Habitat and Arthropod Relationships Supporting the Red-Backed Fairy-Wren in the Australian Tropical Savanna Dry Season

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Abstract

Anthropogenic activities are influencing, and in many cases decreasing, biodiversity in the tropics. In Australia's tropical savanna, mismanaged fire regimes and the introduction of nonnative species are of major concern, and climate change may worsen the situation. Already very fire-prone, Australia's wet-dry northern tropical savanna ecosystem is experiencing intensive burn regimes and also suffers from an invasive grass species which may influence the severity and frequency of fires. This study investigates relationships between fire history, vegetation, arthropods, and a grassland-dwelling insectivorous bird, the red-backed fairy-wren (*Malurus melanocephalus*). We found that fire history predicts grass cover, which in turn influences arthropod abundance and diversity and the presence of red-backed fairy-wrens. In the context of intensive fire regimes, we argue that this species may be suitable as an indicator of ecosystem health in Australia's tropical savanna.

Introduction

The tropics have more biodiversity than other latitudes, but they also have the world's highest prevalence of wildfires, many anthropogenic and mismanaged (Cochrane, 2009). Humans began altering Australia's tropical ecology over 40,000 years ago through hunting and setting fires (Rule et al., 2012) and continue to change Australia's ecosystems. Increasingly frequent wildfires affect Australian ecology, with global climate change potentially exacerbating the situation (Bowman, 2012; Lindenmayer et al., 2010). In monsoonal northern Australia there has been a noticeable heightening of the strength, incidence, and impact of fires, which burn in the austral winter's dry season (Andersen et al., 1998). Over 75% of the area burnt annually in Australia is in the tropical savanna, a habitat occupying most of northern Australia and ~20% of the country's land area. Many bird species in this region suffer under current fire regimes, requiring larger portions of the landscape to remain unburnt for many years (Valentine et al., 2012; Woinarski and Legge, 2013).

In addition to fire, many invasive plants and animals also threaten Australia's native biota (Bowman, 2012). Invasive gamba grass (*Andropogon gayanus*; hereafter, gamba) can increase fire intensity, frequency, and extent (Rossiter-Rachor et al., 2008). In the 1930s, agriculturalists introduced this grass to the Northern Territory from central Africa as feed for cattle and it has since escaped pastureland and naturalized (Rossiter et al., 2003). The governments of Western Australia, Northern Territory, and Queensland have declared this plant a pest because of its vigorous growth and potential negative impacts (Department of Agriculture, Fisheries and Forestry, 2011). As of 2008, this tall perennial had taken over an estimated 15,000 km^2 of the tropical savanna of Australia's "Top End" and studies estimate that gamba could spread to 380,000 km^2. Gamba can reach 4 m in height, with tussocks reaching 70 cm in diameter and shallow roots spreading up to 1 m from the tussocks (Department of Agriculture, Fisheries and Forestry, 2011). This sort of growth means a potentially competitive advantage over native grasses. Because of the increased intensity of gamba-fueled wildfires, significant losses of nitrogen, phosphorus, and other limiting nutrients to the atmosphere may result from the burning of areas invaded by gamba (Rossiter-Rachor et al., 2008). Setterfield et al. (2010) found that a gamba fuel load severely changes the behavior of fire. Because gamba can be eight times taller than native grasses and can have nearly three times the biomass in a given area, gamba-fueled fires can scorch foliage in the canopy. Most trees are normally less affected. They concluded that this could have adverse effects on savanna biota adapted to frequent but less severe fires. Fire regime may influence floral composition and vice versa, thereby also affecting the savanna's diverse animal life.

The combined threat of invasive plants and fire is not limited to Australia. A federal meta-review of the interactions of fire and invasive plants in North America reports that, although in some cases prescribed burning can be a tool for controlling invasive plant species, subjecting communities with already-stressed native plants and/or invasive plants to fire, especially fires of frequencies and intensities different from those to which natives have adapted, can lead to wholesale changes in composition and displacement by invasive species (Zouhar et al., 2008). This same report generalizes that high-intensity fire increases the establishment and spread of invasive plant species compared to low-severity burns (Zouhar et al., 2008). Although not all disturbances result in invasion, disturbances facilitate the establishment of 95% of Australia's major invasive plant species. Examples in North America, the Hawaiian archipelago and South Africa demonstrate that, while some invading species qualitatively change the functions of ecosystems (setting off vicious cycles of altered disturbance regimes which reinforce their invasiveness, for instance), others only quantitatively change ecosystem functioning, not affecting new fire or other disturbance regimes (Sayre, 2003). Invasive plants can change fuel loads to the point where the fire regime becomes altered, establishing an

Figure. 1. Male red-backed fairy-wren. Photo credit: Lantz

Figure 2. Female red-backed fairy-wren. Photo credit: Lantz

"invasive plant/fire regime cycle" with implications for land management (Zouhar et al., 2008). This information illustrates the importance of studying the interactions of invasive plant species and fire globally.

Changes in fire regime and floral composition in the grass-dominated savanna of northern Australia could have many implications for the ecosystem in general. At a fine scale, these forces are expected to influence the red-backed fairy-wren (*Malurus melanocephalus*; hereafter, RBFW), an insectivorous bird inhabiting the wet-dry tropical savanna in northern Australia (Webster et al., 2010). At least in the short term, fire negatively impacts these semi-nomadic birds; they disperse out of recently burnt habitat (Valentine et al., 2007) and RBFWs experiencing late-dry-season fires have lower reproductive success (Murphy et al., 2010). The effect of fire-prone gamba on the RBFW is poorly understood. The presence of gamba alongside native grasses means that insects, potential prey of RBFWs, could be found differentially in the grasses. Food availability partly determines habitat quality for RBFWs and thus influences their selection of habitat. One would expect that the presence of gamba grass would affect arthropods in the area. However, this is poorly understood and one study found no difference in arthropod richness, quantity or community structure between gamba and native vegetation (Parr et al., 2010).

Our objectives in this study are to investigate how fire regime and the vegetative community (especially native versus gamba grasses) are correlated to arthropod group abundance and richness, and how this in turn relates to RBFW habitat selection. It is important to consider dry season arthropod numbers in the larger study of RBFW behavior because the birds may be trophically limited during this season. Rains trigger breeding, likely due to an increase in arthropod abundance during the wet season (Murphy et al., 2010). As with many birds, the RBFWs tendency to flock in the dry season could be explained by facultative foraging for limited and patchily distributed food resources (Pulliam, 1973).

We hypothesized that the effects of fire on the quality of RBFWs' habitat, particularly food availability, might explain RBFW declines in recently burnt areas. We predicted a negative correlation between fire and percent total grass cover and that fire would affect gamba and native grasses differently, suggesting that gamba, which is known to burn more intensely and frequently (Rossiter-Rachor et al., 2008; Setterfield et al., 2010), would be more abundant in recently burnt areas. Additionally, if gamba harbors significantly less arthropod abundance and biodiversity than native grasses due to its structural alteration of the habitat, fire-related nutrient losses, and probable adaptation of arthropods to native grasses, gamba would provide RBFWs with poorer foraging, making it a qualitatively inferior habitat. This would imply a negative effect of gamba on RBFWs in contrast to native grasses. Alternatively, gamba could benefit RBFWs by hosting favored or more abundant prey, or by providing useful habitat in another way, such as good shelter from predators because of its thick growth. We predict that fire directly and indirectly affects arthropods in the short term by reducing both arthropod numbers and grass cover, respectively, which, because it in part comprises habitat, will correlate positively with

Figure 3. Typical savanna at the study site. This location is mostly covered with gamba, but also has some native grasses. The photograph was taken less than a week after a burn in August 2012, approximating conditions in our recently-burnt plots. Photo credit: Lantz

Figure 4. As shown in this photograph, which was taken in January 2013 following the December 2012 burn, lush grass growth can follow relatively low-intensity fire. Photo credit: Lantz

arthropod numbers. Thus, more recently burnt areas will have less grass cover, leading in turn to less arthropod abundance and biodiversity and the subsequent reduction in numbers of RBFWs.

Methods

Study Area and Data Collection

We conducted arthropod surveys to quantify arthropod diversity and abundance at sites with different vegetative communities and fire history at Coomalie Farm, Northern Territory, Australia (13.00°S, 131.18°E) during the dry season in June and July of 2013. The precipitation means in June and July from 1992-2013 were 0.5 and 0.2 mm, respectively. The respective temperature means for these years in June and July were 31.2 and 31.8 ˚C, while the respective highs were 35.8 and 35.8 ˚C and the respective lows were 21.0 and 26.3 ˚C (Australian Government Bureau of Meteorology). The study was part of a larger project on RBFW behavior funded by the National Science Foundation (see Acknowledgements). Vegetation surveys were conducted by all members of the research team.

Vegetation Surveys

We determined the floral composition of 10 m by 10 m plots. On the 4 km^2 core study area, we randomly generated 98 points as plot centers and systematically designated 119 points as plot centers at sites of RBFW sightings through point-count transects and opportunistic sightings. All plot centers were at least 20 m apart from one other. We quantified all

Figure 5. In this photograph, taken in May 2013, the site has recovered from the fire. Photo credit: Lantz

vegetation features and other ground cover found in each plot. For all trees, we recorded diameter at breast height (1.2 m above ground) to the nearest cm, and estimated their height to the nearest 0.5 m. A tree was defined as a woody plant with one or more trunks at 1.2 m above ground. This meant that only the largest trunk would be measured if the trunks split before breast height. Visibility was recorded to the nearest 1 percent by viewing a cover board held at the plot center 1 m off the ground from 7.1 m away in each of the cardinal directions. Canopy cover was taken 5 m from the center in each of the four cardinal directions and recorded to the nearest 5 percent. Percentage of ground covered was estimated to the nearest 5 percent and many potential categories were allowed, e.g., road, gravel, bare ground (leaf litter and other dead organic matter covering the ground still counted in this category, because these are effectively the same thing to RBFWs), herbaceous vegetation (in height classes of <0.5 m, 0.5 m, 1 m, etc.), native and gamba grasses (in height classes of <0.5 m, 0.5 m, 1 m, etc.), saplings (plants that were obviously young trees, but <1.2 m), log piles (height and length were also estimated for these; log piles are perched on by RBFWs), termite mounds (not given a percentage if <0.5 m, but instead counted), bushy *Pandanus* (too short to take DBH, but still likely significant to the RBFWs), etc.

Arthropod Surveys

We conducted arthropod surveys at points randomly selected from the vegetation surveys. We surveyed 60 randomly selected 10 m by 10 m sites available to the RBFWs as habitat (centered on points randomly-generated on the 4 km^2 core study area, not within 20 m of each other). We also conducted surveys at 59 10 m by 10 m sites randomly chosen from the gross number used by RBFWs (based on collaborative bird sightings). Following an uncontrolled burn in July 2013, we opportunistically conducted 14 surveys on transects three days after the burn. We began observing cloud cover, temperature and wind (quantified on the Beaufort Scale) 1 week into the study.

In order to be assured of tractable methods, we modeled the survey protocol after a previous study on the same site (Hinton, 2013). We conducted surveys between 0900-1600 h at predetermined sites, recording the time and randomly picking two opposite cardinal directions. The surveyor faced one direction (N or W first, S or E to follow), scanned for airborne arthropods between 0.1-2.5m for 30s, then walked a 7.1m transect in that direction while counting arthropods seen flushed and on vegetation between 0.1-2.5m. In each direction the surveyor conducted a 30s ground scan at the end of the transect line over 15 cm^2, followed by counting the arthropods shaken from vegetation between 0.1-1.0m over a clipboard for 30s. The same procedure in the opposite direction (S or E) was carried out immediately afterwards. The four scans in each direction took 3-5min and the total time to survey each site was 6-12min. This protocol focuses on potential prey of RBFWs, because it reflects the birds' tendency to stay at around eye level and, by flushing arthropods from vegetation, reflects their predilection for gleaning from grasses.

We modified Hinton's methodology in that we also recorded presence/absence and, when possible, genus or species of ants. We hypothesized that a relationship could exist between ants (common predators of other insects in the savanna system) and RBFW prey or vegetative characteristics. Green tree ants' (Oecophylla smaragdina) nests' presence and size classification were also noted for the same reason. We also estimated the quantity of isopterans (termites) when individually seen.

We only counted living arthropods. By estimation, we assigned size classes (1=<1cm, 2=1-2cm, 3=>2cm) in a way meaningful to RBFW natural history (due to a beak length of ~1cm, the birds likely cannot eat size class 3 prey). Except for ants and the families Mantodea (praying mantids) and Blattodea (cockroaches), we classified all to order.

Statistical Analyses

For vegetation, we converted percentage covered in quadrants by both gamba and other/native grasses to percentage of the whole square plot. We defined arthropod abundance as the total number of individuals counted per site excluding ants, and arthropod richness as the total number of orders (plus two families, see Arthropod Surveys) counted per site excluding ants. For most of the analyses, we excluded ant data (unless specifically mentioned). We tested presence/absence of ants against whether or not sites burnt in the past year using a Contingency Analysis. With two least-squares-fitting regressions, we compared the relative ability of habitat variables, including ant presence/absence, to respectively predict abundance and richness. For fire history, we classified plots by how long since they last burnt at the time of surveying: 55 plots burnt over 12 months before (burn history unknown); 41 plots burnt approximately 12 months before (July 2012); 12 burnt 6 months before (December 2012); 10 burnt 1-2 months before (May 2013); and the 14 plots surveyed in the burnt area burnt 3 days before (July 2013). For most analyses, we collapsed these categories into two: burnt in past year including in July 2012, and unburnt in past year.

We used a non-parametric Spearman Rank Correlation to test for correlations between percent gamba and percent native grasses with arthropod abundance and richness, because these latter parameters were not normally distributed. We used One-way Analysis of Variance (ANOVA) tests to investigate the interactions between percentages of gamba and native grasses and fire history. We also tested for differences in arthropod abundance and richness and percentage native and gamba grasses between sites classified by burn history and RBFW presence/absence with ANOVA analyses. We used pairwise Student's t-tests to compare means of arthropod abundance and richness between burn histories. We investigated the relationship between site fire history and RBFW presence/absence with a likelihood ratio Chi-square test. We combined the total percentage cover of native and gamba grasses (referred to as total percent grass cover) for some analyses. We tested the significance of parameters (whether or not burnt in last year, total percent grass cover and arthropod richness) in determining RBFW presence/absence with nominal logistic fit. We investigated the dependence of arthropod abundance and richness on total percent grass cover with two bivariate fit analyses. We used ANOVA analyses to analyze the variance of total percent grass cover by plot type (used/available) and whether or not burnt in last year.

Results

The data partly support our predictions. As summarized in Figure 1, we found significant relationships between presence/absence of RBFWs, burn history, vegetative composition (proportion gamba versus native grasses) and arthropod abundance and richness.

The inverse relationship between percent cover of the two grass types was not significant (Spearman: p = -0.04, p = 0.67). Percent cover gamba was significantly and positively correlated with arthropod richness (Spearman: rho = 0.34, p = <0.001), but gamba was not correlated with abundance (Spearman: p = 0.11, p = 0.26). The above results for gamba contradict our prediction of less arthropod abundance and richness in gamba. Percent cover native grasses significantly and positively correlated with richness and abundance (Spearman with richness: p = 0.30, p = 0.0012; Spearman with abundance: p = 0.26, p = 0.0051). Arthropod richness was significantly dependent on total percent grass cover with a strong linear fit (bivariate fit analysis: RSquare = 0.195; analysis of variance: F Ratio = 27.33, Prob > F = <0.001), while abundance was non-significantly dependent on total percent grass cover with a weak linear fit (bivariate fit analysis: RSquare = 0.029; analysis of variance: F Ratio = 3.43, Prob > F = 0.067). Arthropod abundance and richness significantly and positively correlated (Spearman: p = 0.76, p = <0.001).

We found a significant difference in percentage gamba and other/native grasses between sites classified by burn history (ANOVA with other grasses: F Ratio = 11.73, d.f. = 4, Prob > F = <0.001; ANOVA with gamba: F Ratio = 3.73, d.f. = 4, Prob > F = 0.007). The sites burned 3 days prior to surveying (in July 2013) had less grass than all others. Percentage of other/native grasses mostly declined in relation to less time since last burn, while percentage gamba was greatest in the July 2012 class (Figure 2). Figure 2 portrays relatively low percentages of gamba across all burn histories, but, of 217 plots surveyed for vegetation,

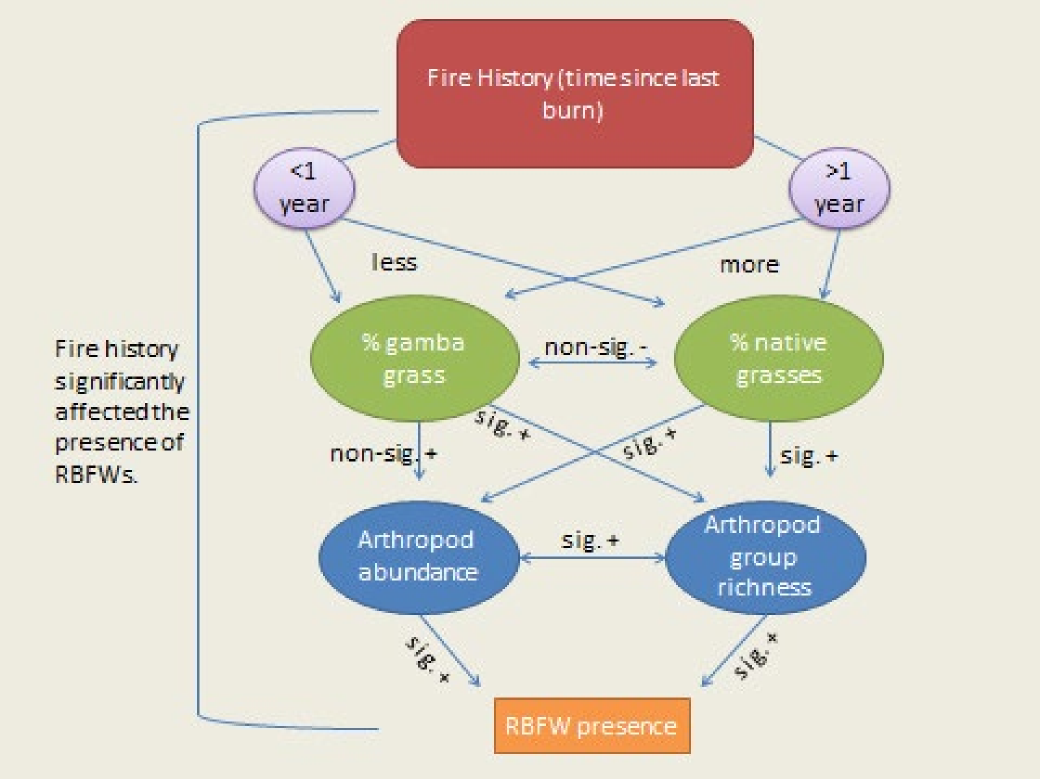


Figure 1. Relationships between fire, grasses, arthropods, and RBFW presence in the 2013 dry season, in a tropical savanna site in Northern Territory, Australia. The significances of the relationships and their directions are denoted as follows: "non-sig." for non-significant; "sig." for significant; "+" for a positive relationship; and "-" for a negative relationship.

103 plots contained gamba and this invasive grass covered 46 percent of each of those on average.

Areas burnt more recently had significantly lower arthropod abundance and richness (ANOVA with abundance: F Ratio = 8.86, d.f. = 4, Prob > F = <0.001; ANOVA with richness: F Ratio = 18.62, d.f. = 4, Prob > F = <0.001). Because we suspected this significance might be solely due to the much lower abundance and richness means for the July 2013 burn sites, we ran pairwise t-tests comparing arthropod abundance and richness means between all burn dates (Table 1). Indeed, running the ANOVA without the July 2013 data, fire date did not significantly explain richness or abundance (ANOVA with abundance and without July 2013: d.f. = 3, F Ratio = 0.812, Prob > F = 0.49; ANOVA with richness and without July 2013: d.f. = 3, F Ratio = 1.34, Prob > F: 0.27). Still, the results of the ANOVA with July 2013 and the t-tests support our prediction of reduced arthropod abundance and richness in more recently burnt habitat.

There was no significant difference in presence/absence of ants between sites burnt and unburnt in the past year (likelihood ratio Chi-square test: Chi-squared value = 0.45, d.f. = 1, p = 0.50). Whether or not a site was burnt in the past year was more predictive of abundance than presence/absence of ants or total percent grass cover (least squares fit whole model parameter estimates: t ratio = 3.76, p = <0.001). Among the variables above, total grass cover and whether or not a site was burnt in the past year significantly predicted richness, but presence/absence of ants did not (total percent grass cover: t ratio = 3.02, p = 0.003; burnt in last year: t ratio = 3, p = 0.003). Thus, the inclusion of ants had no qualitative effect on our findings.

RBFWs tended to use sites with more native/other grass cover than available sites (ANOVA with native: F Ratio = 3.12, d.f. = 1, p = 0.080) and used sites had significantly more gamba than available sites (ANOVA with gamba: F Ratio = 4.70, d.f. = 1, p = 0.033). Sites used by RBFWs had significantly greater arthropod abundance and richness than available sites (ANOVA with abundance: F Ratio = 9.90, d.f = 1, p = 0.002; ANOVA with richness: F Ratio = 11.80, d.f. = 1, p = <0.001). This supports the warrant that habitat selected by the RBFWs will be of higher quality in that they have greater arthropod abundance and richness. Sites used by the RBFWs and sites unburnt in the last year had significantly more total percent grass cover than available sites and those burnt in the last year, respectively (ANOVA: F Ratio = 11.31, d.f. = 1, p = 0.001 and F Ratio = 48.77, d.f. = 1, p = <0.001, respectively).

RBFWs were more likely to use areas that had not burnt recently. Used and available sites differed significantly in their burn history (likelihood ratio Chi-square test: Chi-squared value = 9.99, d.f. = 1, p = 0.002); 86% of sites used by the RBFWs were not burnt in the past year and only 14% were, while 62% of the available sites were not burnt in the past

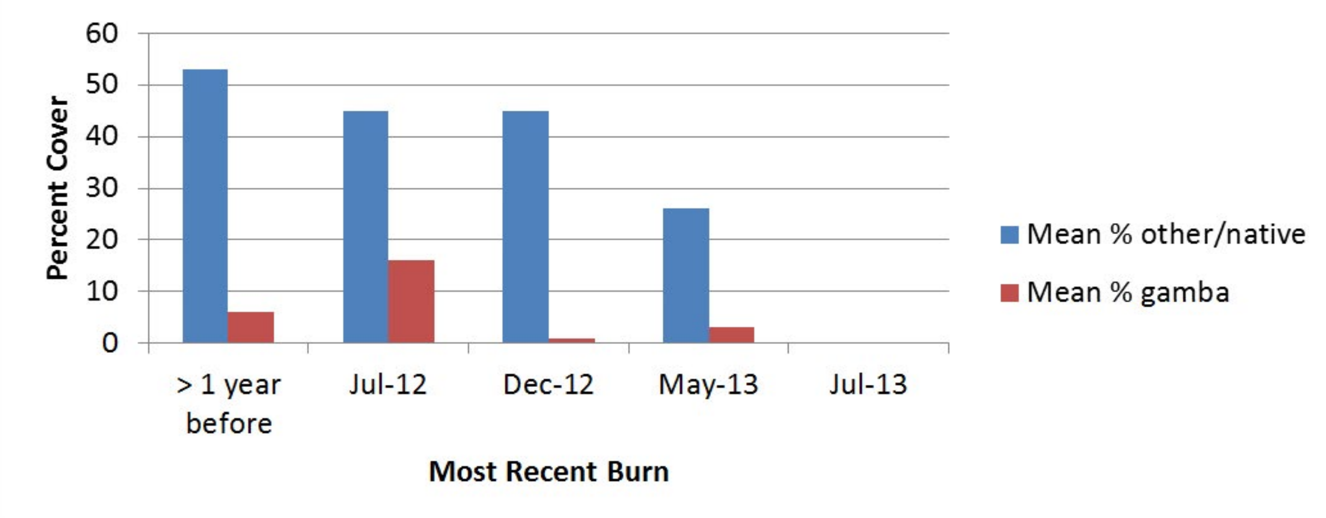
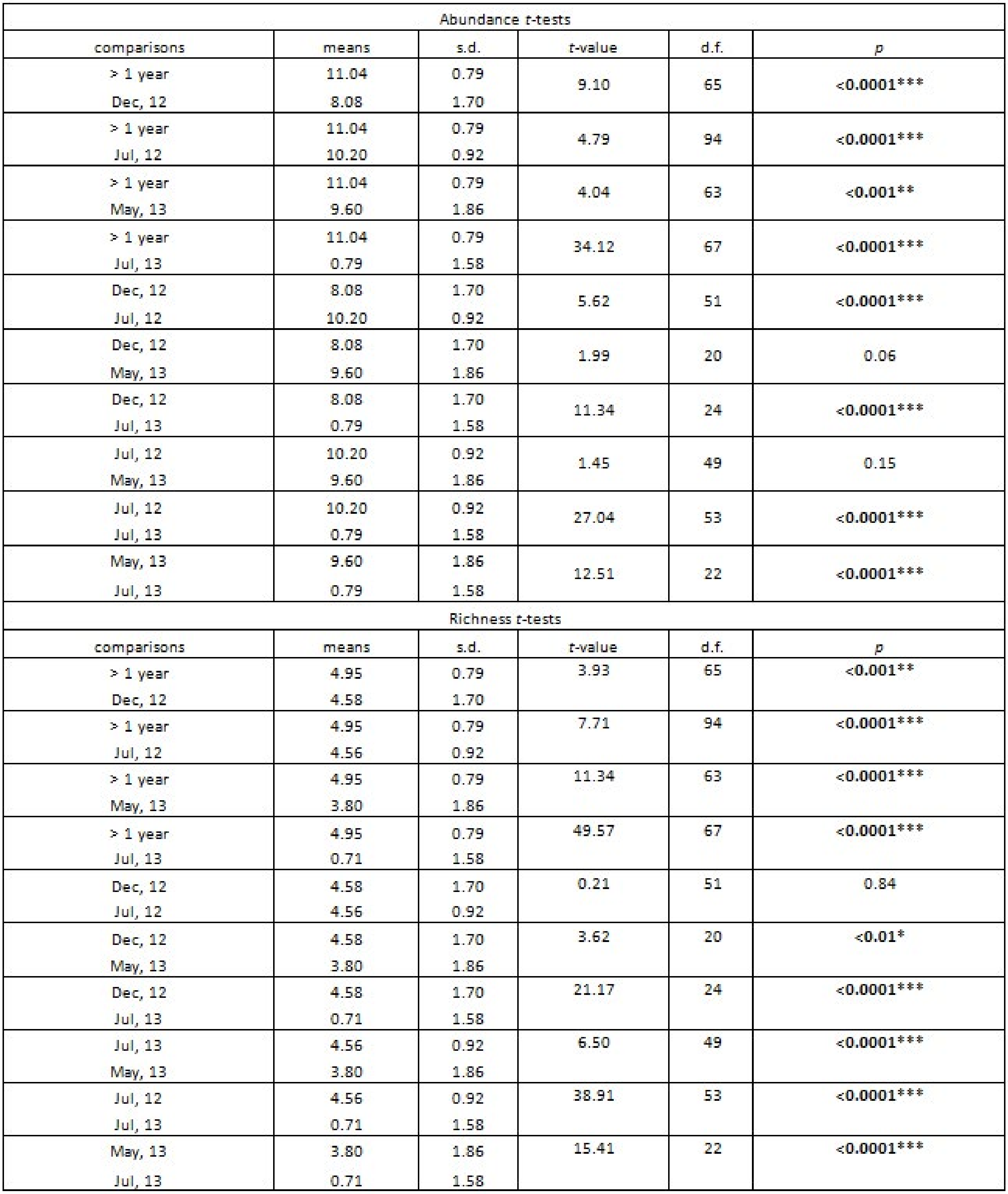


Figure 2. Percent Cover of Grasses by Burn History. A largely negative relationship between percent grass cover and more recent burns.



Abundance *t*-tests

comparisons	means	s.d.	*t*-value	d.f.	*p*
> 1 year	11.04	0.79	9.10	65	**<0.0001*****
Dec, 12	8.08	1.70			
> 1 year	11.04	0.79	4.79	94	**<0.0001*****
Jul, 12	10.20	0.92			
> 1 year	11.04	0.79	4.04	63	**<0.001****
May, 13	9.60	1.86			
> 1 year	11.04	0.79	34.12	67	**<0.0001*****
Jul, 13	0.79	1.58			
Dec, 12	8.08	1.70	5.62	51	**<0.0001*****
Jul, 12	10.20	0.92			
Dec, 12	8.08	1.70	1.99	20	0.06
May, 13	9.60	1.86			
Dec, 12	8.08	1.70	11.34	24	**<0.0001*****
Jul, 13	0.79	1.58			
Jul, 12	10.20	0.92	1.45	49	0.15
May, 13	9.60	1.86			
Jul, 12	10.20	0.92	27.04	53	**<0.0001*****
Jul, 13	0.79	1.58			
May, 13	9.60	1.86	12.51	22	**<0.0001*****
Jul, 13	0.79	1.58			

Richness *t*-tests

comparisons	means	s.d.	*t*-value	d.f.	*p*
> 1 year	4.95	0.79	3.93	65	**<0.001****
Dec, 12	4.58	1.70			
> 1 year	4.95	0.79	7.71	94	**<0.0001*****
Jul, 12	4.56	0.92			
> 1 year	4.95	0.79	11.34	63	**<0.0001*****
May, 13	3.80	1.86			
> 1 year	4.95	0.79	49.57	67	**<0.0001*****
Jul, 13	0.71	1.58			
Dec, 12	4.58	1.70	0.21	51	0.84
Jul, 12	4.56	0.92			
Dec, 12	4.58	1.70	3.62	20	**<0.01***
May, 13	3.80	1.86			
Dec, 12	4.58	1.70	21.17	24	**<0.0001*****
Jul, 13	0.71	1.58			
Jul, 13	4.56	0.92	6.50	49	**<0.0001*****
May, 13	3.80	1.86			
Jul, 12	4.56	0.92	38.91	53	**<0.0001*****
Jul, 13	0.71	1.58			
May, 13	3.80	1.86	15.41	22	**<0.0001*****
Jul, 13	0.71	1.58			

Table 1. In pairwise comparisons, sites burnt most recently (in July 2013) and sites burnt least recently (more than 12 months before) had respectively far less and far more arthropod abundance and richness than every other burn history, and these differences were all highly significant (p = <0.001). Almost all pairwise comparisons of abundance and richness by burn date were highly significant. The p-values of these are bolded and the significance levels are denoted as follows: "" for <0.01; "**" for <0.001; and "***" for <0.0001.*

year and 38% were. In other words, more than 75% of sites burnt in the last year were available (unused by RBFWs), while more than 50% of sites unburnt in the last year were used by the RBFWs. This finding reconfirms RBFWs' aversion to recently-burnt areas.

The intercept of the variables burnt versus unburnt in past year, richness and total percent grass cover significantly determined RBFW presence/absence (nominal logistic fit with parameter estimate: d.f. = 3, p = <0.001). The most significant variable on its own was richness (nominal logistic fit with parameter estimates: d.f. = 3, p = 0.067).

Discussion

At least in the short term, fire negatively affects RBFW habitat quality, as determined by grass cover and arthropod abundance and richness. Reduction of these could explain the finding that RBFWs prefer less recently burnt habitat to more recently burnt habitat. Our prediction that arthropod abundance and richness are reduced in more recently burnt areas was supported. Sites used by the RBFWs had significantly greater arthropod abundance and richness than other available, unused, sites. Reductions in arthropod prevalence and grass cover might cause RBFWs' abandonment of burnt habitat and these parameters of RBFW habitat quality are probably not mutually exclusive.

The significant positive relationship between gamba and arthropod richness and the lack of a significant relationship between gamba and arthropod abundance do not support our prediction that invasive gamba has a negative effect on these measures of arthropods. Still, we found an inverse, though non-significant, relationship between percentage gamba and percentage native grasses. Although Figure 2 seems to portray relatively low percentages of gamba across burn histories for this study site, this does not necessarily mean that gamba is not very invasive there. Where gamba was present, it occupied nearly half of an average plot's area. It grows taller than any native grass on the site and very little vegetation manages to grow underneath or amongst it (A. Rose, personal observation). Australia declared gamba a Weed of National Significance in 2012 (Department of Agriculture, Fisheries and Forestry, 2011) and under the *Weeds Management Act 2001* the Northern Territory government obligates landowners to manage gamba on their property. The Territory assists landowners with controlled burning and herbicide application to control gamba (Department of Natural Resources, Environment, The Arts and Sport, 2011). The landowner of our study site attempts to control the grass by spraying, and by mowing it shortly before it flowers or sets seed and these efforts may have contributed to its seeming lack of invasiveness on Coomalie Farm (Lantz, personal communication).

Because a gamba fuel load increases fire frequency, intensity and severity (Setterfield et al., 2010; Rossiter-Rachor et al., 2008), the replacement of native grasses by gamba might have reverberating effects on northern Australia's savanna biota. A comparison of fire history with percentage gamba and native grasses showed that gamba contradicted a generally negative relationship between less time since fire and grass cover. This implies that gamba grows back more quickly after a burn than do native grasses. Additionally, or alternatively, this could imply greater susceptibility of gamba-dominated areas to fire. We propose a possible positive feedback loop by which gamba promotes fire and recovers more readily from fire than less flammable native grasses. Thus, gamba alters the fire regime and may benefit in its competition with native grasses from this alteration.

Our findings concur with some of those of a similar study conducted at the same site in 2012 (Hinton, 2013). Hinton did show arthropod abundance, percent grass cover and burn history significantly predicted RBFWs' presence at sites, although his analyses did not consider arthropod richness, did not have data distinguishing gamba and native grasses, relied on subjective data for burn history (categories of "unburnt," "partly burnt," and "burnt") with burn category based on visible confirmation of a recent (April-May 2012) controlled burn (i.e., charred grass), and excluded ants. Our results lend credence to Hinton's decision to exclude ants from the analysis, since presence/absence of ants was not significant in relation to whether or not a site had burnt in the past year and did not predict non-Formicidae arthropod abundance and richness. Hinton's data revealed no significant difference in arthropod abundance between burnt and unburnt plots, while ours did due to the surveys in habitat burnt 3 days prior.

Many of our significant results rely on data from this very recently burnt habitat, a potential weakness of this study. Still, we argue that these findings importantly reveal differences related to short-term fire history.

Since the generation times of most arthropods are short and many can proliferate rapidly in response to changing environmental conditions, we argue that relatively immediate effects of fire are generally relevant to their natural history. We argue that our results support a pattern of reduced RBFW habitat quality in more recently burnt areas partly, but not entirely, due to the 15 plots surveyed in the most recently burnt area. Alternatively, because the seasonality of the burn histories varied, phenological differences related to arthropod life history stages might explain some of the differences between plots categorized by burn history. However, we note that sites burnt longest ago (more than 12 months before) had significantly greater arthropod abundance and richness than every other burn history in pairwise comparisons (see Table 1), implying that time since fire affects arthropod numbers regardless of seasonality. A potential source of bias in this study is the counting of mantids and cockroaches as separate groups, giving them the same weight in the analyses as orders (justified by their distinctness and current taxonomic limbo).

Fire-sensitive, insectivorous RBFWs, besides being a behaviorally interesting bird, are a case study for the complex interplay of fire history, habitat, and food resources. Both the severe loss of arthropods from a very recently burnt area and the diminishment of grass cover by fire could explain insectivorous RBFWs' dislike of burnt areas. In the short term, more burnt areas mean less food. These effects of fire also contribute to a better understanding of RBFWs' altered behavior in the fire-prone dry season. RBFWs form large flocks in the dry season (Webster et al., 2010). Because flocks of birds could cooperatively flush out more prey, keep watch for predators and experience safety in numbers, trophic limitation and predator avoidance are possible explanations for this flocking behavior. Our work supports the idea that RBFWs leave burnt areas because of increased predation risk due to reduced cover or because of a decrease in food (Valentine et al., 2007; Webster at al., 2010; Hinton, 2013). Murphy et al. (2010) showed that RBFWs temporarily vacate habitat after fire. Although fire has short term adverse effects on some other Australian bird species (Valentine et al., 2007), RBFWs and arthropods, fires maintain their grass-dominated savanna ecosystem (Cochrane, 2009). Valentine et al. (2007) even found higher overall avian abundances in the short term in a controlled-burn study of Australia's savanna. Arthropod biodiversity has been shown to be negatively affected in the short term by an experimental fire regime, but to stabilize in the long term (Siemman and Haarstad, 1997).

By generally affecting habitat, fire influences birds in ways beyond food availability and grass cover. A review of the effect of fire on Australian avifauna found that inappropriate fire regimes consisting of frequent, low-intensity fires are a major threat to birds, especially to many declining species. Mismanaged fires can be detrimental partly because of compositional and structural changes to vegetation (Woinarski and Recher, 1997). For example, in south-eastern Australia fire history strongly influences the availability of tree cavities, an important habitat feature for birds and other wildlife (Haslem et al., 2012).

Future studies of northern Australia's fire ecology should quantify arthropod biodiversity evenness as well as abundance and richness, determine the focal study species' diet and use this knowledge to more accurately gauge habitat quality (the effects of fire on a particularly favored prey item may explain RBFWs' dislike of burnt areas) or test for predation risk in habitats with differing fire histories. Experimentally burning gamba and native grasses in conjunction with measuring grass regrowth and before-and-after arthropod numbers could help further elucidate the effects of gamba and fire on arthropods. Allowing different periods of time for recovery after the experimental burning would facilitate exploring shorter-to-longer-term effects. For example, arthropods could be sampled periodically following a precise burn date to determine when the abundances of various groups build up and peak.

This study adds to our understanding of fire ecology in the highly biodiverse tropics by considering a model system in an extreme environment affected by an invasive grass and a changing fire regime. This work could help inform future research on RBFWs and other bird species living in the wet-dry tropics, especially as it relates to their dry season behavior. Information on the effects of fire on the relatively common RBFW and its trophic foundation relates to comparable Northern Territory bird species that are threatened and less amenable to study. Endangered species that are probably negatively affected by anthropogenic changes to fire regimes include the tiwi masked owl (*Tyto novaehollandiae melvillensis*, also affected by gamba), the Carpentarian grass-wren

(*Amytornis dorotheae*, also feeds on arthropods) and the Alligator Rivers subspecies of the yellow chat (*Epthianura crocea tunneyi*, also affected by gamba and feeds on arthropods). Critically endangered species that are probably affected by anthropogenic changes to fire regimes include the mallee fowl (*Leipoa ocellata*, also feeds on arthropods) and the tiwi hooded robin (*Melanodryas cucullata melvillensis*, also feeds on arthropods) (Department of Land Resource Management, 2013). This work is also relevant to future studies on Australian savanna ecology in general and could help improve often mismanaged fire practices.

Acknowledgements

A three-year grant provided by the National Science Foundation IRES (International Research Experience for Students) program supported the research. Seven undergraduate students from The College of William and Mary, Cornell University and Tulane University participated in the project's second year of field work. Greg Tito and Payton Phillips of William and Mary, Katheryn Zelak, Vera Ivezic and Kathryn Grabenstein of Cornell, and Erik Iverson and Alexander Rose of Tulane assisted with data collection in the vegetation survey and provided valuable feedback on previous versions of this manuscript. Though focusing on our own research projects, we all collaborated on field work, especially conducting vegetation surveys together. The landowner, Richard Luxton, graciously facilitated the use of Coomalie Farm as the study site.

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