Reduced fire frequency over three decades hastens loss of the grassy forest habitat of an endangered songbird

Zoë L. Stone [a,*], Martine Maron [a], Elizabeth Tasker [b]

[a] School of Earth and Environmental Sciences, Centre for Biodiversity and Conservation Science, The University of Queensland, Brisbane, QLD 4072, Australia
[b] Science, Economics & Insights Division, NSW Dept of Planning, Industry & Environment, Parramatta, NSW 2150, Australia

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ABSTRACT

Fire plays an important role in maintaining grassy forests, and reduced fire frequency has been linked to encroachment of woody plants into grassy forests and woodlands globally. In Australia a range of threatened animals, including the northern population of the endangered eastern bristlebird (*Dasyornis brachypterus*), are dependent on grassy forests. We examined this issue by collating three decades of detailed monitoring and fire data for 43 current and historically-occupied bristlebird sites, and examined the relationships among fire history, bristlebird occupancy and habitat patch size/condition. Habitat patch size declined by over 50% between 1980 and 2009 due to woody plant encroachment. Bristlebird occupancy was associated with reduced habitat loss and time since fire, while reduced fire frequency was the main predictor of decline in grassy cover, a critical habitat element for bristlebirds. Our models suggested habitat loss was strongly influenced by fire history, particularly fire frequency, with reduced habitat loss associated with more-frequent burning. Native grass cover can return quickly, and remained high until 5–10 years post-fire; densest grass cover was found at sites with fire intervals of between 3.5 and 7 years. Active fire management, including regular ecological burning, is imperative for conservation of the eastern bristlebird and other threatened fauna that depend on these grassy forests. The massive changes in global patterns of fire currently occurring, and the threat this poses to biodiversity, make understanding the nuances of fire ecology, including the role of fire frequency, essential to improving conservation management.

1. Introduction

Fire is an ecologically important disturbance for many grass-dominated vegetation types (Andersen et al., 2003; Bond and Keeley, 2005; Bowman et al., 2009). Globally, woody plants are reported to be expanding into grassy communities, especially in high rainfall, humid regions, such as on the margins of rainforest (Bond and Parr, 2010; Staver et al., 2011; Graw et al., 2016; Stevens et al., 2017). This has been linked to reduced fire occurrence and elevated atmospheric CO_2 (Bond and Midgley, 2000; Harrington and Sanderson, 1994; Crowley and Garnett, 1998; Higgins et al., 2000, 2007; Bond and Keeley, 2005; Gooden et al., 2009; Tng et al., 2012). While the loss of rainforest is a widely recognised issue of global conservation concern (e.g. Corlett & Primark, 2008; DellaSala, 2011), for species dependent on grassy vegetation near rainforest, or attributes of both rainforest and adjacent habitat, loss of grassy habitat is equally critical.

Reduced fire frequency has contributed to increased woody cover in tropical African savannas (Sankaran et al., 2005; Heubes et al., 2011), reduced plant diversity in north American grasslands and savannas (Ratajczak et al., 2012), shifting savanna-forest boundaries in Brazil (Hoffmann et al., 2012) and northern Australia (Tng et al., 2012);, and declining extent and condition of grassland habitats embedded in rainforest ('grassy balds') in eastern Australia (Fensham and Fairfax, 2006; Fairfax et al., 2009; Moravek et al., 2013; Butler et al., 2014). Succession to rainforest is a threat to a range of endangered species in Australia, including a suite of small mammals (e.g. Bradford and Harrington, 1999; Jackson et al., 2011; Vernes et al., 2001), insectivorous bats (Broken-Brow et al., 2019) and numerous bird species (Chapman and Harrington, 1997). For birds, changes to fire regimes have been widely documented to be contributing to population declines in fire-prone vegetation types in Australia (Baker, 1997; Woinarski, 1999), North America (Grant et al., 2004) and southern Africa (Sirami et al., 2009). Consequently, there is growing interest in the impacts of changing fire regimes and the role ecological burning can play in conservation, particularly in grassy

ecosystems, which are adapted to more-frequent fire (Bradstock et al., 2002; Bond et al., 2005; Penman et al., 2011; Russell-Smith and Cooke, 2009).

In Australia, the grassy forests of the Great Dividing Range provide critical habitat for a number of threatened species, including many that are endemic and relict Gondwanan species. For instance, cool, high-elevation grassy forests in north-eastern New South Wales (NSW) and south-eastern Queensland (QLD) are home to the endangered Hastings River mouse (*Pseudomys oralis*) and eastern bristlebird (*Dasyornis brachypterus*; Fig. 1). These species rely on dense grassy foliage cover at ground level (Baker, 2000; Stone et al., 2018; Read and Tweedie, 1996), which limits their ability to colonise habitat patches that are separated by rainforest or heavily grazed pasture. Changes to fire regimes are thought to have played a role in the decline of both species (Charley et al., 2021; Tasker and Dickman, 2004). Recent studies have suggested that the grassy forest patches to which they are restricted have declined considerably in condition and extent in the last three decades (Lamb et al., 1993; Rohweder, 2000; Rennison, 2016). However, the role of fire regimes in this change has not been fully established.

Although once found more widely along the coast and ranges of eastern Australia, the eastern bristlebird (*Dasyornis brachypterus*) now occurs in small, isolated populations in Victoria and southern NSW, and an ecologically unique, highly isolated northern population (hereafter 'northern' bristlebird) 700 km away on the QLD-NSW border (OEH, 2012). The species lives in dense, low vegetation cover. It uses heath and shrubland in southern Australia (Baker, 2000) but at its northern limit, is dependent on grassy forest (Holmes, 1989; Lamb et al., 1993; Stone et al., 2018). Until recently, the central and southern populations (500–2000 individuals) were considered relatively stable with their coastal and montane heath habitats largely protected in conservation reserves (Bramwell et al., 1992; Baker, 1997; Baker, 2000), however the 2019–2020 fires in Australia (Collins et al., 2021) burnt much of this habitat and significantly increased the extinction risk of these populations (Charley et al., 2021).

Considered one of the most 'at risk' taxa in Australia (Geyle et al., 2018), the northern bristlebird is found only in patches of high-elevation grassy sclerophyll forest (Charley et al., 2021; Rohweder, 2000). These patches are typically bordered by rainforest and/or (since European colonisation) cleared grazing land. Wildfires have been suggested as a threat to the small remaining populations (Holmes, 1989, 1992; Lamb et al., 1993), but low intensity fires are thought necessary to maintain the grassy habitat (Rohweder, 2000; Sandpiper Ecological Surveys, 2000; Rohweder, 2006). Understanding the threats and required fire regimes for bristlebirds may therefore also contribute to the overall conservation understanding of the ecology of these ecosystems.

We therefore aimed to explore how changing fire regimes have impacted northern bristlebirds and their habitat. To do this we identified all 43 grassy forest patches known to have been occupied by northern
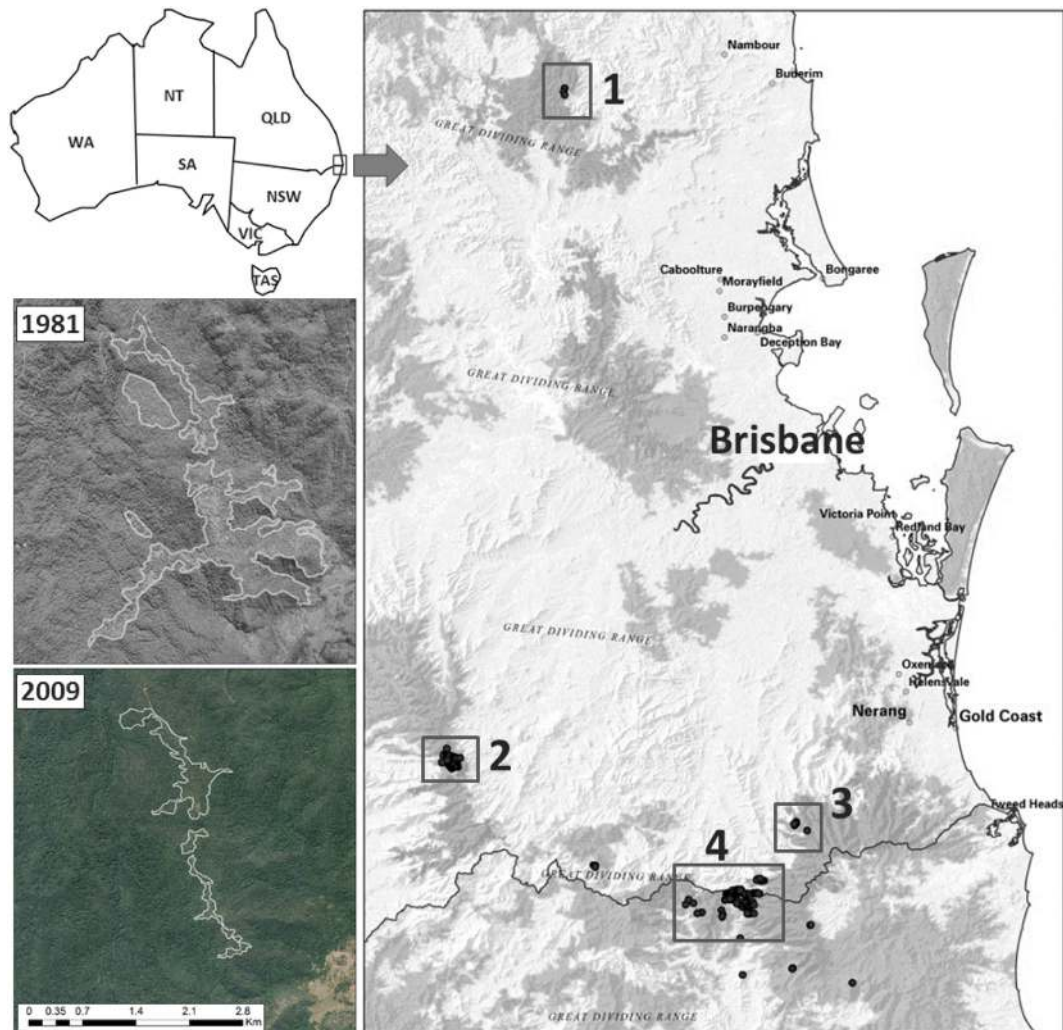

Fig. 1. Right: Historical and current locations (dots) of the northern bristlebird, showing the 43 sites clustered into four main regions: (1) Conondale, (2) Main Range, (3) Lamington and (4) Border Ranges. Left: Changes to grassy sclerophyll forest habitat extent between 1981 and 2009 shown for Conondale as an example.

bristlebirds, of which only 16 are still occupied, and used aerial imagery to quantify changes in the size of those patches over three decades. We mapped habitat using remote-sensed imagery available for 1980 and 2009 and then combined these habitat maps with field data on vegetation condition, as well as fire history from government records, bristlebird monitoring and interviews with land managers. Using these data, we asked:

1. Has the mean size of habitat patches changed between 1980 and 2009?
2. Is continued northern bristlebird presence related to changes in the size of habitat patches or fire history?, and
3. Has fire history influenced habitat condition in these northern bristlebird sites?

2. Methods

2.1. Study area

Our study area comprised all 43 of the known sites currently or historically occupied by the northern bristlebird. Scattered across southeastern QLD and northern NSW, Australia, these sites span the entire known range of the northern bristlebird, and form regional clusters near Conondale, Main Range, Lamington and Border Ranges national parks (Fig. 1). They are situated in a subtropical region and experience warm, wet summers and mild, dry winters (average rainfall of 1500 mm per year, with average maximum air temperature of 29 °C in summer and 22 °C in winter (E & H. Starkey unpubl., daily records 2001–2020).

Territories of bristlebirds that occur close together within a single habitat patch, and that were separated from other habitat patches by >100 m, were termed a 'site'. Sites were mostly delineated based on the original territory mapping by Holmes (1989), supplemented by territory locations identified in more recent surveys (see Section 2.2). Most of the currently occupied sites were located along upper slopes or exposed ridgelines within open sclerophyll forest interspersed with rainforest gullies, and within private properties adjacent to parks. Much of the sclerophyll woodland originally found on lower slopes in the region has been cleared for agriculture, while rainforest is the dominant vegetation at higher elevations and on the more sheltered south-easterly aspects. Both woodland and rainforest vegetation are unsuitable for northern bristlebirds.

2.2. Site occupancy

Site occupancy, defined as the presence of any birds in a patch at any given sampling time, was determined from monitoring that commenced in 1989 (Holmes, 1989) and has been carried out at regular intervals since (Appendix S1). These surveys, which have monitored the entire population since 1989 with consistent personnel, provide a high level of confidence in site occupancy data used in our models. Of the 43 sites included, 16 were occupied in 2016, and the remaining 27 had been occupied at some point during the monitoring period prior to 2016.

2.3. Habitat distribution & canopy cover

Habitat patches were mapped by visually delineating the contiguous area of grassy forest habitat within which all 43 known northern bristlebird sites were located, using 2009 ADS40 stereo-imagery (5 m resolution; sourced from NSW and QLD State governments). Although the habitat boundaries may differ somewhat between 2009 and 2016 (the date of the most recent bristlebird surveys), the 2009 imagery was the most recent available data for the entire study area. Since 2009, increased habitat management had been implemented across northern bristlebird sites, so while 2009 mapping may not reflect 2016 habitat conditions, it still captured the main changes in patch area since 1981.

To compare how the size of habitat patches had changed since 1981,

we mapped the boundaries of the same habitat patches using black and white aerial stereo-imagery taken in 1981 at a scale of 1:25,000 (the best available at the time). Mapping was done at a consistent scale of 1:5000 for 1981 and 2009 to minimise possible confounding from the different image resolutions. More detail on how habitat was defined and mapped is presented in Appendix S1.

From these maps of patches in both 1981 and 2009, habitat patch size and canopy cover were calculated. To examine potential changes in canopy structure over time, we calculated canopy cover for each grassy forest habitat polygon. Supervised classifications were conducted in ArcMap (version 10.7) for both 1981 and 2009 aerial imagery where individual pixels were assigned as either open ground, tree canopy or shadow (i.e. unable to be identified) after being trained on a manually identified subset of pixels (Ibanez et al., 2013). The training subset consisted of at least 500 pixels per class within each site polygon from which the classification could assign remaining pixels. Classifications were validated by manually checking 492 randomly classified pixels (246 open ground, 246 canopy cover). Over 80% of the classified points were correctly classified under the model. Details are provided in Appendix S1, including examples of imagery.

2.4. Fire history

Fire history data were collated for all 43 sites covering the period from 1980 to 2015 (Appendix S2). In summary, data were obtained from a range of sources, including NSW and QLD state fire mapping within National Parks, privately contracted reports, historical site reports and property management strategies, supplemented by personal records of local landholders, consultants, and land managers. Due to detailed fire records kept by stakeholders and the low turnover of residents and local land managers, and the multi-decadal conservation collaboration for management of bristlebird habitat, we are confident that we obtained accurate dates for the majority of fires (or reliable estimated dates, to within a year) for each site dating back to the early 1980s. Although we used the full fire history dataset for subsequent analysis, we also conducted a sensitivity analysis to examine the effects of including or excluding fires with estimated dates on the results. This sensitivity analysis involved performing the same statistical analyses but using only the precise recorded fire history dates (see Appendix S1).

Following previous work looking at the influence of the various components of the fire regime on similar vegetation (e.g. Cary and Morrison, 1995; Morrison et al., 1995; Watson and Wardell-Johnson, 2004; Gosper et al., 2011), we selected (i) time since most recent fire (where a time since fire of '0' was given for sites that had burnt <1 year previously), and; (ii) total number of fires for each site, as our predictor variables. These data were derived using fires recorded between 1981 and 2009 (to match habitat mapping dates) and used to explore the relationship between fire history and changes in habitat patch extent and canopy cover (cf. Methods 2.3). Models of the relationship between fire history (Methods 2.2) and understorey vegetation structure (Methods 2.5) and bristlebird occupancy in 2016 used fire data covering the period 1980–2015 (as both understorey vegetation and occupancy were assessed in 2016). Although the longest recorded interval between any two fires was initially considered as a third predictor variable (per Tasker & Watson unpubl.), it was discarded from the analysis because it was highly correlated with the number of fires variable, and its effect could not be separated.

2.5. Vegetation characteristics

Four to six 20 × 20 m vegetation plots (depending on site size) were measured inside patches within 200 m of known northern bristlebird locations at 38 of the 43 northern bristlebird sites (remaining sites were inaccessible, recently burnt or had become rainforest). Multiple plots were used to capture within-patch variation and were placed randomly within the known territory.

Vegetation surveys were done in May–July 2014 and March––November 2015, spanning winter, and autumn to spring periods. Field work was limited somewhat by access and weather, but each site was measured only once. Sites with different vegetation survey years had their fire variables calculated to match the year vegetation was surveyed (i.e. time since fire was based on 2014 or 2015 depending on vegetation survey).

Grass height was measured along the two central axes of each 20 × 20 m plot at 50 cm intervals and averaged across all plots for a site. The total cover (%) of grasses and other graminoids was estimated within each of the four 10 × 10 m subplots and averaged across all plots for each site to determine total ground cover. In addition, for each grass and graminoid species, individual cover estimates were made within each of the subplots and then averaged for the entire site. Tussock cover was calculated as the total cover of clumping grass species (*Sorghum. leiocladum, Poa sieberiana* and *Themeda triandra*). Further detail on methods used to measure the full suite of vegetation characteristics is presented in Stone et al. (2018).

2.6. Statistical analysis

We used an information-theoretic approach to assess the relative support for various models (summarized in Table 1; Burnham and Anderson, 2002). All analyses were completed using the R statistical computing environment (R Core Team, 2021). We fitted linear (LMMs) and generalized linear mixed-mixed effects (GLMMs) models using the lme4 R package (see below for specific details; Bates et al., 2015). We also used the MuMIn package to compare models (Barton and Barton, 2015).

2.6.1. Change in size of habitat patches and canopy cover

To examine how the extent of grassy forest habitat changed between 1981 and 2009, we used paired *t*-tests to compare size of grassy forest patches, and percent tree canopy cover in patches, between 1981 and 2009. We then modelled change in habitat patch size and canopy cover as a function of fire history. Because some habitat patches contained multiple bristlebird sites, we aggregated occupancy data to the patch-level to ensure these models were fitted at a consistent spatial scale. Additionally, to ensure temporal consistency between the dates of the fire record and the aerial imagery, we only considered fire records between 1980 and 2009 to model patch size. Thus, we created a new dataset, wherein each observation corresponded to a different patch containing variables that describe the change in patch size between 1980 and 2009, and also fire history associated with each site located within a patch. We then used LMMs to examine relationships between the change in patch size and the fire history variables, accounting for region (Conondale, Main Range, Border Ranges and Lamington National Park) using a random intercept term.

2.6.2. Northern bristlebird occupancy

We fitted GLMMs to explore the correlation of fire history and change in habitat patch size and northern bristlebird occupancy of sites in 2016. To achieve this we compared several models: null, fire frequency, time since fire, combined fire history, and habitat change. The fire history model included predictor variables for time since most recent fire (TSF) and number of fires (#Fires), based on all fire records to 2016 (the date of the most recent bristlebird surveys). The habitat change model included predictor variables for change in size of habitat patches (ΔHS) and canopy cover (ΔCC). Our sample size was too small to fit a model combining both fire history and habitat change, when the non-independence of sites within the same region using a random effect (sites = 43, regions = 4) was taken into account. All models were fitted with a logit link function to accommodate the binary (presence/absence) response variable. Additionally, we accounted for the non-independence of sites within the same patch and the non-independence of patches within a region using nested random intercept terms. Although previous research suggested that the fire may have a quadratic relationship to habitat variables (e.g. Morgan and Lunt, 1999; Prober et al., 2007), preliminary analyses could not find adequate support for this relationship, so we fitted the models using only linear relationships.

2.6.3. Grassy understorey structure

We fitted LMMs to explore whether site-level grass structure was related to fire history. Grass variables were selected based on their previously-identified importance for the northern bristlebird (Stone et al., 2018). We modelled mean grass height, grass cover and mean tussock cover using a global fire history model that included TSF and number of fires as predictor variables. For this analysis, fire records between 1980 and 2015 were used (to end at a time corresponding to the start of the vegetation surveys). Similar to the bristlebird occupancy models (Section 2.6.2), these models were fitted using nested random intercept terms to accommodate the non-independence of sites within patches, and patches within regions.

3. Results

3.1. Change in size of habitat patches between 1981 and 2009

The average size of all habitat patches in the region decreased significantly in the 28 years from 1981 to 2009 ($t = -2.902$, df = 22, $p = 0.008$). In 1981 grassy habitat patches where northern bristlebird had been recorded (38 sites) averaged 362 ha (from 10 to 1687 ha) in size, but by 2009 this had declined to an average of 96 ha (from 0 to 928 ha). That is, by 2009 the size of northern bristlebird habitat patches in our study area had declined to only 36% of their initial size in 1981. In contrast, we found no difference in average tree canopy cover within sites between 1981 and 2009 ($t = -1.759$, df = 22, $p = 0.093$), suggesting habitat changes were coming from a change to the site boundary or from changes to the understorey rather than from changes to the density of interior canopy trees (Fig. 2).

3.2. Effect of change in size of habitat patches and fire history on northern bristlebird occupancy

Models of northern bristlebird occupancy that included habitat change and time since fire had the strongest support (Table 2). Models using fire frequency or combined fire history to predict occupancy were less well supported (ΔAICc <2 from the null). While both these models outperformed the null (ΔAICc = 3.11), there was higher uncertainty regarding the habitat loss model, with higher standard errors for the coefficient estimates.
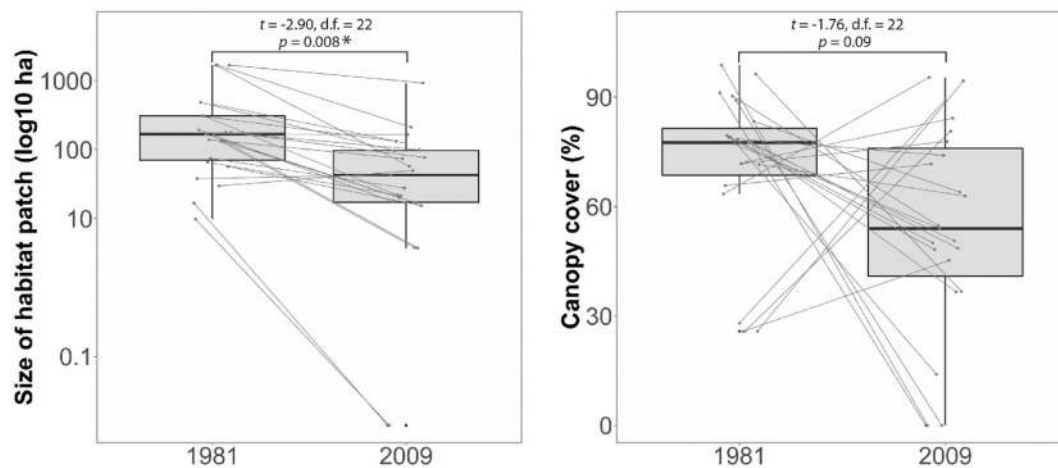
Table 1
List of predictor and response variables used to model fire history in relation to northern bristlebird occupancy and habitat condition.

Response variable	Predictors	Fire dataset
NEBB presence	Time since fire	1981–2016
	Number of fires	
	Change in habitat patch size	
	Change in canopy cover	
Grass cover	Time since fire	1980–2015
	Number of fires	
Grass height	Time since fire	1980–2015
	Number of fires	
Tussock cover	Time since fire	1980–2015
	Number of fires	
Habitat patch change	Time since fire	1980–2009
	Number of fires	

Fig. 2. Average size of grassy forest habitat patches in 1981 and 2009 (left) and average percent canopy cover within patches (right) across all northern bristlebird sites in 1981 and 2009. Boxes represent the median and interquartile range of values while whiskers indicate minimum and maximum values within 1.5 times the median, outlying points shown individually. Points – offset to help visualisation – show data measured at each site for 1981 and 2009, and lines connect measurements recorded at the same site across the two years. Results from paired t-test are displayed.

Table 2
Comparison of generalized linear models of northern bristlebird persistence in response to fire history and change in habitat patch size between 1981 and 2009 (ranging from −100 to +70%). Relative fit of alternative models using standardised coefficients with standard error: time since fire (TSF), number of fires (#Fires), change in size of habitat patch (ΔHS) and change in canopy cover (ΔCC).

Model	df	logLik	AICc	ΔAICc	Model coefficients			
					TSF	#Fires	ΔHS	ΔCC
Habitat patch change	6	−22.89	60.18	0			10.84 (±15.95)	5.56 (±3.03)
Time since fire	4	−26.12	61.27	1.09	−0.56 (±0.46)			
Fire frequency	4	−26.57	62.21	2.04		0.38 (±0.37)		
Null	4	−27.10	63.29	3.11				
Fire history	5	−25.93	63.52	3.35	−0.47 (±0.47)	0.24 (±0.40)		

3.3. Influence of fire on size of habitat and habitat (understorey) condition

The substantial decline in size of grassy forest patches throughout the entire range of the bird (both occupied and abandoned patches) was strongly associated with fire history at sites (Table 3). Habitat loss was associated with reduced fire frequency and longer TSF (Fig. 3). The combined fire history model was well-supported, suggesting that both a *single* long fire return interval (in this case, the most recent) and the overall *long-term* frequency of fires were both detrimental to grassy habitat.

Decline in habitat patch size was more severe when extended fire-free periods occurred. Those habitat patches that did not change ($n = 1$), or expanded in size ($n = 6$) had a mean of 7.3 fires in 28 years (i.e. burnt on average every 4.9 years), compared to sites that contracted in size, which had a mean number of 5.4 fires in 28 years (i.e. burnt on average every 6.6 years).

Habitat condition, specifically grass cover, was also influenced by fire (Table 3), with our fire frequency model – the top performing model – substantially outperforming the null (ΔAICc = 4.31). Fire frequency had a positive effect on grass cover, with more frequent fires associated with increased grass cover (Fig. 4). Sites with the highest grass cover had been burnt within the previous five years, and had between 4 and 8 fires in 28 years (i.e. 3.5–7 year mean fire intervals). Grass cover returned quickly following fire, with cover already above 100% (due to overlapping grasses measured within the understorey strata) by one-year post-fire for most sites and remained stable with increasing time since fire up until 10 years post-fire. None of the fire models were good predictors of grass height or tussock cover, with all performing similarly, or worse, than the null (Table 3).

4. Discussion

The size of grassy habitat patches used by northern bristlebirds nearly halved between 1981 and 2009. Reduced fire frequency was the best predictor of habitat patch contraction and reduced habitat condition. Whether northern bristlebirds still occupied patches in 2016 was also directly related to the habitat loss and time since fire. The rate of habitat decline for this highly imperilled taxon is of great concern, and demonstrates the importance of active fire management in this landscape.

Our results support a growing body of evidence of the vulnerability of rainforest-adjacent grassland/savanna patches to inappropriate fire regimes. The ecosystem presented in this study, while floristically unique to eastern Australia, is similar to many others globally in its dependency on frequent, low intensity fire (Bond et al., 2005; Murphy and Bowman, 2012; Sankaran et al., 2005). The current global emphasis on the increasing incidence and severity of wildfires and their threat to wildlife carries a further risk: that the value of low intensity and regular fires as a tool for habitat maintenance for dependent species and ecological processes may be forgotten. Frequent, low-severity fires may not only maintain grassy diversity and habitat structure (e.g. Morgan and Lunt, 1999; Prober et al., 2007), but can reduce severity of subsequent fires in some vegetation types (Barker et al., 2021). For such habitats, implementing low intensity, frequent fire may thus improve their resilience to future wildfires. Under a changing climate, and increased threat from other factors, such as habitat fragmentation, being able to understand and skilfully manipulate the different components of the fire regime (frequency, season, severity, type and extent of fire) is likely to become increasingly critical.

Table 3

Comparison of alternative mixed effects models exploring the influence of fire history on grass cover, grass height, tussock cover, and change in habitat patch size at all bristlebird sites. All variables were standardised. Fire history coefficients with standard error: time since fire (TSF) and number of fires (#Fires) are indicated.

Model	df	logLik	AICc	ΔAICc	TSF	#Fires
Grass cover						
Fire frequency	5	−170.74	353.35	0		12.32 (±4.31)
Fire history	6	−170.64	355.98	2.63	−3.58 (±7.71)	12.00 (±4.45)
Null	4	−174.23	357.67	4.31		
Time since fire	5	−173.87	359.61	6.26	−7.36 (±8.17)	
Grass height						
Null	4	−149.35	307.91	0		
Fire frequency	5	−148.27	308.41	0.5		4.05 (±2.46)
Time since fire	5	−149.17	310.11	2.2	−2.78 (±4.05)	
Fire history	6	−148.23	311.18	3.26	−1.03 (±3.9)	3.81 (±2.6)
Tussock cover						
Fire frequency	3	−25.77	58.24	0		0.12 (±0.39)
Null	3	−25.81	58.34	0.09		
Fire history	4	−25.04	59.3	1.05	0.82 (±0.71)	0.23 (±0.41)
Time since fire	4	−25.21	59.63	1.38	0.73 (±0.69)	
Habitat patch change						
Fire frequency	4	−14.23	38.82	0		0.10 (±0.04)
Fire history	5	−12.70	39.16	0.34	−0.02 (±0.01)	0.07 (±0.04)
Time since fire	4	−14.83	40.02	1.2	−0.03 (±0.01)	
Null	3	−17.61	42.74	3.74		

4.1. Contraction of grassy patches and effects on bristlebird populations

Elsewhere, grassy forests and savanna woodlands adjacent to rainforest appear to be highly susceptible to colonisation by rainforest and woody shrubs, for instance in other parts of Australia (e.g. Bowman and Fensham, 1991; Bowman, 2000; Stanton et al., 2014 and Tng et al., 2012) and in other regions across the globe (Heubes et al., 2011; Murphy and Bowman, 2012; Hoffmann et al., 2012; Stevens et al., 2017). Our results suggest this is also the case for the grassy forests of sub-tropical eastern Australia. The significant reduction in habitat extent and the corresponding loss of grass cover demonstrated here is of serious concern for northern bristlebirds: the taxon has experienced a precipitous 80% decline in population size over the same period and is considered one of the most imperilled birds in Australia (Geyle et al., 2018).

Northern bristlebirds are territorial, and individual home ranges vary between 2 and 5 ha depending on bird density (Holmes, 1989; D. Charley pers. comm.). For long-term persistence, it has been estimated as a general rule of thumb that effective population sizes of 100 are needed to avoiding inbreeding depression, while effective populations of 1000 will preserve evolutionary potential (Frankham et al., 2014). Given that only three occupied northern bristlebird habitat patches are >100 ha (thus potentially each supporting 20–50 pairs) with the rest <90 ha in size, they almost certainly are insufficient to support sustainable effective populations. Therefore, maintaining sufficiently frequent low intensity burning within current patches still grassy enough to carry fire in moderate conditions, though essential, will not be enough. Reclamation of now-marginal encroached habitat will be necessary to increase the extent of grassy habitat not only for northern bristlebirds but the range of co-occurring species they represent. If not, the territories within this small, highly fragmented population – at very high risk of local extinction due to inbreeding depression and stochastic events (Shaffer, 1981; Wilcox, 1986; Clark et al., 1990) – are likely to blink out one by one in the near future.

In contrast to our finding that frequent, low intensity fires maintain these grassy forests, there is evidence that severe wildfires may cause the loss of isolated subpopulations. This occurred for the only remaining substantial population in QLD after moderately severe wildfire in 1991. Severe fires may also cause mass germination of shrubs with dormant soil seedbanks (Gordon et al., 2017). At a number of the NSW sites, a severe wildfire in 2001 resulted in mass emergence of *Acacia* species (S. King, pers. comm.), rapidly converting the understorey of these sites from continuous grass to shrubby wattles, which shaded out the grassy layer and would no longer carry low intensity fire.

Under suboptimal management, feedback loops may occur that subsequently maintain sites in undesirable stable states. Under low-moderate fire weather conditions, small, degraded habitat patches
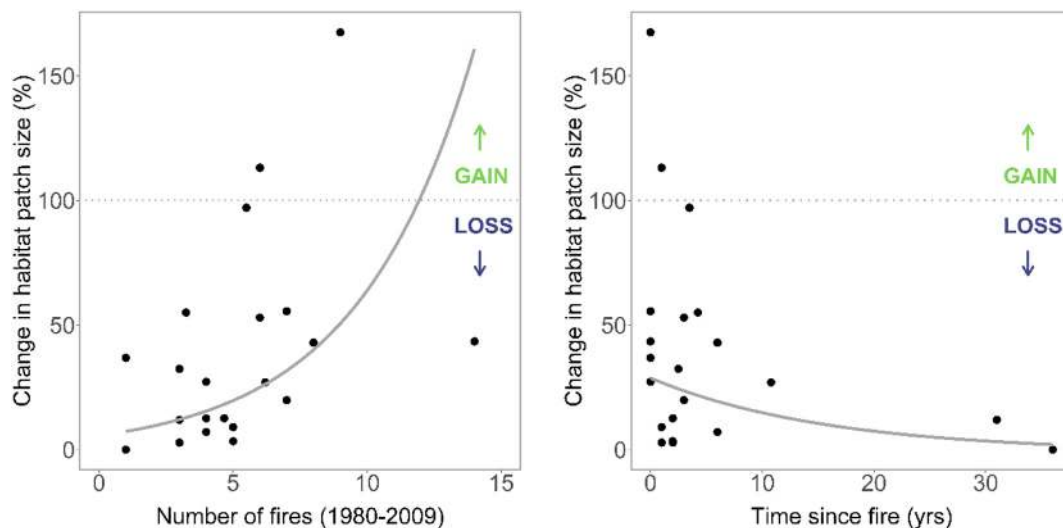

Fig. 3. The relationship the total number of fires (left) and time since fire (right) on the change in habitat remaining between 1980 and 2009 across northern bristlebird sites. Shown are data (dots) and model predictions from fitted GLMMs (grey line). Dotted line indicates no change in habitat patch size (= 100%), with sites experiencing habitat loss below (< 100%), and sites that have had habitat gain above (> 100%).
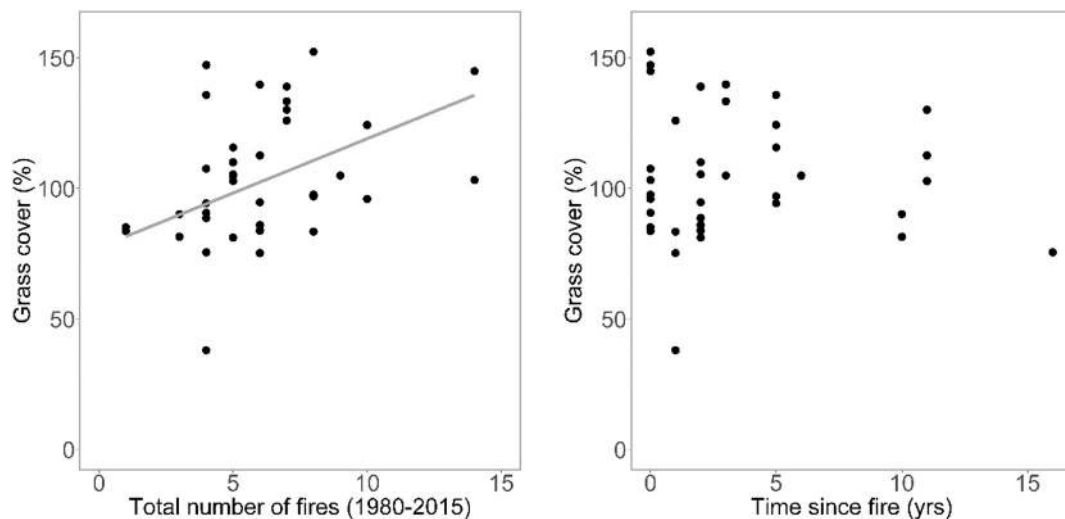
Fig. 4. The relationship the total number of fires from 1980 to 2015 (left) and time since fire (right) on grass cover across northern bristlebird sites. Total number of fires is plotted against model predictions from fitted GLMM (grey line). Time since previous fire is shown as number of years, hence sites with a time since fire of '0' may have been burnt at any time within the previous 12 months and may have high grass cover.

may be less likely to burn because of the loss of continuous ground fuel, and leaf litter being moister. However, in severe fire weather, when the conditions enable flames to connect more patchy fuels (Bradstock, 2010; Zylstra et al., 2016) shrub-invaded (i.e. 'degraded' bristlebird habitat) patches will become available to burn. Under severe conditions, fires are also likely to be more extensive, threatening bristlebirds over a larger area than their limited home ranges and poor dispersal ability allows them to recolonise.

Northern bristlebirds live in a highly productive landscape where high rainfall and basalt soils result in a highly competitive environment (Low, 2011). Rainforests can readily replace grassy forests in the absence of fire (Unwin, 1989; Chapman and Harrington, 1997; Butler et al., 2014), similar to the shift from grassy forest to monsoon rainforest in far north Australian savannas (Bowman and Fensham, 1991). In our study region, frequent, low-intensity fires in grassy patches are likely to maximise landscape (gamma) diversity by maintaining and enhancing the structural and floristic differences between grassy eucalypt forests and the adjacent rainforests (e.g. Baker et al., 2021; Broken-Brow et al., 2019). Our findings are also consistent with research showing that frequent fires can limit the establishment and dominance of woody plants by top-killing juveniles and saplings, thus keeping them in a 'fire trap' (Hoffmann, 1999; Grady and Hoffmann, 2012; Werner, 2012; Hoffmann et al., 2020).

4.2. Mechanisms of effects of altered habitat on bristlebirds

Grass cover was strongly influenced by fire frequency, and following a fire, grass cover returns quickly (provided prior abundance/health) and remains fairly stable up to 5–10 years post-fire within our sites. As a 'rat in a feathered suit' (Kristo 1997, in Baker (1998)), the northern bristlebird runs on the ground much more than it flies, using the space under grasses for foraging, and thick tall clumps for nesting. Changes in grass cover are therefore likely to strongly impact foraging, survival and exposure to predators, and can also reduce the quality of the invertebrate food sources (Stone et al., 2019). Increased fire frequency to maintain thick grass cover, and thus provide protection, 'runways' and foraging opportunities underneath it, is apparently essential for northern bristlebirds. Many of the other threatened animals of the grassy forests of the region also depend on dense grass for cover (Vernes et al., 2001), and food (Tasker and Dickman, 2004).

4.3. Conservation implications

Our research indicates a lack of sufficiently frequent fire in grassy forests is contributing substantially to a loss of northern bristlebird habitat. The decline in fire frequency in the region is likely a combination of three factors. First, since the 1980s a strong conservation emphasis on rainforest protection in the study region (Shoo et al., 2014) - an understandable reaction to a previous era of destructive logging and clearing and recognition of the high diversity and endemism of the region's rainforests (resulting in creation of the Gondwana Rainforests World Heritage Area) - also led to an aversion to fire. Undervaluing grassy forests compared to neighbouring rainforest habitats is a globally common phenomenon (Parr et al., 2014). Second, the increasing density of human settlement, changing land-use practices, the arrival of 'tree-changers' less familiar with fire, and increasing regulation have also undoubtedly contributed. It is notable that in our study region virtually all the remaining occupied sites are located on private property (10 out of 11 current sites) where landowners have continued burning, largely to maintain a grassy understory for low-intensity cattle grazing. Third, and perhaps most significantly, is the loss of Indigenous fire management of these grassy ecosystems since European colonisation. There is increasing evidence that for systems finely balanced on the boundary between flammable and fire-resistant alternative stable states, Indigenous cultural burning was a critical factor in determining the vegetation that resulted (Fletcher et al., 2021; Mariani et al., 2022).

While too-frequent fire is a major conservation threat to many species (Gallagher et al., 2021), and is a key threatening process in NSW (NSW Scientific Committee 1998), for grassy forests in highly productive regions such as ours, the threat is just the opposite (Baker et al., 2020). Increased shrub growth rates as a result of increasing CO_2 fertilisation (Bond and Midgley, 2000) appear to be pushing grassy ecosystems in wet, fertile landscapes in this direction at an accelerating rate.

By maintaining a diversity of fire regimes (and in particular, fire *frequencies*) across the landscape, the full range of diversity can best be maintained (Swan et al., 2020). Without active fire management, the species dependent on these grassy ecosystems are likely to disappear within our lifetime.

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CRediT authorship contribution statement

Zoë L. Stone: Conceptualization, Methodology, Formal analysis, Validation, Investigation, Resources, Writing – original draft, Writing – review & editing. **Martine Maron:** Conceptualization, Methodology, Writing – original draft, Supervision. **Elizabeth Tasker:** Conceptualization, Methodology, Validation, Resources, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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