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Effect of fire on insectivorous bat activity in northern Australia: does fire intensity matter on a local scale?

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Abstract.   Fire is notably becoming more intense, frequent and widespread due to climate change. In northern Australia, inappropriate fire regimes have been implicated in mammal declines, yet nothing is known about how different aspects of fire regimes affect bats in this region. This study aimed to determine how fire intensity, associated with seasonality, affects insectivorous bats on a local scale. An experimental M BACI approach was used on five site replicates across Cape York Peninsula, where ultrasonic detectors were used to determine the activity of insectivorous bats in response to low intensity burns (LIBs) and high intensity burns (HIBs) on a local scale. Total bat activity increased due to LIBs, but showed no response to HIBs. Activity of edge-open guild bats also increased due to LIBs but decreased in response to HIBs. Activity of open guild bats was unaffected by LIBs, but exhibited a strong positive response to HIBs. Activity of closed guild bats showed no response to fire, or fire intensity. Responses were likely derived from changes in habitat structure and prey availability. Given that each bat guild responded differently to each fire intensity, this lends support to the 'pyrodiversity begets biodiversity' concept, which is currently the basis for many fire management practices for conservation in northern Australia.

Keywords: bat conservation, bat guilds, burn regime, ecomorphological guild, mammal decline, microbats, pyrodiversity, savanna.

Introduction

Fire is used as a management tool for biodiversity conservation and protecting infrastructure (Fensham 2012; Queensland Parks and Wildlife Service 2013). There is increasing subscription to the concept that 'pyrodiversity begets biodiversity' (Martin and Sapsis 1992). Theoretically, diversity within the fire regime maximises environmental heterogeneity and the number of niches, and therefore biodiversity (Martin and Sapsis 1992; Bradstock *et al*. 1995; van Wilgen *et al*. 2003). However, there is little evidence to support this at a regional or habitat scale (Parr and Andersen 2006; Pastro *et al*. 2011). As anthropogenic climate change increases the intensity and frequency of fires, it is important to understand the effects of both wildfires and prescribed burns (often referred to as 'ecological burns') on different fauna (Williams *et al*. 2009).

Fire has been a significant part of Australia's ecology since the arrival of Aboriginal peoples (Bowman 1998). The application and suppression of fire has changed drastically over the past 100 years (Fensham 2012). In northern Australia,

fire occurs extensively throughout the year due to arson, carbon farming, hazard reduction, and wildfire (Fensham 2012; Williams *et al*. 2012). Inappropriate fire regimes have been implicated as one of the leading causes of the northern Australian mammal decline (Woinarski *et al*. 2004; Legge *et al*. 2008; Radford *et al*. 2014; Lawes *et al*. 2015). There is a tentative consensus among land managers and conservationists that patch mosaic burns, applied throughout a savanna woodland landscape are the most effective in maintaining biodiversity (Parr and Brockett 1999). It is unknown how these fires affect insectivorous bat fauna (hereafter referred to as bats) of northern Australia.

Bats comprise approximately half the mammalian diversity in northern Australia (Van Dyck and Strahan 2008), and eight species are listed as threatened under state, territory or federal legislation. Despite this, there are very few published studies on bat ecology in northern Australia, and only a limited number examining the effects of fire on bats in this region (Milne *et al*. 2005; Inkster-Draper *et al*. 2013; Broken-Brow *et al*. 2019; Broken-Brow 2020). In the absence of further

information, the findings relating to the effects of fire on one species, or group of species, are often used to develop fire regimes for the conservation of all wildlife (Woinarski 1990; Legge *et al*. 2019). Furthermore, the results from fire studies (e.g. examining fire frequency) are often extrapolated without considering fire intensity. It is unsurprising then that fire management practices generally do not consider the requirements of bat species.

The effects of fire may be attributed to specific aspects of an individual fire, such as intensity (often associated with seasonality) and extent, or the fire regime timing, which considers the frequency and time since last burn. Fire intensity is highly variable in tropical ecosystems, with two fire intensities generally recognised and used by land managers: low intensity burns (LIBs) and high intensity burns (HIBs) (Woinarski and Legge 2013). These fire intensities are often related to season, where LIBs and HIBs commonly occur in early or late dry season, respectively (Russell-Smith and Edwards 2006). For this reason, a landscape is commonly exposed to both levels of fire intensity in a single year (Northern Australia Fire Information 2019).

It is essential to compare the local and landscape-based response of wildlife to different fire intensities to gather evidence for whether pyrodiversity begets biodiversity. Bats are a useful faunal group to study the effects of fire because they are volant, allowing them to respond almost immediately to fire (Lacki *et al*. 2009; Nimmo *et al*. 2019), and are diverse in their hunting strategies and diet (Churchill 2008). Species are often grouped together into guilds that share similar foraging strategies and microhabitat requirements, on the basis of their echolocation call characteristics and wing shape (Schnitzler and Kalko 2001; Denzinger and Schnitzler 2013; Denzinger *et al*. 2016). In practice, bat guilds represent functional groups (Schnitzler and Kalko 2001; Suarez-Rubio *et al*. 2018), which are used to understand patterns in species richness (Brown *et al*. 2000) and response to changing environments (Mancini *et al*. 2019; Newbold *et al*. 2020). A decrease, or disappearance, of a functional group is often associated with a decrease in ecological or functional diversity, when species within that group are negatively affected by an environmental change (Storkey 2006; Suarez-Rubio *et al*. 2018; Newbold *et al*. 2020).

Of the studies that have investigated the response of bats to fire in northern Australia, none have examined the effect of intensity or seasonality. In southern Australia, bat responses to wildfire have been examined, with species being neutrally or positively affected by a severe wildfire (Law *et al*. 2018), and bat activity was higher on sites with lower burn intensity compared with higher burn intensity after another severe wildfire (Jemison *et al*. 2012; Law *et al*. 2019). Similarly, further afield, Braun de Torrez *et al*. (2018) found the activity of the Florida bonneted bat (*Eumops floridanus*) to be positively associated with less intense burns. Other studies globally have found certain bat species and assemblages to have positive (Buchalski *et al*. 2013), negative (Saunders 2015) and neutral (Cox *et al*. 2016) responses to HIBs, or associated seasonality. The variation in findings among studies is likely due to differences in site factors, as well as the extent of the burns. All but the most recent aforementioned studies (Law *et al*. (2018) and Law *et al*. (2019) being the exceptions) were conducted only after the burn, and therefore may lack

power to identify causal relationships. The present study aimed to critically evaluate the local effects of fire intensity, associated with seasonality, on bat activity in northern Australia.

Methods

Site locations

The study was conducted across northern Cape York Peninsula, Queensland, Australia: on the Steve Irwin Wildlife Reserve (SIWR; 12°38′S, 142°18′E) in the west, and Kutini-Payamu (Iron Range) National Park, Cape York Peninsula Aboriginal Land (KPNP; 12°44′S, 143°16′E) in the east. The climate is characterised by a monsoonal wet season (December–April) and a dry season (May–November). Wet season rainfall is relatively consistent across Cape York Peninsula, with a mean monthly rainfall of ~330 mm, whereas the dry season has a higher mean monthly rainfall in the east (49 mm) compared with the west (22 mm: Bureau of Meteorology 2019). The data were collected between November 2016 and October 2017, when the dry season rainfall was average, and when wet season rainfall was slightly below average at KPNP (282 mm). Monthly temperatures were average for both areas (Bureau of Meteorology 2019). The habitat of the region is predominantly tropical savanna woodland, with some rainforest, heathland and monsoonal paperbark (*Melaleuca* spp.) wetlands.

The open woodland at the study sites was dominated by Darwin stringybark (*Eucalyptus tetrodonta*) and Melville Island bloodwood (*Corymbia nesophila*) with limited understorey, and groundcover dominated by native grasses. These woodlands are managed using fire for ecological conservation, fuel reduction, and carbon farming under the Australian Government Carbon Farming Initiative. Typically, they are burnt biennially with LIB; however, they are also subject intermittently to HIB through arson, and storm burns for weed control. Storm burns refer to high intensity, small scale prescribed burns conducted in the early wet season (Queensland Parks and Wildlife Service 2013). All of the study sites were burnt in 2014 or 2015, with fire excluded from 2016 until the experiment began, representing the maximum possible amount of time since last burn.

Experimental design

The study used a multiple before–after control–impact (M BACI) experimental design, with five site replicates (two at KPNP and three at SIWR). Sites were located at least 5 km apart to maximise sampling independence. Within each site three 1-ha treatment plots were established: control (no burn), HIB and LIB. Plots were located within 1 km of each other, and separated by a fire break (e.g. a gully or track) (Fig. 1).

Fire treatment

Burn treatments were applied by land managers for the purposes of this experiment and were restricted to a few hectares around each plot. The LIBs were most comparable to early dry season ecological burns; however, the scale was reduced to a smaller area, whereas the HIBs were similar to prescribed 'storm burns'. Fire intensity was not measured, but local experienced land managers (Sites 1 and 2: G. Featonby, Ranger in Charge, Queensland Parks and Wildlife Service;

Sites 3–5: B. Lyon and A. Dawson, Rangers, Australia Zoo) managed the experimental fires to match commonly observed intensities. Seasonal environmental conditions (such as soil moisture and curing of vegetative ground cover) and burn timing were used to achieve each burn intensity. Across all treatment sites, similar fuel loads (vegetation) were present before the burns. LIBs were conducted in the early dry season, in the cool of the morning, resulting in a patchy reduction in

ground cover (primarily grass), with no observable reduction in vegetation above the ground cover layer and scorch heights of less than 1 m. HIBs were conducted in the late dry season at the hottest time of the day, resulting in the elimination of almost all ground cover and notable reduction in understorey cover, with scorch heights up to 10 m. Based on research conducted by Andersen *et al.* (2005) in a similar habitat in northern Australia, LIBs and HIBs were expected to be ~2100 kW m^{-1} and 7700 kW m^{-1} respectively.
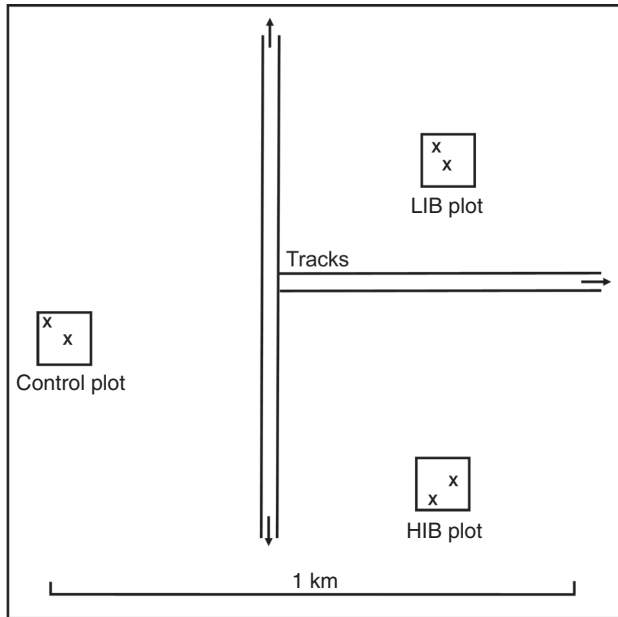

Fig. 1. Plot design for a site. × indicates a bat detector location.

Sampling

Within each plot, two Anabat Express bat detectors with omnidirectional microphones (Titley Scientific, Brendale, Qld) were placed in a randomly chosen location, 1.5 m above the ground. Plots were sampled for four consecutive nights, without rain, within the two weeks preceding the treatment. Sampling was repeated in the same locations 2–4 weeks after treatment. This sampling regime occurred twice at each site, once for LIB treatment (only the LIB and control plots sampled), and once for HIB treatment (only the HIB and control plots sampled).

Bat activity was analysed using Anabat Insight 1.7.2 (Titley Scientific 2019). Noise files were filtered from the dataset using the software-supplied 'All Bats' filter, then checked manually to ensure bat calls were not missed. Relative bat activity was quantified by counting the number of 'passes' per night. A pass was defined as at least three consecutive echolocation pulses. The study region has 24 insectivorous bat species, and bat calls were grouped into three ecomorphological guilds – open space, edge-open space, and closed space foraging guild – based on echolocation characteristics (see Table 1 for species guild groupings). Bat

Table 1.   Bat foraging guilds and species (from Broken-Brow *et al.* 2019)

Foraging guild	Species	Common name
Closed	*Hipposideros ater*	Dusky leaf-nosed bat
	Hipposideros cervinus	Fawn leaf-nosed bat
	Hipposideros semoni	Semon's leaf-nosed bat
	Murina florium	Flute-nosed bat
	Nyctophilus bifax	Eastern long-eared bat
	Nyctophilus geoffroyi	Lesser long-eared bat
	Phoniscus papuensis	Golden-tipped bat
	Rhinolophus megaphyllus	Eastern horseshoe bat
	Rhinolophus robertsi	Greater large-eared horseshoe bat
	Rhinolophus sp. (undescribed)	Intermediate horseshoe bat
Edge-open	*Chalinolobus nigrogriseus*	Hoary wattled bat
	Hipposideros diadema	Diadem leaf-nosed bat
	Miniopterus australis	Little bent-winged bat
	Miniopterus orianae oceanensis	Eastern bent-winged bat
	Myotis macropus	Large-footed myotis
	Pipistrellus adamsi	Forest pipistrelle
	Scotorepens sanborni	Northern broad-nosed bat
	Vespadelus troughtoni	Eastern cave bat
Open	*Chaerephon jobensis*	Greater northern free-tailed bat
	Ozimops lumsdenae	Northern free-tailed bat
	Ozimops ridei	Ride's free-tailed bat
	Saccolaimus flaviventris	Yellow-bellied sheath-tailed bat
	Saccolaimus mixtus	Papuan sheath-tailed bat
	Saccolaimus saccolaimus nudicluniatus	Bare-rumped sheath-tailed bat

Table 2.   Models tested using AICc values

Model	Fixed effects	Random effects	Hypothesis
M1	Treatment Period	Site	Null fire effect (base model)
M2	Treatment Period Fire type	Site	Null fire intensity (base model)
M3	Treatment Period Treatment × period	Site	Interaction represents the response of bats to fire
M4	Treatment Period Fire intensity Treatment × period Treatment × period × fire intensity	Site	Interactions represent the response of bats to fire, and fire intensity respectively

calls could not be identified to species, due to lack of reference calls in the study region.

Statistical analysis

Statistical analyses were conducted using R 3.5.0 (R Core Team 2019) run within RStudio 1.0.136 (RStudio 2019). The activity data were $\log_{10}(x+1)$ transformed to conform to assumptions of normality. Akaike Information Criterion values corrected for small sample size (AICc) were calculated to determine the best fit of four models for total bat activity, and the activity of each guild (Table 2).

For each bat activity grouping, a mixed model analysis of variance (ANOVA) was conducted on the best-fit model, and random effects for closed bat guild were plotted using the *merTools* package (Knowles *et al*. 2019) in R Studio. Probability values were tested against a 5% level of significance ($P < 0.05$). Log-transformed activity data were back-transformed to their original scale for presentation of results.

Results

Over 320 detector-nights, a total of 133 809 files were recorded. Of these, 19 805 contained bat passes, with open, edge-open, and closed guilds representing ~31%, 56%, and 13% respectively. The AICc values for each of the models are shown in Table 3, ranked by best fit (most parsimonious). For total bat activity, and the activity of edge-open and open guild bats, the model representing the interaction between fire and fire intensity was the best fit. For closed guild bat activity, the base model with only treatment and period was the best fit.

Mean total bat activity was significantly affected by fire intensity ($F_{3,290} = 5.25$, $P = 0.0015$), with the mean being more than 1.5 times higher from LIBs. There was no detectable effect of HIBs (Fig. 2).

Mean open guild bat activity differed significantly due to fire intensity ($F_{3,289} = 3.80$, $P = 0.0107$) (Fig. 3): at HIB sites activity increased due to the fire, but not at LIB sites.

Edge-open bat activity differed significantly due to fire ($F_{1,289} = 4.06$, $P = 0.045$), and differed significantly due to fire

Table 3.   The AICc values for each model, ranked by best fit
K, number of estimated parameters; AICc, Akaike Information Criterion values corrected for small sample size; ΔAICc, delta Akaike Information Criterion corrected; AICc Wt, Akaike Information Criterion corrected weight; Cum. Wt, cumulative Akaike Information Criterion corrected weight; LL, log-likelihood

| Model	K	AICc	AICc	AICc Wt	Cum. Wt	LL
All bats						
M4	10	351.93	0	0.94	0.94	−165.58
M1	5	359.16	7.22	0.03	0.97	−174.48
M3	6	359.54	7.61	0.02	0.99	−173.63
M2	6	360.52	8.58	0.01	1	−174.11
Open guild						
M4	10	284.58	0	0.61	0.61	−131.9
M1	5	287.07	2.49	0.17	0.78	−138.43
M3	6	287.3	2.71	0.16	0.94	−137.5
M2	6	289.15	4.57	0.06	1	−138.43
Edge-open guild						
M4	10	531.4	0	0.86	0.86	−255.31
M3	6	536.91	5.51	0.05	0.92	−262.31
M1	5	537.12	5.72	0.05	0.97	−263.45
M2	6	537.94	6.54	0.03	1	−262.82
Closed guild						
M1	5	71.79	0	0.42	0.42	−30.79
M2	6	71.83	0.04	0.41	0.84	−29.77
M3	6	73.79	2	0.16	0.99	−30.75
M4	10	79.52	7.73	0.01	1	−29.37
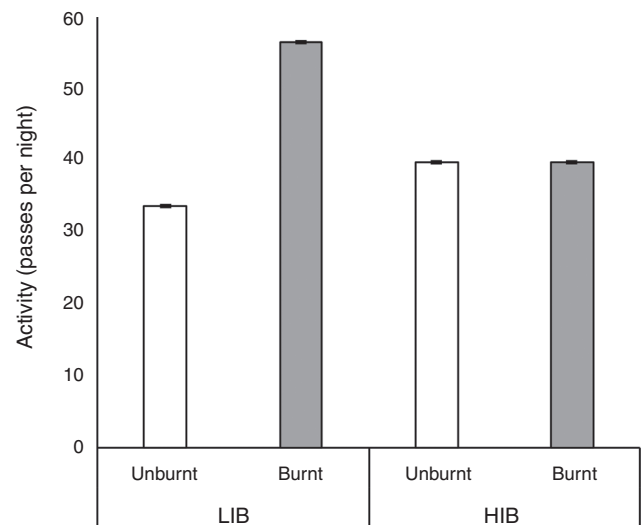
Fig. 2.   Estimated mean total bat activity in low intensity (LIB) and high intensity (HIB) unburnt (white) and burnt (grey) plots. Error bars represent the standard error. The means are adjusted for the effect of period and site.

intensity ($F_{3,289} = 4.32$, $P = 0.0053$). LIBs resulted in edge-open bat activity nearly double that of unburnt sites, whilst HIBs resulted in a slight decrease in activity (Fig. 4).

The best-fit model, null fire effect base model, indicated that closed guild bat activity was not affected by fires or fire intensity (Fig. 5).
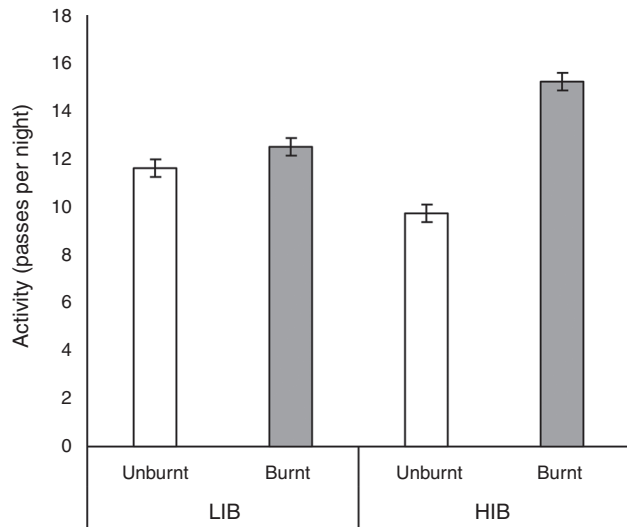
Fig. 3. Estimated mean open guild bat activity in low intensity (LIB) and high intensity (HIB) unburnt (white) and burnt (grey) plots. Error bars represent the standard error. The means are adjusted for the effect of period and site.

Fig. 5. Estimated mean closed guild bat activity in low intensity (LIB) and high intensity (HIB) unburnt (white) and burnt (grey) plots. Error bars represent the standard error. The means are adjusted for the effect of period and site.

Fig. 4. Estimated mean edge-open guild bat activity in low intensity (LIB) and high intensity (HIB) unburnt (white) and burnt (grey) plots. Error bars represent the standard error. The means are adjusted for the effect of period and site.
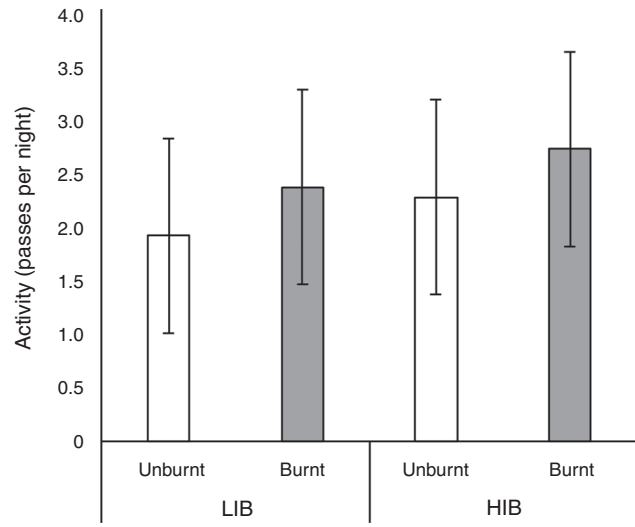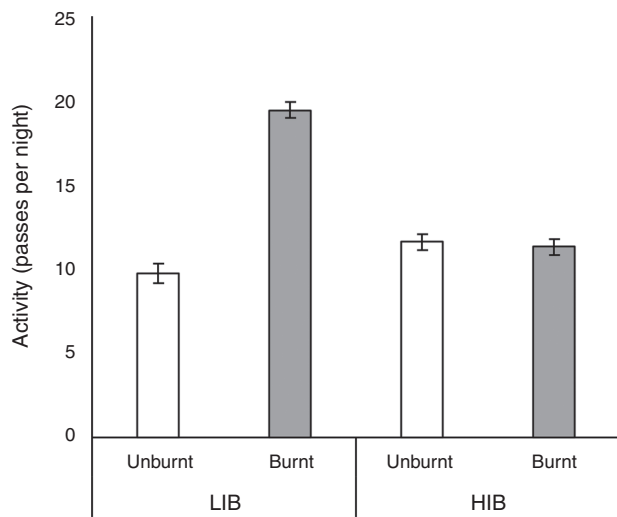
Table 4. The random effects (site) variance and standard deviation for each of the bat groups

| | Random effects (site) | |
	Variance	Standard deviation
All bats	0.0084	0.0914
Open guild	0.0846	0.2908
Edge-open guild	0.1159	0.3404
Closed guild	0.3901	0.6245

Fig. 6. Random effect ranges of site on closed guild bat activity.

Table 4 shows the variance and standard deviation of the random effects (site) for each of the best-fit models. The random effects variance for closed guild bat activity was considered high (0.3901 ± 0.625) compared with the other bat groups. Closed guild bat activity was associated with sampling site, with Sites 1 and 2 being markedly different from the remaining three sites (Fig. 6).
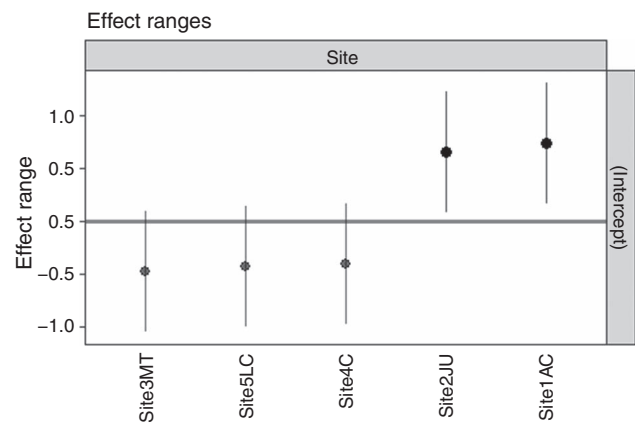
Discussion

The present study demonstrates that total bat activity, and the activity of open and edge-open guild bats was significantly affected by fire intensity at a local scale. However, each guild group responded differently to HIBs and LIBs. This is not surprising, as different fire intensities will affect habitat clutter and insect prey availability in different ways (Broken-Brow *et al*. 2019; Broken-Brow 2020). Fire of any intensity will reduce the level of vegetative clutter in tropical ecosystems, at least initially (Fensham 2012). HIBs are known to markedly

reduce the number of sapling trees, large trees, and total tree basal area (Radford *et al*. 2008). Although LIBs may affect stem or tree survival, the magnitude of such a loss is relatively small and dependent upon fire frequency (Williams *et al*. 1999). There is abundant evidence in the literature of bats responding positively to a reduction in clutter (e.g. Kusch and Schotte 2007; Adams *et al*. 2009), including a reduction in ground cover (Rainho *et al*. 2010), due to increased accessibility and the reduced energetic requirements of flying and foraging in more open habitats (Norberg and Rayner 1987; Speakman and Thomas 2003).

Insect prey abundance is usually affected by fire. There is some evidence that insect prey abundance exhibits a postfire pulse (Lacki *et al*. 2009; Doty *et al*. 2016). However, a study by Radford and Andersen (2012) in a habitat type similar to that of the present study reported that numbers of grass-layer invertebrates declined dramatically immediately after LIBs. It is likely that differences in habitats, insect collection method, timing, seasonality and fire factors will influence the results (Teasdale *et al*. 2013). However, there is a paucity of information regarding changes in abundance or availability of bat prey specifically after fire of any intensity. It is assumed that pyrophilic insects will exhibit a postfire pulse after LIBs or HIBs, whereas numbers of fire-sensitive species will decline markedly after HIBs (New 2014).

Total bat activity responded positively to LIBs, but not to HIBs. This was mostly driven by the response of edge-open guild bats, which contributed more than half of the total bat activity. Edge-open guild bats responded positively to LIBs, but also showed a slightly negative response to HIBs, so it is likely that fire of any intensity will affect the activity of bats in this guild. Inkster-Draper *et al*. (2013) also observed an increase in total bat activity after a LIB in northern Australia.

Open guild bats showed no response to LIBs but had a strong positive response to HIBs. Given that open guild bats are less adapted to clutter than edge-open guild bats (Schnitzler *et al*. 2003; Denzinger and Schnitzler 2013), it is likely that this response is due to a substantial reduction in vegetative clutter from HIBs.

Closed guild bat activity did not change in response to fire or fire intensity. There are three plausible explanations for this finding. First, this may have been an accurate measure of response; it is consistent with a response documented for *Rhinolophus megaphyllus* (a closed guild species) by Inkster-Draper *et al*. (2013) in a similar habitat. Second, the activity of closed guild bats might have been too low to detect significant effects, with estimated means being less than five passes per night. Third, the random effect of 'site' was shown to contribute to the results. Responses at sites on the western side of Cape York Peninsula were different from those on the eastern side, which indicate that landscape-level factors influenced the response of closed guild bats to fire. Eastern sites were located in a mosaic of long-unburnt habitat (rainforest), whereas western sites were located in a more homogenous landscape of frequently burnt woodland.

Landscape factors such as proximity to long-unburnt vegetation or recently burnt vegetation (Radford *et al*. 2015), access to refugia (Brennan *et al*. 2011; Berry *et al*. 2015) or weather (Pettit and Naiman 2007) have been demonstrated to affect the activity of bats and other mammalian groups; this is important to consider when interpreting the findings of this study, and those of other studies, regarding the effects of fire on bats. It is also important to note that different guilds may be disproportionately affected by landscape-scale factors. More generally, the landscape scale at which bat response is measured can affect the results (Gehrt and Chelsvig 2003; McConville *et al*. 2013). Buchalski *et al*. (2013) investigated the effects of fire severity on bats and only measured effects at the local scale, not the broader landscape scale. Future studies should maximise the number of site replicates so that variation due to landscape factors can be accounted for; ideally, these sites would be stratified across the landscape to assess the influence of proximity to long-unburnt refugia and recently burnt vegetation.

Survey timing may have influenced the results of this study in two ways. First, seasonality represents a confounding factor, as it often determines fire intensity. Seasonality may affect insect abundance independent from the influence of fire (Grimbacher and Stork 2009) or bat activity (Pettit 2011; Burns 2016). Given that seasonality and fire intensity are inextricably linked in northern Australia, their relative effects are inseparable. Second, many faunal groups are known to exhibit a postfire pulse, or severe rapid decline, sometimes followed by a period of 'stabilisation' (Woinarski and Recher 1997; Moretti *et al*. 2006; Kelly *et al*. 2010). The sampling in the present study was undertaken 2–4 weeks after treatment, and it is uncertain if the bat response in this period is representative of a postfire pulse, temporary decline or lasting effect. The study by Broken-Brow (2020) in the same habitat and location showed that open guild bats exhibited a pyrophilic pulse within one week postburn, but by 14 days activity had returned to prefire levels.

Whilst the present study shows that fire intensity, associated with seasonality, has a significant impact on bats in northern Australia, it should be noted that there are other aspects of fire such as extent, frequency, and time since last burnt that are also likely to influence the response of bats.

Conclusion

The findings from this study contribute to our understanding of how fire regimes affect volant mammals at a local scale, and how fire could be managed to improve biodiversity. Given that different bat guilds responded positively, negatively, or not at all to different fire intensities, a mosaic of fire intensities across a landscape would maximise the activity and presence of all guilds that contribute to diversity. In the absence of species richness measures, the study of functional groups in this case supports the concept that pyrodiversity promotes biodiversity. Further research into species-specific responses (with a focus on threatened species) and the effects of fire frequency should be undertaken to inform fire management practices.

Conflicts of interest

The authors declare no conflicts of interest. Hardware and software are listed in the Methods for descriptive purposes, not as an endorsement.

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