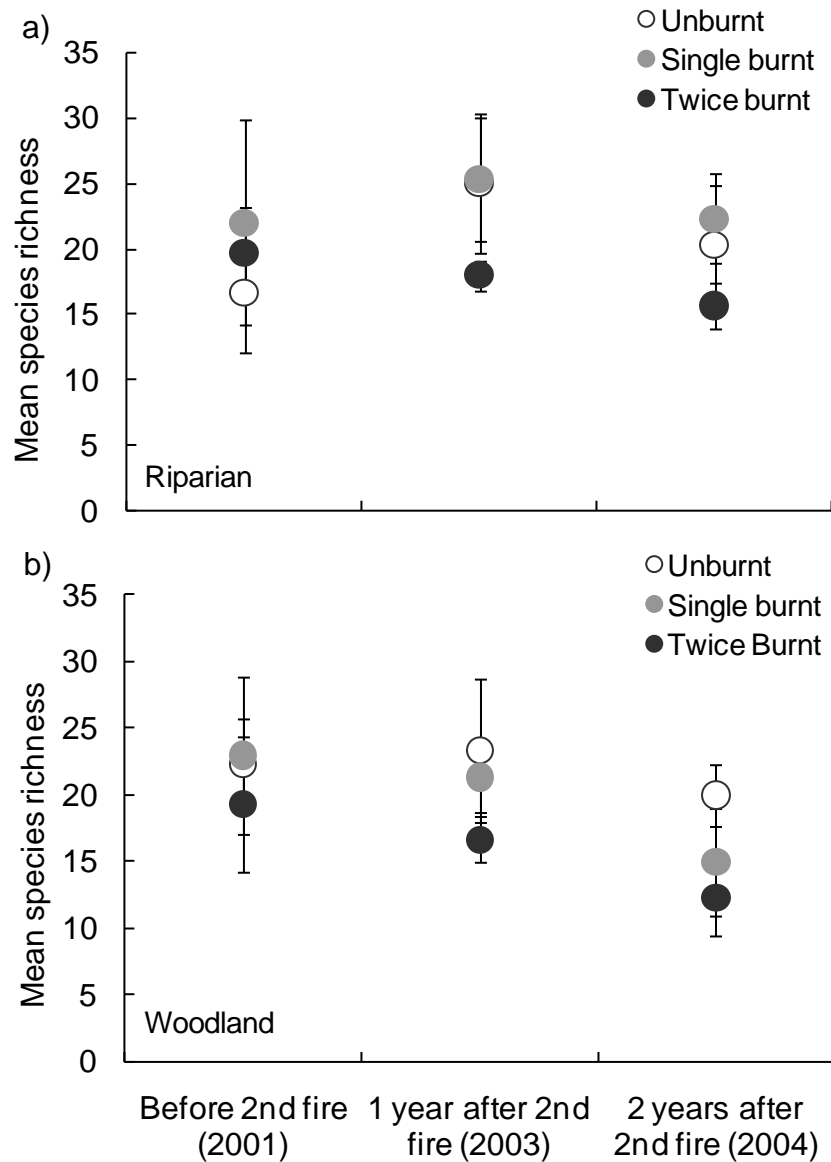
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4 Fig. 1. Map of study region in northern Australia. First inset shows location of study
 5 sites along tributaries of the Burdekin River, north-eastern Queensland. Second inset
 6 (not to scale) shows fire treatment plots and habitat for Bend Creek (dashed line
 7 indicates separation of habitats; R = riparian, W = adjacent woodland). Fire treatment
 8 placement was randomly imposed along other creeks.

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4 Fig. 2. Mean number of species (\pm 95%CI) per site observed in fire treatments over time

5 in a) riparian habitat, and b) woodland habitat. Note that in a) the unburnt fire treatment

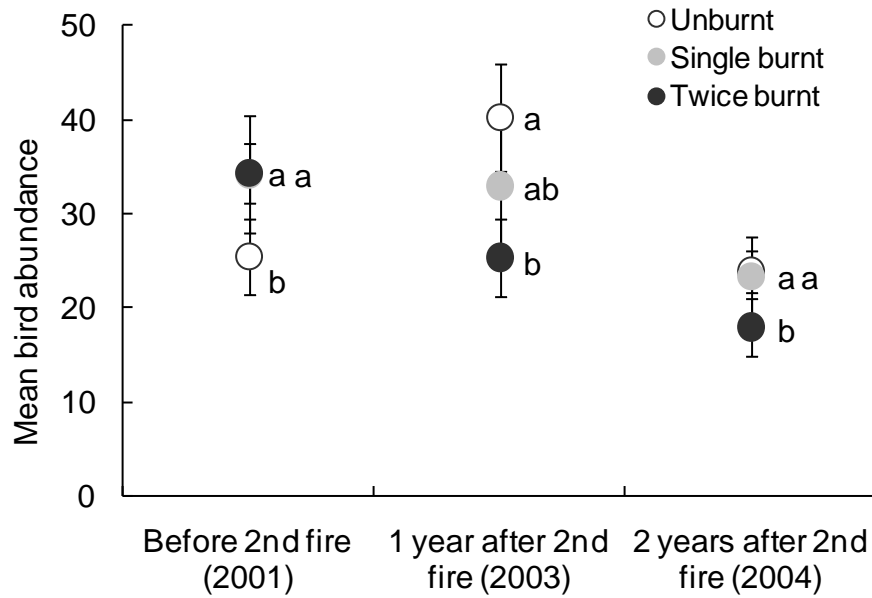
6 in the “1 year after 2nd fire’ time period is obscured by the single burnt fire treatment.

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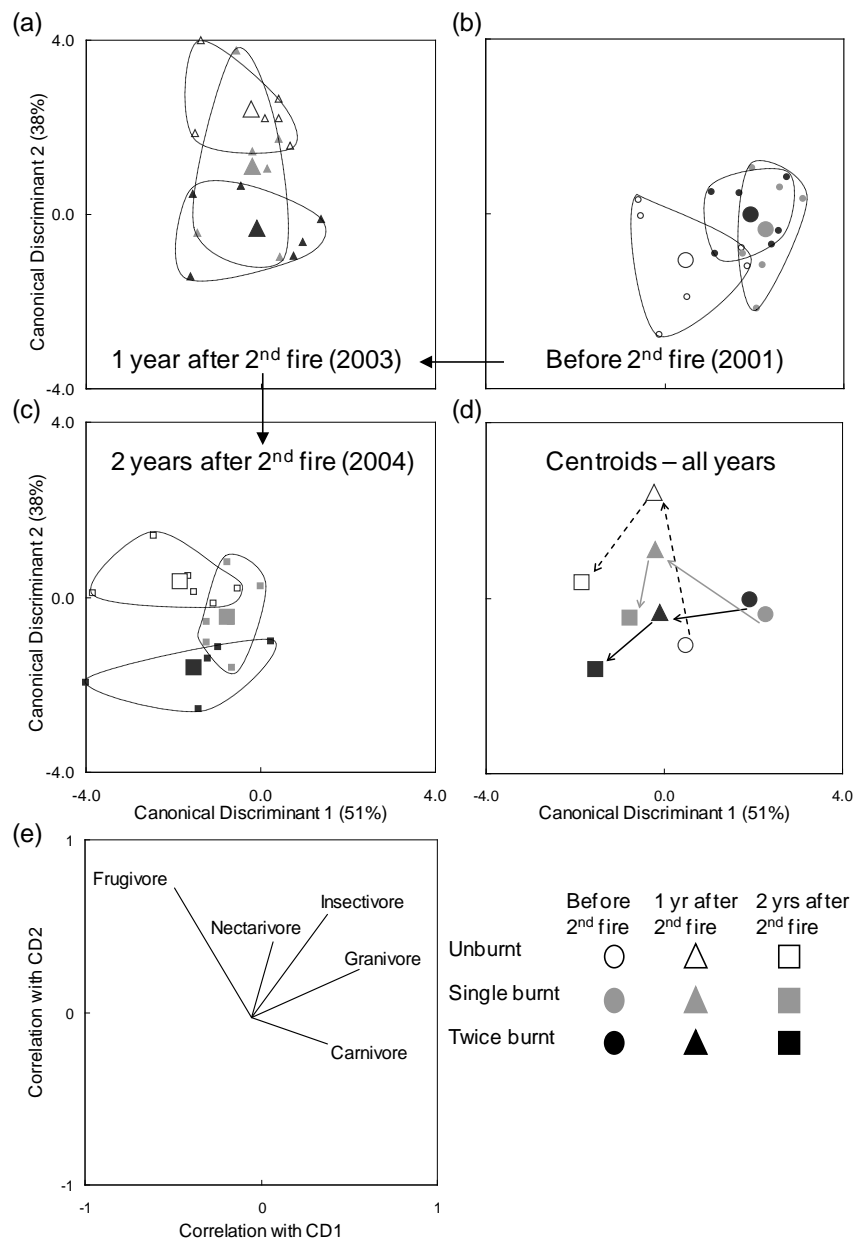


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4 Fig. 3. Mean bird abundance (\pm 95% CI) per site in fire treatments over time. Letters
 5 indicate differences between fire treatments within each year of survey based on post-
 6 hoc Tukey HSD tests ($\alpha < 0.05$). Note that the single burnt fire treatment in the 'Before
 7 2nd fire' time period is obscured by the twice burnt fire treatment.

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2 Fig. 4. Canonical Discriminant Analysis of feeding group in fire treatments over time.

3 a-c) The position of each site (small symbols) and centroids (large symbols) of fire

4 treatments (woodland and riparian sites separated) displayed in each year. Dashed lines

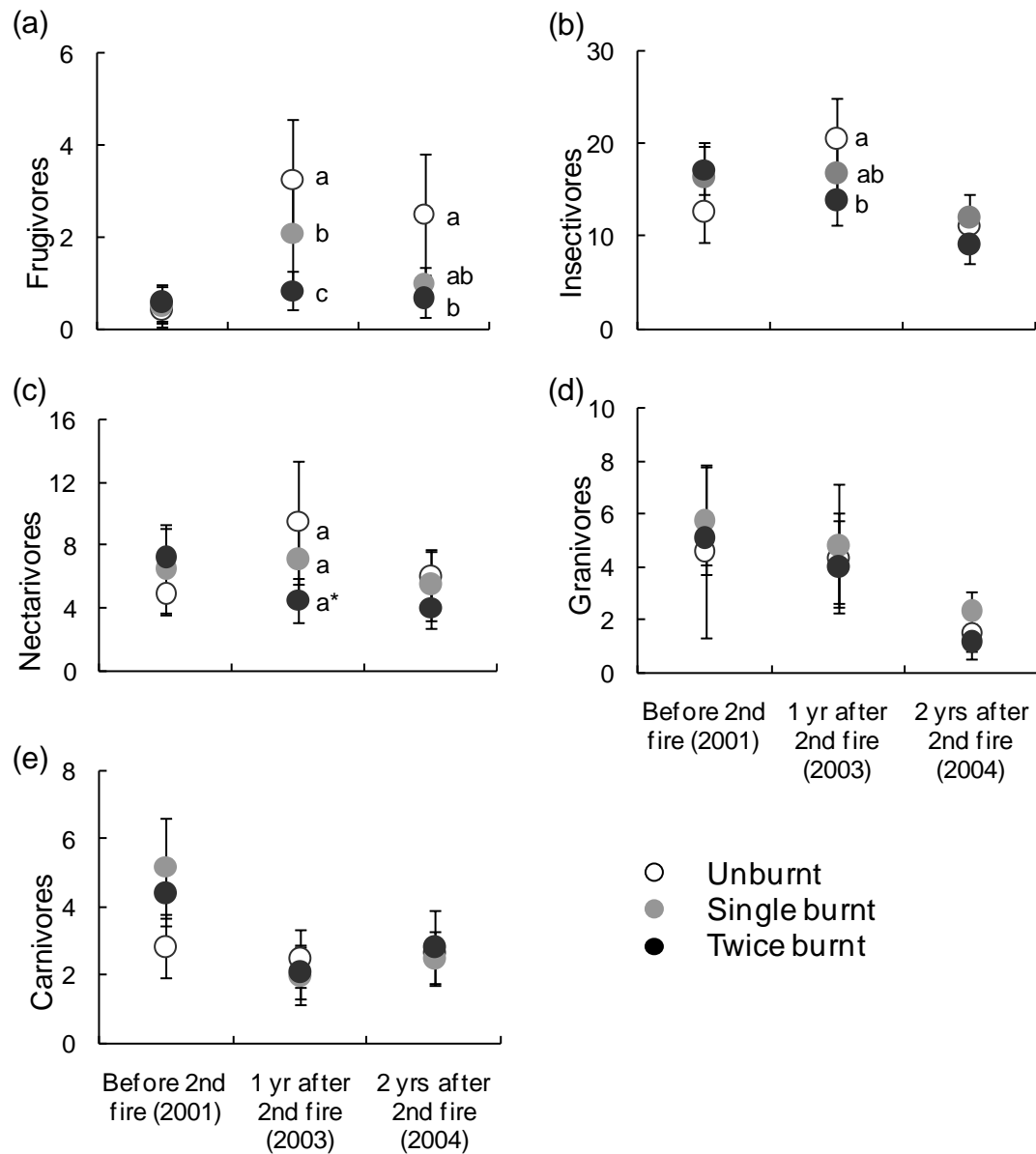
5 define the range of sites within each fire treatment*year combination. d) Centroids for

6 each group. Arrows show change in centroid over time. e) The correlation between

7 feeding groups and the canonical value.

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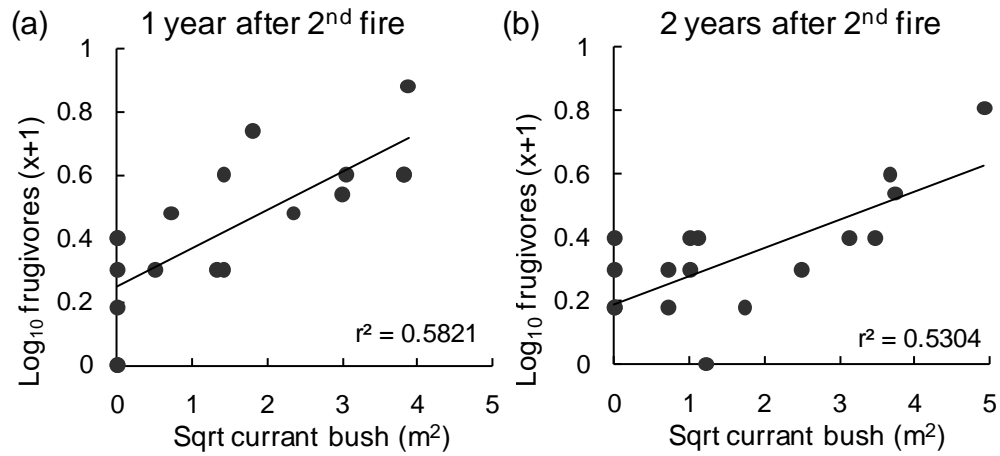
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3 Fig. 5. Untransformed mean feeding group abundance (\pm 95% CI) of a) frugivores, b)
 4 insectivores, c) nectarivores, d) granivores and e) carnivores per site in fire treatments
 5 over time. Letters within graph indicate significant differences between fire treatments
 6 within each year of survey based on post-hoc Tukey HSD tests ($\alpha < 0.05$) and the
 7 asterisk (*) indicates that there was a strong trend ($0.06 < P \leq 0.05$) for the twice burnt
 8 sites to have lower abundances than the unburnt sites.

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4 Fig. 6. Associations of mean frugivore abundance per site and the mean amount of
 5 currant bush per quadrat within a site (10 x 20m) following the second fire. Lines on
 6 graph show linear trend lines (with the r^2 value displayed).

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1 Appendix 1. ANOVA F-values for select species from 3-way ANOVA within each year of survey. Significant values are in bold (* $P < 0.5$, **
 2 $P < 0.01$, *** $P < 0.001$) and values approaching significance are identified ($0.06 > P \geq 0.05$). Letters beside significant values indicate results
 3 from post-hoc Tukey HSD tests (fire treatment: U = unburnt, S = singularly burnt, T = twice burnt) or which habitat had highest abundances
 4 (habitat: W = woodland, R = riparian). Species with a significant response to the 2nd fire are highlighted in bold. F-values for the blocking factor
 5 Creek are not shown.

Species	Before 2 nd fire (2001)			1 year after 2 nd fire (2003)			2 years after 2 nd fire (2004)		
	Fire treatment _{df=2,10}	Habitat _{df=1,10}	Fire treatment *Habitat _{df=2,10}	Fire treatment _{df=2,10}	Habitat _{df=1,10}	Fire treatment *Habitat _{df=2,10}	Fire treatment _{df=2,10}	Habitat _{df=1,10}	Fire treatment *Habitat _{df=2,10}
<i>Carnivores</i>									
Pied butcherbird	11.976** S & T > U	124.116*** W	11.976**	0.567	16.520** W	0.619	1.004	4.463	0.480
Grey butcherbird	0.454	33.843*** R	2.885	0.560	23.946** R	0.547	3.979 [^] T > S	9.541* R	0.645
<i>Frugivores</i>									
Great bowerbird	0.493	0.281	0.493	8.557** U & S > T	0.332	11.013**	1.570	0.240	1.186
Mistletoebird	0.683	0.155	1.739	5.396* U > T	0.014	1.316	6.094* U > T	0.001	0.685
<i>Granivores</i>									
Red-winged parrot	0.679	0.642	1.348	6.879* S > T	3.713	2.657	3.983 [^] U > T	0.068	1.718
Peaceful dove	2.156	0.111	1.089	0.080	0.003	0.581	0.455	7.723* R	3.182
Pale-headed rosella	0.825	0.770	0.377	0.861	0.061	0.145	1.068	1.047	0.944
<i>Insectivores</i>									
Black-faced cuckoo-shrike	4.750* T > U	0.101	4.273*	1.087	2.886	0.148	0.388	4.665 [^] R	2.997
Dollarbird	1.980	3.337	0.064	1.667	20.000** R	1.667	0.454	16.848** R	2.627
White-throated gerygone	1.517	0.496	0.585	0.637	0.004	0.657	Only one individual observed – no tests performed		
Magpie-lark	0.285	2.185	0.352	0.368	0.044	0.105	0.791	6.060* R	0.484
Australian magpie	0.118	8.857* W	0.048	0.132	0.304	0.804	0.354	1.687	0.306

Short fire-return-intervals and birds

Red-backed fairy-wren	3.888 [^] U > S & T	1.927	1.173	2.318	5.163* W	2.079	0.424	7.809* W	0.424
Yellow-throated miner	1.728	5.293* W	0.092	2.270	3.845	2.270	1.221	0.010	0.561
White-throated honeyeater	0.152	5.636* R	2.843	4.786* U > T	0.283	1.707	27.022*** S & U > T	2.157	0.749
Olive-backed oriole	0.333	1.748	0.199	1.731	1.199	0.127	1.315	0.322	0.902
Striated pardalote	4.402* S & T > U	1.115	0.673	0.172	0.080	0.189	1.251	2.256	1.587
Weebill	0.898	5.560* W	0.428	0.121	9.574* W	0.092	3.162	6.134* W	0.278
Apostlebird	2.431	0.170	1.366	2.895	0.258	0.841	2.576	4.896 [^] R	1.025
<i>Nectarivores</i>									
Blue-faced honeyeater	1.404	0.047	0.145	0.104	0.569	3.221	0.758	3.737	0.351
Yellow honeyeater	2.054	3.552	0.450	2.284	1.247	0.538	3.328	3.280	1.590
Little friarbird	2.506	0.424	3.994 [^]	0.037	0.110	1.432	0.454	2.286	0.122
Noisy friarbird	2.422	0.286	0.074	7.329* S & U > T	1.538	0.582	0.776	0.551	0.053
Rainbow lorikeet	0.536	1.938	2.794	2.021	0.008	0.365	4.559* S > T	1.014	0.506

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