

Quantifying the impacts of Australian bushfires on native forests and gray-headed flying foxes

K. Baranowski^{a,1,2}, C.L. Faust^{a,1,3}, P. Eby^{b,c,4}, N. Bharti^{a,*,5}

^a Department of Biology, Center for Infectious Disease Dynamics, The Pennsylvania State University, University Park, PA 16802, USA

^b Centre for Ecosystem Science, University of New South Wales, Sydney, NSW 2052, Australia

^c Environmental Futures Research Institute, Griffith University, Nathan, QLD 4111, Australia

ARTICLE INFO

Article history:

Received 21 October 2020

Received in revised form 29 March 2021

Accepted 29 March 2021

Keywords:

Mega-fires

Pteropus

Habitat loss

Climate change

ABSTRACT

Climate change is increasing the frequency and intensity of wildfires in many regions of the world. Changing fire regimes have been shown to delay vegetation recovery and shift distribution of ecosystems, increasing the importance of understanding the short- and long-term impacts of these changes. The unusually severe 2019–2020 Australian bushfire season has been linked to climate change and the impacts on wildlife and ecosystems are still being studied. We use remotely sensed thermal data to assess the differences between annual fire seasons from 2012 to 2019 in eastern Australia to understand the unique characteristics of the 2019–2020 anomalous fire season. We use spatial and temporal monitoring data of the vulnerable gray-headed flying fox (*Pteropus poliocephalus*) and its habitat to examine evidence for fire impacts on these important forest pollinators. We analyze roost occupancy in response to a previous fire season and use these results to identify roosts that are particularly affected by the 2019–2020 fires. During the 2019–2020 anomalous fire season, mega-fires, defined as contiguous fires over 10,000 hectares (ha) each, burned over 60% of the total affected area and occurred mostly in forested areas. This is in contrast to previous fire seasons in which smaller, scattered fires burned mostly non-forested areas. While we found little evidence that gray-headed flying fox reacted directly to fires in a previous season, unburned winter habitat was a key predictor of roost occupancy. The 2019–2020 anomalous fire season burned nearly ten times the amount of total habitat (33.7%) across the gray-headed flying fox range compared to the previous season. Critical winter habitats, including a species in fire refugia, were also substantially more burned in the anomalous fire season. Much of the winter habitat that burned in the anomalous fire season was within high or extreme severity fires (41.7%), causing substantial canopy consumption of these species. This work highlights the utility of remotely sensed thermal data for rapidly mapping fire impacts to wildlife and vegetation and highlights areas of habitat key for the conservation of these vulnerable populations.

© 2021 The Authors. Published by Elsevier B.V.
CC-BY 4.0

* Corresponding author.

E-mail address: nita@psu.edu (N. Bharti).

¹ These authors contributed equally.

² ORCID: 0000-0003-4720-1398

³ ORCID: 0000-0002-8824-7424

⁴ ORCID: 0000-0001-5441-2682

⁵ ORCID: 0000-0003-1940-7794

1. Introduction

Fire is essential for the maintenance of biodiversity across ecosystems globally (Bowman et al., 2009). Fire-adapted animal and plant species can thrive in nutrient-rich ash postfire (Bradstock et al., 2008) and some are dependent on fire for new generations (Krawchuk et al., 2009). Despite the vital role of fires, extensive high-intensity fires can have negative impacts on ecosystem health by reducing biodiversity (Pastro et al., 2011; Berry et al., 2015; Lindenmayer et al., 2014) and causing declines in wildlife populations (Lawes et al., 2015; Leahy et al., 2016). Uncontrolled fires can also harm human health (Liu et al., 2015) and damage property (Blanchi et al., 2010). The negative impacts of fire on ecosystems can be long-lasting (Bowd et al., 2018) and new fire regimes can delay or prevent the recovery of ecosystems altogether (Gill et al., 2013). Climate change-induced heat and drought have extended the length of fire seasons and augmented burnable areas across the globe (Jolly et al., 2015). Increases in the size and frequency of large fires have been documented across North America (Westerling et al., 2006; Barbero et al., 2015; Gillett et al., 2004). It is increasingly important to understand the impact of these emerging fire regimes that reduce the resiliency of affected ecosystems and the biodiversity they support to better manage them presently and mitigate future negative outcomes.

Australia is particularly vulnerable to climate-driven changes in fire regimes. While fire occurrence is a product of complex management practices, local conditions, history, and chance (Pausas and Keeley, 2009; Oliveras and Bell, 2008; Gill, 2008), Australian wildfires, often called bushfires, are tightly linked with local weather conditions and climate oscillations (Camac et al., 2017; Cai et al., 2009). Fire intensity (thermal energy release) and severity (loss in organic matter) (Keeley, 2009) are important characteristics that determine a fire's impact on organisms and their ecosystems. Many forested ecosystems found across Australia, namely eucalypts (tribe Eucalypteae within Myrtaceae), are adapted to current fire regimes and most species can either reseed or resprout quickly from lignotubers or epicormic tissue post-fire, including high-severity fires (Bennett et al., 2016; Clarke et al., 2015; Collins, 2020). However, frequent high-severity fires can lead to demographic shifts in eucalypts (Collins, 2020), prevent recovery of forests, and promote domination of alternative ecosystems (Fairman et al., 2016; Bowman et al., 2014). High-intensity fires can lead to increased losses of biomass, damage epicormic tissue growth beyond immediate recovery, and have long-term impacts on the landscape (Denham et al., 2016; Bennett et al., 2016). Both the frequency and extent of bushfires are predicted to increase with climate change (Fasullo et al., 2018), raising questions of whether forested ecosystems will be able to persist and support endemic wildlife in shifting fire regimes. In 2019, local weather and climate conditions in eastern Australia gave rise to an unusually dry spring combined with an accumulation of fuels (Nolan et al., 2020; Lindenmayer et al., 2020). This created favorable conditions for the subsequent anomalous bushfires, which burned an unusually high extent within forested ecosystems (Boer et al., 2020), and dominated international headlines for months.

The location and extent of the 2019–2020 bushfires impacted habitat of many vulnerable and threatened species (Ward et al., 2020; Department of Planning Industry and Environment, 2020) and may have increased extinction risk for some endemic species (Lam et al., 2020). Although fires can increase resources for some species in the short-term (Bradstock et al., 2008), surviving animal populations can also decline because of higher predation risk and loss of resources (Lawes et al., 2015; Leahy et al., 2016). Higher mortality combined with lower reproduction can also lead to delayed populations declines (Sutherland and Dickman, 1999; Lawes et al., 2015). Declines in biodiversity of small mammals and birds are more pronounced after more severe (Chia et al., 2016; Friend, 1993; Lindenmayer et al., 2014) and larger bushfires (Berry et al., 2015; Pastro et al., 2011; Lawes et al., 2015). The scale and intensity of 2019–2020 fires were a consequence of climate change (Van Oldenborgh et al., 2020), suggesting that conservation activities will need to incorporate the impacts of climate-induced fires into future planning. The responses of vulnerable and endangered populations are particularly critical to understand, especially for preserving biodiversity and maintaining ecosystem health with changing fire regimes.

Bat species are important bioindicators of environmental stressors (Jones et al., 2009; Fidelino et al., 2020). Understanding the response of bats to this anomalous bushfire can provide insight into its impacts on the ecosystem. Radio-tracking of insectivorous bats during prescribed fires in North America showed movement away from smoke, suggesting a behavioral response to ignition and low direct mortality (Dickinson et al., 2009). Research on bat responses to fires has primarily used acoustic surveys to measure activity and occupancy of insectivorous bats in the months and years following fires in North America and Australia. These studies have shown an increase in activity in burned areas immediately following fires and extending to several years post-burn, likely driven by changes in vegetation structure that reduces clutter (Buchalski et al., 2013; Burns et al., 2019), increases in prey (Doty et al., 2016; Law et al., 2019), and increased availability of roosting sites (Lacki et al., 2009; Perry, 2011). However, responses to fires depend on the specific ecology of each bat species (Blakey et al., 2019; Steel et al., 2019), timing of fire during the reproductive cycle (Buchalski et al., 2013), and severity of the fire (Buchalski et al., 2013; Burns et al., 2019; Steel et al., 2019).

The gray-headed flying fox (*Pteropus poliocephalus*) lives throughout southeastern Australia and is one of four *Pteropus* species on the continent. Habitat loss and human disturbances led to an estimated 30% population decline from 1989 to 2001 and lead to the species being listed as 'Vulnerable' (McIlwee and Martin, 2002; Tidemann and Nelson, 2011; Dickman and Fleming, 2002; Threatened Species Scientific Committee, 2001). More recent reports show the population has been fairly stable over the last 20 years, although differences in counting methods over time have impacted the accuracy of this estimate (Westcott et al., 2015). Gray-headed flying foxes consume native fruits and nectar, and likely play an important role in vegetation recovery through pollination and seed dispersal (Eby, 1991a, 1995, 1998; Hall and Richards, 2000; Mcconkey and Drake, 2006; Roberts et al., 2012). While their typical foraging range from large communal roost sites is 20–30 km, they can travel hundreds of kilometers during seasonal movements (Roberts et al., 2012; Welbergen et al., 2020). However, the evidence for

conservation implications of bushfires on *Pteropus poliocephalus* populations, or any nectar- and fruit-dependent flying fox species, is not known. Old World fruit bats (Pteropodidae) rely less on echolocation, so they would not be as affected by changes in habitat structure postfire, which is observed in echolocating insectivorous bats. We expect changes in fruit and nectar resources following fire will impact foraging activity and roost occupancy. The majority of gray-headed flying fox resources resprout post-fire (Table B.1), but the nectar resources provided by these species will depend on fire intensity and severity. Low intensity burns have been documented to result in bud loss and delay flowering 1 year and high intensity fires can delay flowering for a few species up to 3 years (Law et al., 2000), but more research is needed on species specific responses to fire severity. To our knowledge, the only study conducted on fire responses in Old World fruit bats observed the sensitivity of Madagascar flying fox (*Pteropus rufus*) roosts to fire disturbances (Jenkins et al., 2007). Our study presents a novel evaluation of the response of an Australian flying fox species to fire, with implications for management and conservation of these important pollinators and seed dispersers (Eby, 1991a).

We integrate remotely sensed thermal data and longitudinal roost monitoring data to better understand the impact of fires on gray-headed flying fox populations and develop a pipeline for rapidly mapping priority areas for monitoring and conservation. Specifically, we used thermal satellite data to quantify the extent and distribution of fires in the recent anomalous fire season (2019–2020). We compared fire distribution, forested areas affected, and extent from 2012 to 2020 to investigate how this anomalous fire season compared to previous years. We then focused on fire extent within the gray-headed flying fox habitat range and quantified fire severity for the subset of foraging habitat in New South Wales where fire severity has been systematically assessed in 2019–2020. We hypothesized that roost occupancy would decrease with greater extents of burned surrounding habitats. We tested this for the 2012–2013 fire season using longitudinal roost survey data in Queensland. We use responses to this previous fire to identify the roosts that are most likely to be impacted by the 2019–2020 anomalous bushfire season and highlight these roosts and surrounding habitat for critical conservation prioritization.

2. Materials and methods

This study focuses on the eastern Australian states of Queensland, New South Wales, Australian Capital Territory, and Victoria (Fig. 2a) that encompass the range of gray-headed flying foxes. This region of Australia has the nation's highest human population density, high biodiversity and the largest tracts of remaining forest habitats (Williams et al., 2011).

2.1. Acquisition and processing of spatial fire and forest data

We retrieved fire incidence data from NASA's Fire Information for Resource Management System (FIRMS) Visible Infrared Imaging Radiometer Suite (VIIRS) Active Fire and Thermal Anomalies for September 1 to March 1 of each fire season from 2012 to 2020 (LANCE FIRMS, 2020). Raw VIIRS data has been validated for long-lasting fires (Oliva and Schroeder, 2015) and has higher spatial and temporal resolution than other remotely sensed products. VIIRS data has low false positive active fire cases (Schroeder et al., 2014) and high concordance with LANDSAT imagery (Oliva and Schroeder, 2015).

We converted VIIRS thermal anomaly points to a raster to cartographically generalize burned area. To account for the wide range in scan and track pixel size of these data (320–800 m) we created 440 m and 1120 m rasters of fire extent which represent the hypotenuses of the highest and lowest resolution pixels, respectively. We present data on burned area at the highest resolution in the main text and the lowest spatial resolution in the SI. We also created a modified raster of the 440 m generalized burned area that incorporated small forested gaps in the thermal anomaly data created by drift from the satellite passage. We calculate burned area in each year from 2012 to 2019 to summarize key fire metrics including: total burned area, number of individual fires (as number of unconnected polygons), proportion of area burned by 'moderately sized' fires (> 100 ha), and proportion of area burned by 'mega'-fires (> 10,000 ha, as defined in Adams (2013)). Here we define 'individual' fires as fires that were spatially separated by unburned areas, we do not assume they were independent ignition events.

We evaluated the ability of the VIIRS data to accurately assess fire extent by comparing our near-real time burned area assessments to the Australian Government's National Indicative Aggregated Fire Extent Dataset, a product first released in February 2020 and updated monthly until June 2020 (Commonwealth of Australia, 2020). We evaluated discrepancies between the two datasets of fire extent using Normalized Difference Vegetation Index (NDVI) values in March 2020 derived from Sentinel-2 imagery (GMES-GSEG-EOPG-TN-09-0029, 2012; Planet Team, 2020). We used the National Vegetation Information System (NVIS) to identify the forest types and compared efficacy of each method to differentiate burned and unburned vegetation in these discrepancy areas.

To quantify fire impacts on forests, we used a global dataset of 30 m resolution tree canopy cover estimates derived from LANDSAT imagery in the Global Forest Change dataset v1.6 (Hansen et al., 2013). We define forested areas as tree cover of 20% or more in a pixel (Montreal Process Implementation Group for Australia and National Forest Inventory Steering Committee, 2018) and the product only includes trees taller than 5 m. We resampled forested areas to 440 m resolution using maximum combined area selection, again using a 20% tree cover threshold to distinguish forest and non-forest pixels, and assessed fire extent in forests. We tracked the size and abundance of forest fragments because fragmentation of forests affects plant mortality and growth, often in a localized area and over the short-term (Laurance et al., 2018; King et al., 2018), and has the potential to affect flying fox resources.

2.2. Temporal and spatial extent of gray-headed flying fox habitat

Spatial data on gray-headed flying fox habitat (State Government of NSW and Department of Planning Industry and Environment, 2008) is based on a comprehensive survey of diet species, which includes both blossom and fruit resources across a variety of ecosystems (Eby and Law, 2008). Because this spatial data was created in 2008, we incorporated more recent forest loss using spatial and temporal forest cover data (described above; Fig. A.9). Incorporating forest loss allowed us to estimate habitat loss for gray-headed flying foxes and provide temporal estimates of resource availability for specific roosts. This remotely sensed forest data doesn't include any new forest growth from 2013 to 2018 (Hansen et al., 2013) and likely overestimates net forest loss. However, this is unlikely to omit important resources for gray-headed flying foxes; eucalypts can take several decades to mature after planting (Cremer et al., 1978), and young trees are likely to be immature or produce less nectar than mature stands (Law and Chidel, 2009, 2008; Wilson and Bennett, 1999). Spatial habitat data is specific to native vegetation and doesn't include resources in cleared or urban environments, which some populations of gray-headed flying foxes may rely on (Parry-Jones and Augee, 1991; Williams et al., 2006).

We refer to roost-adjacent resources as *foraging* resources throughout the paper to reflect the immediately available resources for a particular roost. We defined *total foraging habitat* as all native habitat within a 50 km radius of a known flying fox roost (details below) (Eby, 1991b; Tidemann et al., 1999). We defined *winter foraging habitat* as areas that contain at least one of five species (*Eucalyptus robusta*, *E. tereticornis*, *E. siderophloia*, *Melaleuca quinquenervia*, and *Banksia integrifolia*) within a 50 km radius of a known roost. While there are 13 gray-headed flying fox diet species that can flower during winter, the selected five species represent the most annually reliable and productive species during critical resource bottlenecks in winter months (Eby and Law, 2008).

2.3. Gray-headed flying fox roost-level responses to fire

To examine how wildfires may impact gray-headed flying fox populations, we used longitudinal monitoring data of flying fox (*Pteropus* species) roost sites in the states of Queensland and New South Wales. Roost counts are conducted approximately quarterly. Location and occupancy data (count estimates in Queensland and presence/absence in New South Wales) are publicly available through the National Flying Fox Monitoring Program (Westcott et al., 2011; Flying Fox Monitoring Program, 2020; National Flying Fox Monitoring Program, 2020).

To explore evidence of fire impacts, we focused on modeling occupancy of gray-headed flying foxes (presence/absence of at least one animal) at roosts over time. Four seasons preceding and following the 2012–2013 wildfire season (from September 2011 to March 2014) were included to account for known seasonal variation in occupation (Vardon et al., 2001) in addition to fire impacts (Fig. A.2). Observations recorded during the fire season (September 2012–March 2013) were excluded. The dataset was truncated to only include roosts that had a minimum of four observations in pre- and post-fire periods, resulting in 146 roosts in Queensland. Continuously occupied roosts ($n = 11$) and completely unoccupied roosts ($n = 29$) were further excluded. Only satellite roosts, defined as roosts that had both presence and absence of gray-headed flying foxes in the observation period, were used for this analysis (dataset FF1, Table 1). We focused on satellite roosts because these are most likely to have responses to disturbances and reflect the natural nomadic behavior of gray-headed flying foxes (Welbergen et al., 2020).

Presence and absence of gray-headed flying foxes (π) at satellite roosts were fit with logistic mixed effects models, with i indicating temporal observations and roost identities (j) included as random effects (ζ):

$$\text{logit}\{\pi_{ij}\} = \beta_1 + \beta_2 x_{2j} + \beta_3 x_{3ij} + \zeta_j$$

Univariate and multivariate regressions were evaluated with several predictor variables (x_n), including: presence of another flying fox species, area of total foraging habitat, area of winter foraging habitat, distance to closest burned area, proportion of foraging habitat burned, proportion of winter foraging habitat burned, latitude, and season (Tables A.1, A.8). Total foraging and winter foraging habitat were quantified as the sum of hectares that contained diet species within a 50 km radius to incorporate the maximum foraging distance (Eby, 1991b; Tidemann et al., 1999). Logistic mixed effects models were created using *glmmTMB*, residual diagnostics were carried out with *DHARMa*, and model selection was done with AIC, all in R version 3.6.1 (R Core Team, 2019; Brooks et al., 2017; Bolker et al., 2009; Hartig, 2020).

2.4. Quantification of burned gray-headed flying fox foraging habitat

To quantify relevant foraging habitats impacted by each fire season, we first identified all roosts that were occupied at any point in the 5 years preceding the fires for both the 2012–2013 (dataset FF2) and 2019–2020 (dataset FF3) fire seasons (Table 1). We used the locations of these roosts to quantify total foraging habitat and winter foraging habitat. A generalized additive model with a beta distribution and logit link function was used to summarize the proportion of burned winter foraging habitat by latitude and year for occupied roosts. Models were created and evaluated in R version 3.6.1 with the package *mgcv* (Wood, 2011). While fire severity estimates were not available for the past fire seasons or all of eastern Australia, New South Wales mapped fire severity for the 2019–2020 fire season (New South Wales Department of Planning Industry and Environment, 2020). We examined the distribution of fire severity across the gray-headed flying fox habitat range to better understand the impact of these fires on the animals. We clipped the fire severity map to within the adjusted 2018 gray-headed flying fox habitat

Table 1
Datasets for assessing fire impacts on flying foxes.

Name of flying fox Dataset	Time period	Criteria for inclusion	Number of roosts meeting inclusion criteria	Geographic extent	Downstream analysis
FF1	09/2011–03/2014 (excluding 09/2012–03/2013 fire season)	Minimum of 4 observations at a satellite roost (not continuously occupied or unoccupied)	106	Queensland only	Generalized logistic regression model (outcome variable is presence/absence)
FF2	09/2007–09/2012	Presence of flying foxes at roost	248	New South Wales and Queensland	Roost-level foraging habitat quantification for 2012–2013 (including burned area)
FF3	09/2015–09/2019	Presence of flying foxes at roost	324	New South Wales and Queensland	Roost-level foraging habitat quantification for 2019–2020 (including burned area)

spatial layer and quantified the distribution of habitat within each of four severity classes, ranging from low severity (burnt surface with unburnt canopy) to extreme severity (full canopy consumption). We also assessed fire severity in foraging rain-forest habitats to consider impacts of fire on important fire refugia.

3. Results

We first map the extent of fire across the eastern states of Australia to demonstrate differences in scale and distribution between years (Section 3.1). Based on these results, we identified a prior fire season (2012–2013) that had a similar total burned area to the recent 2019–2020 season. The 2012–2013 fire season, hereafter known as the previous focal fire season, was used for comparison to the recent 2019–2020 fire season, hereafter referred to as the anomalous fire season. Specifically, we used gray-headed flying fox roost occupancy in the years surrounding the previous fire season to identify impacts of fire on gray-headed flying foxes (Section 3.2). We compared the extent of fires within total and winter foraging habitats between the previous focal and anomalous fire seasons (Section 3.3), and present preliminary evaluations of fire severity in gray-headed flying fox foraging habitats in New South Wales for the anomalous fire season.

3.1. Fire extent between years

Between 2012 and 2020 in the eastern states of Australia, the total burned area of each annual fire season from September to March from near-real time VIIRS data ranged from 2.40 million hectares (Mha) in 2015–2016 to 8.48 Mha in 2012–2013 (Fig. 1a; Table A.2). The area burned in the 2012–2013 fire season was most similar to the 2019–2020 fire season (5% less than 2012–2013) and affected more than twice the area burned in most of the intervening years. We assessed the similarities and differences in the distribution, extent, and impact of these two fire seasons.

During the previous focal fire season, individual bushfires burned much smaller areas and were more numerous than in the anomalous fire season. There were 67,722 individual fires that burned 8.48 Mha (Fig. 1a) mostly in savannahs and open woodlands with low levels of canopy cover (< 20% canopy cover, Fig. 2b). In contrast, the anomalous fire season burned 8.03 Mha but consisted of only 29,148 individual fires, many burning areas that were an order of magnitude larger than the previous focal fire season (Fig. 1). The majority (62.5%) of the burned area in the anomalous fire season was concentrated in 67 mega-fires (Figs. 1, 2c). The burned area calculations presented here reflect data collection at a spatial resolution of 440 m, calculations using coarser resolutions to account for variation in the size of scan pixels lead to much larger estimates of burned areas but show a similar distribution of fire sizes (Tables A.2, A.3, Figs. A.3–A.5).

The impact of fires on forested areas was drastically different between the previous focal fire season and the anomalous fire season. In the previous focal fire season, the vast majority of total burned area was in non-forested areas, whereas in the anomalous fire season, the majority of total burned area occurred in forested areas (Fig. 2d). Even though 1.1 Mha of forest was cleared in eastern Australia between 2012 and 2018 (Fig. A.9), the area of forest burned was still substantially greater in the anomalous fire season. The mega-fires that accounted for the majority of the burned area occurred primarily in large, contiguous forests in New South Wales (Fig. 2c). Fires burned entire forest patches of all sizes, as demonstrated by the reduction in total number of forest patches (Fig. A.10). Fires also effectively fragmented large contiguous forests (> 1,000,000 ha) and left behind moderately sized forest fragments (> 1,000 ha) (Fig. 2e).

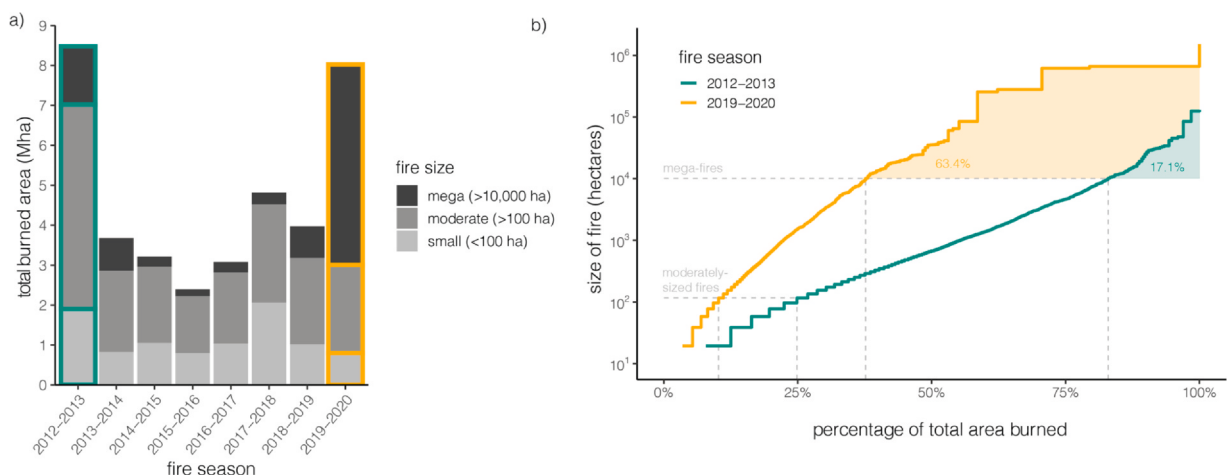


Fig. 1. Total burned area and distribution of fire sizes from 2012 to 2020. (a) Total burned area in eastern Australia between September and March for years from 2012 to 2020. (b) Cumulative burned area by sizes of individual fires for previous focal and anomalous fire seasons. The distribution of fire sizes showed much larger fires in the 2019–2020 anomalous fire season compared to the previous focal fire season of 2012–2013. In anomalous fire season, the majority of burned area (63.4%) was within mega-fires (> 10,000 ha) as denoted by the shaded area.

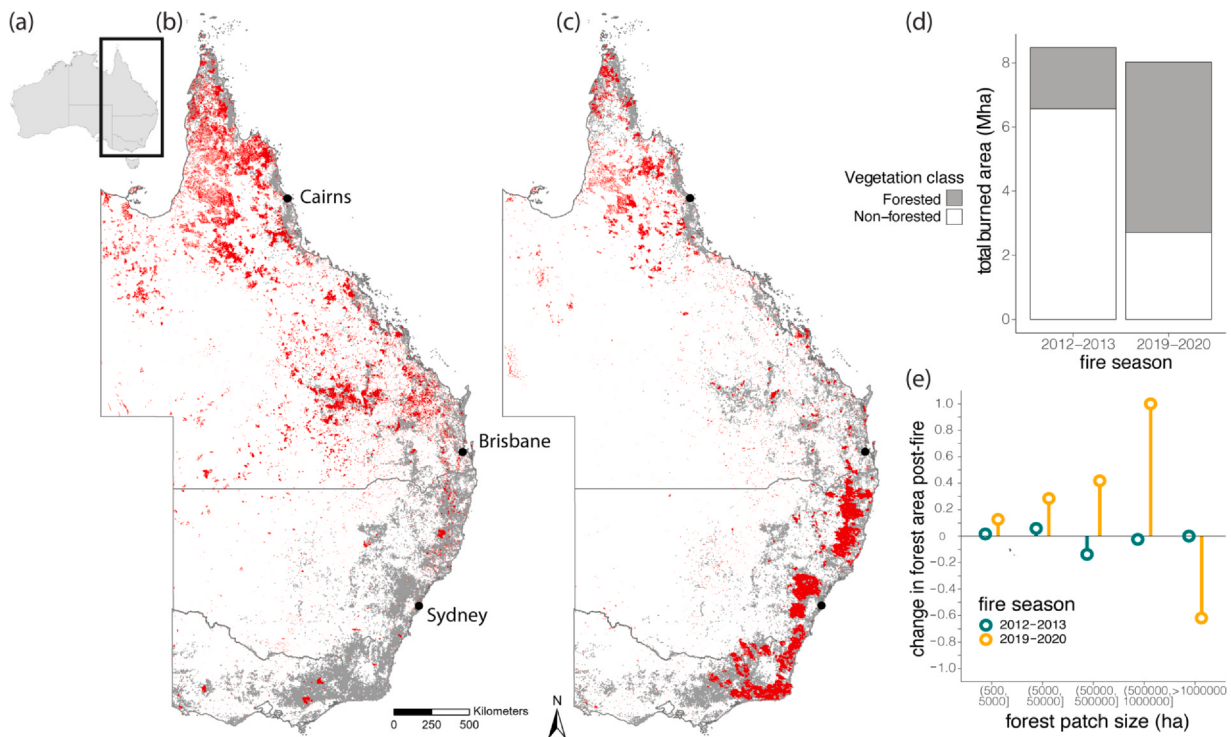


Fig. 2. Extent of forest cover and burned areas in eastern Australia in focal fire seasons (2012–2013 & 2019–2020). (a) The eastern region of Australia, the states of Queensland (QLD), New South Wales (NSW), Australian Capital Territory (within NSW), and Victoria (VIC). Fire extent (red) in the previous focal fire season (b, 2012–2013) and the anomalous fire season (c, 2019–2020) overlaid on forest cover (> 20% canopy cover per pixel shaded in gray) from the respective years. (d) Burned area in forested and non-forested areas in the anomalous and previous focal season. (e) In the anomalous fire season, fire reduced the area of the largest patches of forest, resulting in an increase in the number of moderately sized forest fragments in the short term. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.2. Occupancy of gray-headed flying foxes at roosts and evidence of response to fires in previous focal year (2012–2013)

Based on 1706 observations at 106 satellite roosts, the model that best explained the presence of gray-headed flying foxes included: total unburned area of winter foraging habitat, meteorological season, co-occupation of black flying foxes, and an annual effect (year pre- vs. year post-fire). The best fit logistic regression did not include direct fire metrics (i.e. distance from roost to burned area, total area burned in foraging radius, and foraging habitat burned).

We found that satellite roosts with a greater amount of unburned winter habitat were more likely to be occupied by gray-headed flying foxes at any time of the year (adjusted odds ratio (aOR): 9.89, 95% confidence interval (CI): 1.43, 67.95). Additionally, gray-headed flying foxes were more likely to be observed at roosts during winter (aOR: 1.64, 95% CI: 1.14, 2.37) and spring (aOR: 2.38, 95% CI: 1.62, 3.50) compared with autumn (summer was not significantly different). The presence of gray-headed flying foxes at a roost was also significantly associated with occupancy of black flying foxes (aOR: 70.15, 95% CI: 41.90, 117.0). Finally, gray-headed flying foxes were more likely observed at these roosts in the year following the focal fires compared to the year before (aOR: 1.46, 95% CI: 1.11, 1.93).

3.3. Impacts of focal fire seasons on gray-headed flying fox habitat

We found that fire extent mapped with the remotely sensed thermal data provided more accurate identification of burned gray-headed flying fox habitat over most of their habitat range in the anomalous fire season when compared to the National Indicative Aggregated Fire Extent Dataset (Fig. A.7). This government vector data, used in comparable studies (Ward et al., 2020; Boer et al., 2020), lacks national standardization, is less frequently updated, and is intentionally precautionary on the sized of burned areas (Department of Agriculture Water and the Environment, 2020). We find this government product overestimated fire extent in high crown cover and taller stand eucalypt forests (trees > 10 m and particularly relevant for flying fox habitat). Conversely, the government product more accurately identified fire extent in areas with lower crown cover and vegetation less than 10 m (Fig. A.7) at the southern extent of the flying fox range than did the VIIRS data. Therefore, the VIIRS thermal data would not be ideal to map fire extent in near-real time for all species' habitats, but more accurately and rapidly assessed burned area in most gray-headed flying fox habitats.

Table 2
Summaries of gray-headed flying fox habitats burned in focal fire seasons.

Fire season	Total habitat burned ^a Area (%)	Extent of habitat included in foraging habitat	Burned foraging habitat per roost Mean (range)	Proportion foraging habitat burned per roost Mean (range)	Burned winter foraging habitat per roost Mean (range)	Proportion winter foraging habitat burned per roost Mean (range)
Previous focal fire season 2012–2013	318,484 ha (3.7%)	80.0%	7,950 ha (0–26,854 ha)	3.5% (0–19.86%)	2,795 ha (0–19,671)	4.0% (0–23.1%)
Anomalous fire season 2019–2020	2.8 Mha (33.7%)	87.5%	30,891 ha (0–313,190 ha)	12.2% (0–63.7%)	8,717 ha (0–140,462)	11.1% (0–68.5%)

^a Analysis of habitat in Queensland and New South Wales.

The anomalous fire season burned substantially more gray-headed flying fox habitat across southeastern Queensland and New South Wales when compared to the previous focal fire season (Table 2, Fig. 3, Fig. A.12). The greatest amount of foraging habitat burned at a single roost in the anomalous fire seasons was similar to the total habitat burned across the entire range from the previous focal fire season (Table 2). During the anomalous fire season, 77 of 324 roosts had greater than 20% of their total foraging habitat burned, whereas not a single roost experienced that magnitude of burned foraging habitat during the previous focal fire season. Winter habitat was also greatly impacted in the anomalous fire season (Fig. 3i). At each roost, the percentage of winter foraging habitat burned was highly correlated with the percentage of total habitat burned, but winter habitat covers a much smaller spatial extent throughout the region (Fig. 3c–h), making the scale of these declines particularly important.

A greater proportion of the five critical winter diet species burned in the anomalous fire season (single species maximum: 35.5%, median: 25.4%) compared to the previous focal fire season (single species maximum: 6.1%, median: 4.8%) (Fig. A.13). Even *Melaleuca quinquenervia*, a winter resource that is found in fire refugia (swamps, floodplains, and riparian zones), experienced burning across 13.8% of its distribution in the anomalous fire season, compared to 4.1% in the previous focal fire season (Fig. A.13).

In New South Wales, where fire severity has been systematically assessed for the anomalous fire season, larger areas of winter foraging habitat were burned by high/extreme severity fires than low/moderate severity fires (Table A.6). We find that of the winter foraging habitat that burned, 35.2% burned in low and moderate severity fires that mostly impacted understory vegetation with minimal scorch of the canopy, compared to the 41.7% of winter foraging habitat burned that was in high or extreme severity fires resulting in full canopy scorch and partial or full canopy consumption. Similar proportions of the total foraging areas burned were burned by low or moderate severity fires (36.7%) and high or extremely severe fires (41.0%) during the anomalous season. Rainforests within the foraging range of occupied roosts were also extensively burnt by the anomalous fires season (Table A.7). However, the rainforest habitats that burned were mostly within low/moderate severity fires (36.4%) rather than high/extreme severity fires (19.5%).

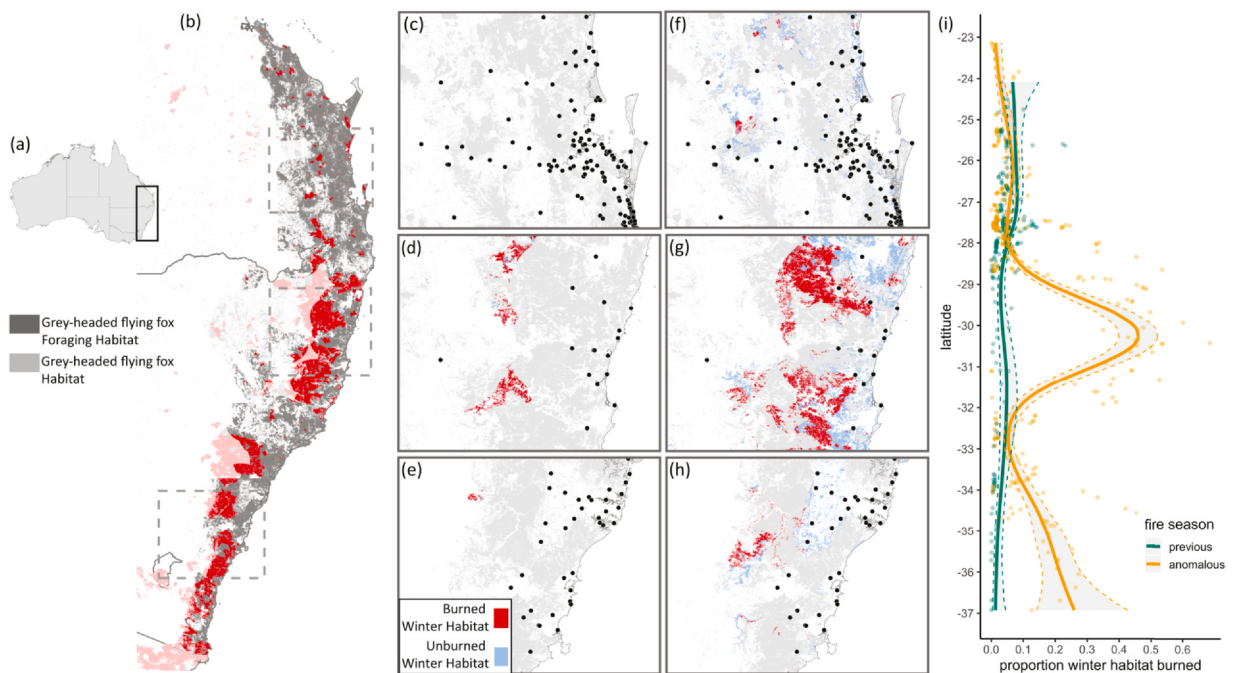


Fig. 3. Extent of 2019–2020 anomalous fire season in flying fox habitats (a) Area of interest, gray-headed flying fox habitat in Queensland and New South Wales is indicated on the map of Australia. (b) Burned flying fox habitat within foraging radii indicated in dark red for roosts that were recently occupied in 2019–2020. Light red indicates burned habitat outside the 50 km foraging range of roosts. Areas of interest in boxes are shown in winter habitat in panels c–h. Panels (show roosts in black points and all available winter habitat outside (c–e) and inside (f–h) roost foraging radii. Light gray highlights total foraging habitat, red indicates burned winter habitat, and blue indicates unburned winter habitat. (i) The proportion of burned winter habitat within foraging radii for each roost is shown in individual points and a GAM fit to year and latitude explains 48.1% of the variation in the proportion of winter habitat burned. Smoothing terms for latitude for each year were significant (2012: 5.931, $p < 0.001$; 2019: 8.505, $p < 0.001$). The proportion of winter habitat burned was overall significantly higher in 2019 compared to 2012 (est: 0.398, $p < 0.001$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

The anomalous 2019–2020 bushfires were extensive in their size, impact on forest ecosystems, and reduction of resources within gray-headed flying fox habitats in eastern Australia. Our analyses highlight the impacts of these fires on the already threatened gray-headed flying foxes, including drastic reductions in immediately available foraging resources, particularly key winter resources. We demonstrate that VIIRS remotely sensed data is accurate for mapping fire extent in most gray-headed flying fox habitats and provides a rapid measurement for monitoring and conservation planning. Monitoring gray-headed flying fox population responses, quantifying the impacts of fire severity on key resources, and understanding the longer-term resilience of vegetation to these extreme fires will be essential next steps for designing management and mitigation strategies in the coming years as fire regimes shift with global climate change.

Our analysis identified 67 mega-fires across eastern Australia during the anomalous fire season, with the largest fire burning almost 1.6 Mha. Mega-fires are associated with higher intensity burns, longer recovery periods, major alterations of canopy structure, and greater direct and indirect mortality (Stephens et al., 2014). While wildlife can often persist or relocate in smaller fires, larger fires are devastating in the short- and long-term for many species (Berry et al., 2015; Stephens et al., 2014). The high number of mega-fires in 2019–2020 and the concentration of these fires in forested areas will have long-term consequences for these ecosystems.

The anomalous sizes and locations of fires in 2019–2020 affected extensive areas of key forest habitat, supporting other work done with government spatial products (Boer et al., 2020). Diet species of gray-headed flying foxes are adapted to current fire regimes. The majority are facultative resprouters that resprout from epicormic buds or lignotubers quickly after experiencing fire (Bennett et al., 2016; Vivian et al., 2008) (Table B.1). Immediate regeneration occurs when fire intensity is low and the epicormic tissue in the bark is not scorched (Gill, 1997; Denham et al., 2016), which is reflective of some areas in the anomalous fire season. Assessments by New South Wales suggested many areas would have limited capacity to support wildlife immediately following fires (State of New South Wales and Department of Planning Industry and Environment, 2020). Six months following canopy scorch (high/extreme severity fires), rapid surveys found some regeneration but also noted tree mortality (Eco Logical Australia, 2020). Furthermore, the extensive drought (Fig. A.8) and extreme heat conditions preceding the fires (Nolan et al., 2020) may reduce or delay the full flowering potential of gray-headed flying fox diet species in the short-term (Law et al., 2000). More research on how these resource species respond to fire and how responses vary with post-fire climate conditions and fire severity is required.

We examined determinants of gray-headed flying foxes roost occupation in Queensland in the years surrounding the previous focal fire season. Although we found higher rates of occupation in the year following the fire, we don't believe this is a response to fire as no direct fire metrics (amount of forest burned, distance to fires, time since fires) were predictive of this increase in occupation. The increase in the year postfire could be a northward movement of gray-headed flying foxes into Queensland tracking resources unrelated to the fires. The highly mobile nature of this species (Welbergen et al., 2020) makes understanding local responses to fires particularly difficult. We were not able to measure immediate disturbance of roosts or changes in foraging activity, which have been previously described as fire responses in some species of bats (see Section 1). However, we were able to show that unburned winter habitat, rather than total foraging habitat, is a key predictor of occupation, which highlights these specific resources as important indicators of roost suitability. This is supported by research showing that winters associated with low volumes of resources lead to high adult mortality and low reproduction (Hall et al., 1991). We also found black flying foxes were a useful predictor of occupation of roosts in Queensland. Black flying foxes and gray-headed flying foxes have similar diets (Palmer, 1997), so correlation in occupation is expected for this region where their ranges overlap. However, they are also competitors for these resources and we would expect the presence of black flying foxes to decrease the abundance of gray-headed flying foxes at roosts, rather than affecting presence, though an explicit evaluation of this hypothesis is outside the scope of the study.

We highlight the significantly larger amount of gray-headed flying foxes' total and winter foraging habitats that burned during the anomalous fire season compared to the previous focal fire season. Gray-headed flying foxes could theoretically respond to large proportions of forage habitat burning by migrating to unaffected (or less affected) roosts. However, our analysis of forest loss demonstrates that 264,695 ha of gray-headed flying fox habitat was lost between 2012 and 2018 due to deforestation (Table A.5). Roosts that were largely unaffected by fire are concentrated in Queensland and are surrounded by habitat limited in extent due to historical forest loss and overlap with black flying foxes. There are alternative roosts in these areas that are located urban environments and unaffected by bushfires, but these come with costs (Parry-Jones et al., 2016). Urban areas contain a variety of mostly anthropogenic food resources that are more consistently available but have different nutritional qualities than native resources. The predictability of these resources supports prolonged roost occupation near humans (Paez et al., 2017) and can increase human-flying fox conflict. Australian flying foxes carry and transmit Lyssavirus and Hendra virus. Spillover into humans and other animal species is more likely in urban settings (Plowright et al., 2011). Limited options for high-quality alternative habitats following the anomalous bushfire season create a precarious position for gray-headed flying foxes' recovery from these extreme events.

To fully understand gray-headed flying fox responses to fires, the responses of both roosts and resources to fire severity need to be included in future work. Fire severity impacts tree mortality (Vivian et al., 2008) and the interval between high severity fires influences long term survival of tree species and subsequent vegetation composition (Collins, 2020). We showed a range of fire severities within foraging habitats during the anomalous fire season, but were limited to data from New South Wales and only during the 2019–2020 fires. Remote sensing methods for quantifying loss of biomass have been developed and could be

used to quantify fire severity in future studies (Keeley, 2009; Escuin et al., 2008). The flying fox monitoring program provides a unique dataset to examine impacts on roost occupation and count. Studies examining the foraging activity and movement of gray-headed flying foxes could provide more detailed data towards understanding population-level responses to fires.

Previous studies have proposed preserving and restoring critical resources to draw flying foxes out of human settlements to reduce risk of viral transmission (Plowright et al., 2015). Our results suggest the areas of unburned winter habitat near heavily impacted roosts (blue, Fig. 3c–h) should be immediately protected from land clearing, as these are now lifelines for these roosts. Long-term efforts to conserve flying foxes should focus on restoring native forests by increasing overall area while limiting negative edge effects of forest fragmentation by joining existing patches (Bradshaw, 2012; Haddad et al., 2015; Ries et al., 2004). Monitoring the timing and intensity of resource flowering in response to disturbance (i.e. drought, fire, temperature extremes) and impacts on nomadic flying fox movements and roost colonization will be essential for informing conservation efforts. Strategic restoration of native forests can also help mitigate negative impacts of changing fire regimes on a diversity of native species. Replanting efforts can increase habitat extent and help support the many species dependent on eucalypts for food, refuge, and breeding sites (Bennett, 2016) as bushfires are expected to become more frequent under climate change.

Australia's recent large bushfires affected eucalypt forest communities that are resilient to high severity wildfire (Collins, 2020), but long-term persistence of these ecosystems is uncertain if extreme bushfires become more frequent. In southeastern dry eucalypt forests, vegetation burned by high severity fires is more likely to experience high severity fires in subsequent years (Barker and Price, 2018). This positive feedback of repeated burning with high severity fires has also been observed in North America (Van Wagtendonk et al., 2012; Harris and Taylor, 2017), and is thought to be driven by rapid and dense plant growth after high severity fires that result in high fuel loads. Frequent, severe fires can push ecosystems beyond recovery and to alternative states, as observed in shifts from tree to shrub in Australian alpine ecosystems (Camac et al., 2017). Additionally, it is expected that wildfire will encroach on less fire-resilient vegetation communities as increases in extreme drought dry fuels below critical thresholds within fire refugia (Collins et al., 2019). Habitats containing *Melaleuca quinquenervia*, a species typically found in fire refugia, burned in far greater extents in the anomalous fire season compared to the previous focal fire season (Fig. A.13). We found that 40% of rainforests habitats within foraging ranges of roosts in New South Wales were burned, although mostly by low and moderate severity fires (Table A.7). Burning in fire refugia is supported by rapid surveys (Eco Logical Australia, 2020), but more fine-scale evaluation is required and beyond the scope of this study. Postfire climate can promote recovery or facilitate additional fires that might push these systems beyond resilience (Adams, 2013). Empirical evidence from the US also demonstrates that, with climate change, postfire weather conditions show reduced capacity for forest recovery (Stevens-Rumann and Morgan, 2019).

5. Conclusion

Using remotely sensed active fire data, we accurately quantified burned areas in the anomalous 2019–2020 bushfire season in eastern Australia and assessed impacts of fire extent and fire severity on flying fox habitats. This study highlights the fire's substantial impact on foraging habitat, particularly winter resources, of gray-headed flying foxes and identifies the most affected roosts, which will be important to monitor in the coming years. Understanding how vegetation and gray-headed flying foxes respond to extreme fire events will improve our ability to help build resilience into these systems as climate change alters the frequency and severity of fires in Australia and other ecosystems globally.

Author Contributions

N.B. conceived the research. K.B., C.L.F., and N.B. designed the research. K.B. analyzed fire extent. C.L.F. analyzed forest cover and impact of fire. K.B. and C.L.F. analyzed impact of fire on gray-headed flying fox habitat. K.B. and C.L.F. wrote the first draft of the manuscript; all authors contributed to revising the manuscript; all authors approved of the final manuscript.

Funding

This work was funded by the U.S. National Science Foundation (grant no. CNH-L: 1716698 and GRFP: DGE1255832), the US Defense Advanced Research Projects Agency PREEMPT program (Cooperative Agreement #D18AC00031), and the Huck Institutes of the Life Sciences at The Pennsylvania State University, USA. The content of the information does not necessarily reflect the position or the policy of the U.S. government, and no official endorsement should be inferred.

Data availability statement

Data analyzed in this study are available in public repositories (see Sections 2.1, 2.2, and 2.3 and readme.md file on GitHub) and the scripts to analyze and visualize data are available on GitHub (https://github.com/bhartilab/aus_fires_2020).

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.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2021.e01566](https://doi.org/10.1016/j.gecco.2021.e01566).

References

- Adams, M.A., 2013. Mega-fires, tipping points and ecosystem services: managing forests and woodlands in an uncertain future. *For. Ecol. Manag.* 294, 250–261.
- Barbero, R., Abatzoglou, J.T., Larkin, N.K., Kolden, C.A., Stocks, B., 2015. Climate change presents increased potential for very large fires in the contiguous United States. *Int. J. Wildland Fire* 24, 892–899.
- Barker, J.W., Price, O.F., 2018. Positive severity feedback between consecutive fires in dry eucalypt forests of southern Australia. *Ecosphere* 9, e02110.
- Bennett, A.F., 2016. Eucalypts, wildlife and nature conservation: from individual trees to landscape patterns. *Proc. R. Soc. Vic.* 128, 71–86.
- Bennett, L.T., Bruce, M.J., Machunter, J., Kohout, M., Tanase, M.A., Aponte, C., 2016. Mortality and recruitment of fire-tolerant eucalypts as influenced by wildfire severity and recent prescribed fire. *For. Ecol. Manag.* 380, 107–117.
- Berry, L.E., Lindenmayer, D.B., Driscoll, D.A., 2015. Large unburnt areas, not small unburnt patches, are needed to conserve avian diversity in fire-prone landscapes. *J. Appl. Ecol.* 52, 486–495.
- Blakey, R.V., Webb, E.B., Kesler, D.C., Siegel, R.B., Corcoran, D., Johnson, M., 2019. Bats in a changing landscape: linking occupancy and traits of a diverse montane bat community to fire regime. *Ecol. Evol.* 9, 5324–5337.
- Blanchi, R., Lucas, C., Leonard, J., Finkel, K., 2010. Meteorological conditions and wildfire-related house loss in Australia. *Int. J. Wildland Fire* 19, 914–926.
- Boer, M.M., Resco De Dios, V., Bradstock, R.A., 2020. Unprecedented burn area of Australian mega forest fires. *Nat. Clim. Chang.* 10, 171–172.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.-S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* 24, 127–135.
- Bowd, E.J., Lindenmayer, D.B., Banks, S.C., Blair, D.P., 2018. Logging and fire regimes alter plant communities. *Ecol. Appl.* 28, 826–841.
- Bowman, D.M., Balch, J.K., Artaxo, P., Bond, W.J., Carlson, J.M., Cochrane, M.A., D'Antonio, C.M., Defries, R.S., Doyle, J.C., Harrison, S.P., 2009. Fire in the Earth system. *Science* 324, 481–484.
- Bowman, D.M., Murphy, B.P., Neyland, D.L., Williamson, G.J., Prior, L.D., 2014. Abrupt fire regime change may cause landscape-wide loss of mature obligate seeder forests. *Glob. Chang. Biol.* 20, 1008–1015.
- Bradshaw, C.J., 2012. Little left to lose: deforestation and forest degradation in Australia since European colonization. *J. Plant Ecol.* 5, 109–120.
- Bradstock, R., Davies, I., Price, O., Cary, G., 2008. Effects of climate change on bushfire threats to biodiversity, ecosystem processes and people in the Sydney region. Final report to the New South Wales department of environment and climate change: climate change impacts and adaptation research project, 50831, 65.
- Brooks, M.E., Kristensen, K., Benthem, K.J.V., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R. J.* 9, 378–400.
- Buchalski, M.R., Fontaine, J.B., Heady III, P.A., Hayes, J.P., Frick, W.F., 2013. Bat response to differing fire severity in mixed-conifer forest California, USA. *PLoS One* 8, e57884.
- Burns, L.K.L., Loeb, S.C., Bridges, W.C., 2019. Effects of fire and its severity on occupancy of bats in mixed pine-oak forests. *For. Ecol. Manag.* 446, 151–163.
- Cai, W., Cowan, T., Raupach, M., 2009. Positive Indian Ocean dipole events precondition southeast Australia bushfires. *Geophys. Res. Lett.* 36, L19710.
- Camac, J.S., Williams, R.J., Wahren, C.H., Hoffmann, A.A., Veski, P.A., 2017. Climatic warming strengthens a positive feedback between alpine shrubs and fire. *Glob. Chang. Biol.* 23, 3249–3258.
- Chia, E.K., Bassett, M., Leonard, S.W.J., Holland, G.J., Ritchie, E.G., Clarke, M.F., Bennett, A.F., 2016. Effects of the fire regime on mammal occurrence after wildfire: site effects vs landscape context in fire-prone forests. *For. Ecol. Manag.* 363, 130–139.
- Clarke, P.J., Lawes, M.J., Murphy, B.P., Russell-Smith, J., Nano, C.E., Bradstock, R., Enright, N.J., Fontaine, J.B., Gosper, C.R., Radford, I., 2015. A synthesis of postfire recovery traits of woody plants in Australian ecosystems. *Sci. Total Environ.* 534, 31–42.
- Collins, L., 2020. Eucalypt forests dominated by epicormic resprouters are resilient to repeated canopy fires. *J. Ecol.* 108, 310–324.
- Collins, L., Bennett, A.F., Leonard, S.W., Penman, T.D., 2019. Wildfire refugia in forests: severe fire weather and drought mute the influence of topography and fuel age. *Glob. Chang. Biol.* 25, 3829–3843.
- Department of Agriculture Water and the Environment, 2020. National Indicative Aggregated Fire Extent Dataset [Online]. <http://www.environment.gov.au/fed/catalog/search/resource/details.page?uuid=%7B9ACDCB09-0364-4FE8-9459-2A56C792C743%7D>. (Accessed 01/09/2020).
- Cremer, K.W., Cromer, R.N., Florence, R.G., 1978. Stand establishment. In: Hillis, W.E., Brown, A.G. (Eds.), *Eucalypts for Wood Production*. CSIRO, Canberra.
- Denham, A.J., Vincent, B.E., Clarke, P.J., Auld, T.D., 2016. Responses of tree species to a severe fire indicate major structural change to Eucalyptus–Callitris forests. *Plant Ecol.* 217, 617–629.
- Department of Agriculture Water and the Environment, 2020. National Indicative Aggregated Fire Extent Dataset Metadata [Online]. <http://www.environment.gov.au/fed/catalog/search/resource/details.page?uuid=%7B9ACDCB09-0364-4FE8-9459-2A56C792C743%7D>. (Accessed 10/01/2020).
- Department of Planning Industry and Environment, 2020. NSW Fire and the Environment 2019–20 Summary: biodiversity and landscape data and analyses to understand the effects of the fire events. State of NSW and Department of Planning, Industry and Environment.
- Dickinson, M.B., Lacki, M.J., Cox, D.R., 2009. Fire and the endangered Indiana bat. In: Hutchinson, Todd F. (Ed.), *Proceedings of the 3rd Fire in Eastern Oak Forests Conference*; 2008 May 20–22; Carbondale, IL. General Technical Report NRS-P-46. Newtown Square, PA: US Department of Agriculture, Forest Service, Northern Research Station, pp. 51–75.
- Dickman, C., Fleming, M., 2002. Pest, or passenger pigeon? The New South Wales Scientific Committee's assessment of the status of the grey-headed flying-fox. *Managing the grey-headed flying-fox as a threatened species in NSW*. Mosman, NSW: Royal Zoological Society of NSW, 20–28.
- Doty, A.C., Stawski, C., Law, B.S., Geiser, F., 2016. Post-wildfire physiological ecology of an Australian microbat. *J. Comp. Physiol. B* 186, 937–946.
- Eby, P., 1995. Biology and Management of *Pteropus* in New South Wales. Species Report. NSW National Parks and Wildlife Service, Hurstville.
- Eby, P., 1991a. "Finger-winged night workers?": managing forests to conserve the role of Grey-headed Flying Foxes as pollinators and seed dispersers. In: Lunney, D. (Ed.), *Conservation of Australia's Forest Fauna*. Royal Zoological Society of New South Wales.
- Eby, P., 1991b. Seasonal movements of grey-headed flying-foxes, *Pteropus poliocephalus* (Chiroptera: Pteropodidae), from two maternity camps in northern New South Wales. *Wildl. Res.* 18, 547–559.
- Eby, P., 1998. An analysis of diet specialization in frugivorous *Pteropus poliocephalus* (Megachiroptera) in Australian subtropical rainforest. *Aust. J. Ecol.* 23, 443–456.
- Eby, P., Law, B., 2008. Ranking the feeding habitat of grey-headed flying foxes for conservation management. Department of Environment and Climate Change (NSW), Sydney.
- Eco Logical Australia, 2020. Northeast NSW Post Fire Rapid Fauna Surveys. Prepared for World Wide Fund for Nature-Australia.

- Escuin, S., Navarro, R., Fernández, P., 2008. Fire severity assessment by using NBR (Normalized Burn Ratio) and NDVI (Normalized Difference Vegetation Index) derived from LANDSAT TM/ETM images. *Int. J. Remote Sens.* 29, 1053–1073.
- Fairman, T.A., Nitschke, C.R., Bennett, L.T., 2016. Too much, too soon? A review of the effects of increasing wildfire frequency on tree mortality and regeneration in temperate eucalypt forests. *Int. J. Wildland Fire* 25, 831–848.
- Fasullo, J., Otto-Bliesner, B., Stevenson, S., 2018. ENSO's changing influence on temperature, precipitation, and wildfire in a warming climate. *Geophys. Res. Lett.* 45, 9216–9225.
- Fidelino, J.S., Duya, M.R.M., Duya, M.V., Ong, P.S., 2020. Fruit bat diversity patterns for assessing restoration success in reforestation areas in the Philippines. *Acta Oecol.* 108, 103637.
- Flying Fox Monitoring Program, 2020. Flying Fox Monitoring Data. 1.0 ed. <https://www.data.qld.gov.au/dataset/flying-fox-monitoring-program>, Queensland Government.
- Friend, G.R., 1993. Impact of fire on small vertebrates in mallee woodlands and heathlands of temperate Australia: a review. *Biol. Conserv.* 65, 99–114.
- Gill, A.M., 2008. Underpinnings of fire management for biodiversity conservation in reserves. Department of Sustainability and Environment: Melbourne.
- Gill, A.M., Stephens, S.L., Cary, G.J., 2013. The worldwide "wildfire" problem. *Ecol. Appl.* 23, 438–454.
- Gill, A.M., 1997. Eucalypts and fires: interdependent or independent. In: *Eucalypt Ecology: Individuals to Ecosystems*, pp. 151–167.
- Gillett, N., Weaver, A., Zwiers, F., Flannigan, M., 2004. Detecting the effect of climate change on Canadian forest fires. *Geophys. Res. Lett.* 31, L18211.
- GMES-GSEG-EOPG-TN-09-0029, 2012. SENTINEL-2 Payload Data Ground Segment (PDGS). Products Definition Document (ESA).
- Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* 1, e1500052.
- Hall, L., Martin, L., O'Brien, G., Kelly, R., Luckhoff, H., 1991. Flying fox populations in crisis in southeast Queensland. In: *Australian Mammal Society 1991 Annual Meeting Abstracts*, 29.
- Hall, L.S., Richards, G., 2000. Flying Foxes: Fruit and Blossom Bats of Australia. UNSW Press.
- Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S., Tyukavina, A., Thau, D., Stehman, S., Goetz, S., Loveland, T., 2013. High-resolution global maps of 21st-century forest cover change. *Science* 342, 850–853.
- Harris, L., Taylor, A.H., 2017. Previous burns and topography limit and reinforce fire severity in a large wildfire. *Ecosphere* 8, e02019.
- Hartig, F., 2020. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R package version 0.3.3.0. <https://CRAN.R-project.org/package=DHARMa>.
- Jenkins, R.K., Racey, P.A., Andriafidison, D., Razafindrakoto, N., Razafimahatratra, E., Rabearivelo, A., Ratsimandresy, Z., Andrianandrasana, R.H., Razafimanahaka, H.J., 2007. Not rare, but threatened: the endemic Madagascar flying fox *Pteropus rufus* in a fragmented landscape. *Oryx* 41, 263–271.
- Jolly, W.M., Cochrane, M.A., Freeborn, P.H., Holden, Z.A., Brown, T.J., Williamson, G.J., Bowman, D.M., 2015. Climate-induced variations in global wildfire danger from 1979 to 2013. *Nat. Commun.* 6, 1–11.
- Jones, G., Jacobs, D.S., Kunz, T.H., Willig, M.R., Racey, P.A., 2009. Carpe noctem: the importance of bats as bioindicators. *Endanger. Species Res.* 8, 93–115.
- Keeley, J.E., 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. *Int. J. Wildland Fire* 18, 116–126.
- King, A.J., Melbourne, B.A., Davies, K.F., Nicholls, A.O., Austin, M.P., Tuff, K.T., Evans, M.J., Hardy, C.M., Cunningham, S.A., 2018. Spatial and temporal variability of fragmentation effects in a long term, eucalypt forest fragmentation experiment. *Landsc. Ecol.* 33, 609–623.
- Krawchuk, M.A., Moritz, M.A., Parisien, M.-A., Van Dorn, J., Hayhoe, K., 2009. Global pyrogeography: the current and future distribution of wildfire. *PLoS One* 4, e5102.
- Lacki, M.J., Cox, D.R., Dodd, L.E., Dickinson, M.B., 2009. Response of Northern Bats (*Myotis septentrionalis*) to prescribed fires in Eastern Kentucky Forests. *J. Mammal.* 90, 1165–1175.
- Lam, S.S., Waugh, C., Peng, W., Sonne, C., 2020. Wildfire puts koalas at risk of extinction. *Science* 367, 750.
- Lance Firms NRT VIIRS 375 m Active Fire product VNP14IMG NASA's Earth Science and Data Information System 2020. doi: 10.5067/FIRMS/VIIRS/VNP14IMG. NRT.001:NASA.
- Laurance, W.F., Camargo, J.L., Fearnside, P.M., Lovejoy, T.E., Williamson, G.B., Mesquita, R.C., Meyer, C.F., Bobrowiec, P.E., Laurance, S.G., 2018. An Amazonian rainforest and its fragments as a laboratory of global change. *Biol. Rev.* 93, 223–247.
- Law, B., Chidel, M., 2008. Quantifying the canopy nectar resource and the impact of logging and climate in spotted gum *Corymbia maculata* forests. *Austral Ecol.* 33, 999–1014.
- Law, B., Mackowski, C., Schoer, L., Tweedie, T., 2000. Flowering phenology of myrtaceous trees and their relation to climatic, environmental and disturbance variables in northern New South Wales. *Austral Ecol.* 25, 160–178.
- Law, B., Kathuria, A., Chidel, M., Brassil, T., 2019. Long-term effects of repeated fuel-reduction burning and logging on bats in south-eastern Australia. *Austral Ecol.* 44, 1013–1024.
- Law, B.S., Chidel, M., 2009. Canopy nectar production and the impact of logging and climate in Grey Ironbark *Eucalyptus paniculata* (Smith) forests. *Pac. Conserv. Biol.* 15, 287–303.
- Lawes, M.J., Murphy, B.P., Fisher, A., Woinarski, J.C., Edwards, A.C., Russell-Smith, J., 2015. Small mammals decline with increasing fire extent in northern Australia: evidence from long-term monitoring in Kakadu National Park. *Int. J. Wildland Fire* 24, 712–722.
- Leahy, L., Legge, S.M., Tuft, K., McGregor, H.W., Barmuta, L.A., Jones, M.E., Johnson, C.N., 2016. Amplified predation after fire suppresses rodent populations in Australia's tropical savannas. *Wildl. Res.* 42, 705–716.
- Lindenmayer, D.B., Blanchard, W., Mcburney, L., Blair, D., Banks, S.C., Driscoll, D.A., Smith, A.L., Gill, A., 2014. Complex responses of birds to landscape-level fire extent, fire severity and environmental drivers. *Divers. Distrib.* 20, 467–477.
- Lindenmayer, D.B., Kooyman, R.M., Taylor, C., Ward, M., Watson, J.E.M., 2020. Recent Australian wildfires made worse by logging and associated forest management. *Nat. Ecol. Evol.* 4, 898–900.
- Liu, J.C., Pereira, G., Uhl, S.A., Bravo, M.A., Bell, M.L., 2015. A systematic review of the physical health impacts from non-occupational exposure to wildfire smoke. *Environ. Res.* 136, 120–132.
- McConkey, K.R., Drake, D.R., 2006. Flying foxes cease to function as seed dispersers long before they become rare. *Ecology* 87, 271–276.
- McIlwee, A., Martin, L., 2002. On the intrinsic capacity for increase of Australian flying-foxes (*Pteropus* spp., Megachiroptera). *Aust. Zool.* 32, 76–100.
- Montreal Process Implementation Group For Australia And National Forest Inventory Steering Committee, 2018. Australia's State of the Forests Report 2018. Commonwealth of Australia, Canberra, Australia.
- National Flying Fox Monitoring Program, 2020. National Flying-Fox Monitoring Viewer [Online]. <http://www.environment.gov.au/webgis-framework/apps/ffc-wide/ffc-wide.jsf>. (Accessed 15 February 2020).
- New South Wales Department of Planning Industry and Environment, 2020. Fire Extent and Severity Mapping (FESM). In: D. R. S. R. M. T. (Ed.), NSW Rural Fire Service. <https://data.gov.au/dataset/ds-ns-w-c28a6aa8-a7ce-4181-8ed1-fd221dfcfc8/details?q=#:~:text=Fire%20severity%20is%20a%20metric,of%20biomass%20caused%20by%20fire&text=The%20statewide%20severity%20map%20has,different%20fires%20across%20the%20landscape>.
- Nolan, R.H., Boer, M.M., Collins, L., Resco De Dios, V., Clarke, H., Jenkins, M., Kenny, B., Bradstock, R.A., 2020. Causes and consequences of eastern Australia's 2019–20 season of mega-fires. *Glob. Chang. Biol.* 26, 1039–1041.
- Oliva, P., Schroeder, W., 2015. Assessment of VIIRS 375 m active fire detection product for direct burned area mapping. *Remote Sens. Environ.* 160, 144–155.
- Oliveras, I., Bell, T., 2008. An analysis of the Australian literature on prescribed burning. *J. For.* 106, 31–37.
- Paez, D.J., Giles, J., McCallum, H., Field, H., Jordan, D., Peel, A.J., Plowright, R.K., 2017. Conditions affecting the timing and magnitude of Hendra virus shedding across pteropod bat populations in Australia. *Epidemiol. Infect.* 145, 3143–3153.
- Palmer, C., 1997. Ecology of the Black Flying Fox, *Pteropus alecto*, in the Seasonal Tropics of the Northern Territory: Resource Tracking in a Landscape Mosaic and Role in Seed Dispersal (Masters Degree). Northern Territory University.

- Parry-Jones, K., Augee, M., 1991. The diet of Flying-foxes in the Sydney and Gosford areas of New South Wales, based on sighting reports 1986–1990. *Aust. Zool.* 27, 49–54.
- Parry-Jones, K., Webster, K.N., Divljan, A., 2016. Baseline levels of faecal glucocorticoid metabolites and indications of chronic stress in the vulnerable grey-headed flying-fox, *Pteropus poliocephalus*. *Aust. Mammal.* 38, 195–203.
- Pastro, L.A., Dickman, C.R., Letnic, M., 2011. Burning for biodiversity or burning biodiversity? Prescribed burn vs. wildfire impacts on plants, lizards, and mammals. *Ecol. Appl.* 21, 3238–3253.
- Pausas, J.G., Keeley, J.E., 2009. A burning story: the role of fire in the history of life. *Bioscience* 59, 593–601.
- Perry, R.W., 2011. A review of fire effects on bats and bat habitat in the eastern oaks region. In: Dey, D.C.S., Michael, C., Clark, S.T.A.C.Y.L., Schweitzer, C.A.L.L.E.J. (Eds.), *Proceedings of the 4th Fire in Eastern Oak Forests Conference*, Springfield, MO. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA, pp. 170–191.
- Planet Team, 2020. Sentinel-2 (ESA) image courtesy of Planet Application Program Interface: In Space for Life on Earth. San Francisco, CA.
- Plowright, R.K., Foley, P., Field, H.E., Dobson, A.P., Foley, J.E., Eby, P., Daszak, P., 2011. Urban habituation, ecological connectivity and epidemic dampening: the emergence of Hendra virus from flying foxes *Pteropus* spp.). *Proc. R. Soc. B Biol. Sci.* 278, 3703–3712.
- Plowright, R.K., Eby, P., Hudson, P.J., Smith, I.L., Westcott, D., Bryden, W.L., Middleton, D., Reid, P.A., Mcfarlane, R.A., Martin, G., Tabor, G.M., Skerratt, L.F., Anderson, D.L., Cramer, G., Quammen, D., Jordan, D., Freeman, P., Wang, L.-F., Epstein, J.H., Marsh, G.A., Kung, N.Y., Mccallum, H., 2015. Ecological dynamics of emerging bat virus spillover. *Proc. R. Soc. B Biol. Sci.* 282, 20142124.
- R Core Team, 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ries, L., Fletcher JR, R.J., Battin, J., Sisk, T.D., 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annu. Rev. Ecol. Evol. Syst.* 35, 491–522.
- Roberts, B.J., Catterall, C.P., Eby, P., Kanowski, J., 2012. Long-distance and frequent movements of the flying-fox *Pteropus poliocephalus*: implications for management. *PLoS One* 7, e42532.
- Schroeder, W., Oliva, P., Giglio, L., Csiszar, I.A., 2014. The New VIIRS 375 m active fire detection data product: algorithm description and initial assessment. *Remote Sens. Environ.* 143, 85–96.
- State Government of NSW & Department of Planning Industry and Environment, 2008. Grey-headed Flying-fox Foraging Habitat. In: S. A. E. E. D. (Ed.), *PORTAL*. <https://data.nsw.gov.au/data/dataset/grey-headed-flying-fox-foraging-habitat2f40a>.
- State of New South Wales & Department of Planning Industry and Environment, 2020. NSW Fire and the Environment 2019–20 Summary: biodiversity and landscape data and analyses to understand the effects of the fire events. Environment, Energy and Science Department of Planning, Industry and Environment, Sydney, NSW, Australia. <https://data.nsw.gov.au/data/dataset/grey-headed-flying-fox-foraging-habitat2f40a>.
- Steel, Z.L., Campos, B., Frick, W.F., Burnett, R., Safford, H.D., 2019. The effects of wildfire severity and pyrodiversity on bat occupancy and diversity in fire-suppressed forests. *Sci. Rep.* 9, 16300.
- Stephens, S.L., Burrows, N., Buyantuyev, A., Gray, R.W., Keane, R.E., Kubian, R., Liu, S., Seijo, F., Shu, L., Tolhurst, K.G., 2014. Temperate and boreal forest mega-fires: characteristics and challenges. *Front. Ecol. Environ.* 12, 115–122.
- Stevens-Rumann, C.S., Morgan, P., 2019. Tree regeneration following wildfires in the western US: a review. *Fire Ecol.* 15, 15.
- Sutherland, E.F., Dickman, C.R., 1999. Mechanisms of recovery after fire by rodents in the Australian environment: a review. *Wildl. Res.* 26, 405–419.
- Threatened Species Scientific Committee, 2001. *Pteropus poliocephalus* (Grey-headed Flying-fox): Advice to the Minister for the Environment and Heritage from the Threatened Species Scientific Committee (TSSC) on Amendments to the list of Threatened Species under the Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act). Australian Government.
- Tidemann, C.R., Nelson, J.E., 2011. Life expectancy, causes of death and movements of the grey-headed flying-fox (*Pteropus poliocephalus*) inferred from banding. *Acta Chiropterol.* 13, 419–429.
- Tidemann, C.R., Vardon, M.J., Loughland, R.A., Brocklehurst, P.J., 1999. Dry season camps of flying-foxes (*Pteropus* spp.) in Kakadu World Heritage Area, north Australia. *J. Zool.* 247, 155–163.
- Van Oldenborgh, G.J., Kriksen, F., Lewis, S., Leach, N.J., Lehner, F., Saunders, K.R., Van Weele, M., Hausteine, K., Li, S., Wallom, D., Sparrow, S., Arrighi, J., Singh, R.P., Van Aalst, M.K., Philip, S.Y., Vautard, R., Otto, F.E.L., 2020. Attribution of the Australian bushfire risk to anthropogenic climate change. *Nat. Hazards Earth Syst. Sci. Discuss. (In Review)*.
- Van Wagtenonk, J.W., Van Wagtenonk, K.A., Thode, A.E., 2012. Factors associated with the severity of intersecting fires in Yosemite National Park, California, USA. *Fire Ecol.* 8, 11–31.
- Vardon, M.J., Brocklehurst, P.S., Woinarski, J.C., Cunningham, R.B., Donnelly, C.F., Tidemann, C.R., 2001. Seasonal habitat use by flying-foxes, *Pteropus alecto* and *P. scapulatus* (Megachiroptera), in monsoonal Australia. *J. Zool.* 253, 523–535.
- Vivian, L.M., Cary, G.J., Bradstock, R.A., Gill, A.M., 2008. Influence of fire severity on the regeneration, recruitment and distribution of eucalypts in the Cotter River Catchment, Australian Capital Territory. *Austral Ecol.* 33, 55–67.
- Ward, M., Tulloch, A.I.T., Radford, J.Q., Williams, B.A., Reside, A.E., Macdonald, S.L., Mayfield, H.J., Maron, M., Possingham, H.P., Vine, S.J., O'connor, J.L., Massingham, E.J., Greenville, A.C., Woinarski, J.C.Z., Garnett, S.T., Lintermans, M., Scheele, B.C., Carwardine, J., Nimmo, D.G., Lindenmayer, D.B., Kooyman, R.M., Simmonds, J.S., Sonter, L.J., Watson, J.E.M., 2020. Impact of 2019–2020 mega-fires on Australian fauna habitat. *Nat. Ecol. Evol.* 4, 1321–1326.
- Welbergen, J.A., Meade, J., Field, H.E., Edson, D., McMichael, L., Shoo, L.P., Praszczalek, J., Smith, C., Martin, J.M., 2020. Extreme mobility of the world's largest flying mammals creates key challenges for management and conservation. *BMC Biol.* 18, 101.
- Westcott, D.A., Heersink, D.K., Mckeown, A., Caley, P., 2015. Status and Trends of Australia's EPBC-Listed Flying-Foxes. CSIRO, Australia.
- Westcott, D.A., Mckeown, A., Murphy, H.T., Fletcher, C.S., 2011. A monitoring method for the grey-headed flying-fox, *Pteropus poliocephalus*. CSIRO published Guidelines.
- Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western US forest wildfire activity. *Science* 313, 940–943.
- Williams, K., Ford, A., Rosauer, D., De Silva, N., Mittermeier, R., Bruce, C., Larsen, F., Margules, C., 2011. Forests of East Australia: the 35th biodiversity hotspot. In: Zachos, F., Habel, J.C. (Eds.), *Biodiversity Hotspots: Distribution and Protection of Conservation Priority Areas*. Springer, Berlin, Heidelberg.
- Williams, N.S., McDonnell, M.J., Phelan, G.K., Keim, L.D., Van Der Ree, R., 2006. Range expansion due to urbanization: Increased food resources attract Grey-headed Flying-foxes (*Pteropus poliocephalus*) to Melbourne. *Austral Ecol.* 31, 190–198.
- Wilson, J., Bennett, A., 1999. Patchiness of a floral resource: flowering of red ironbark *Eucalyptus tricarpa* in a box and ironbark forest. *Vic. Nat.* 116, 48–53.
- Wood, S., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. R. Stat. Soc. B* 73, 3–36.