Animal Conservation

Animal Conservation. Print ISSN 1367-9430

Resilient responses by bats to a severe wildfire: conservation implications

L. Ancillotto[1], L. Bosso[1], P. Conti[2] & D. Russo[1]

1 Wildlife Research Unit, Dipartimento di Agraria, Università degli Studi di Napoli Federico II, Portici, Italy
2 Ente Parco Nazionale del Vesuvio, Ottaviano, Italy

Keywords
BACI experimental design; bat assemblage; forestry; Mediterranean; resilience; wildfire.

Correspondence
Danilo Russo, Wildlife Research Unit, Dipartimento di Agraria, Università degli Studi di Napoli Federico II, via Università 100, Portici, Italy.
Email: danrusso@unina.it

Editor: Karl Evans
Associate Editor: Elissa Cameron

Received 16 March 2020; accepted 15 September 2020

doi:10.1111/acv.12653

Abstract

Wildfires shape ecosystems globally, yet little is known on their effects on wildlife distribution and spatial behaviour. We used bats as models to test the effects of fire on ecosystems because they are multi-habitat specialists and feature ecological and life traits such as behavioural plasticity and longevity that make them able to respond to both short- and long-term environmental changes. We aimed at testing the effects of a severe wildfire on a Mediterranean bat assemblage in terms of occupancy, activity and individual fitness. Here, we measure the effects of fire on activity levels and occupancy by a Mediterranean bat assemblage at the Vesuvius National Park, in Southern Italy, over 4 years, encompassing a year when a severe wildfire occurred. By comparing bat occurrence and activity at burnt versus unburnt sites with a Before-After/Control-Impact approach, we found that bat responses to wildfires are species specific and depend on the time elapsed since the fire. Species that rely more strongly on forest areas showed a strong short-term adverse response in terms of occupancy and activity, while species adapted to open habitats showed no response 1 year after the wildfire. However, most species showed a general positive effect due to the passage of fire 2 years after its occurrence, probably because of vegetation regrowth. The wildfire event was also associated with reduced reproduction in at least one species, and to worse individual body conditions 1 year after the wildfire. Our results show that most bats in a Mediterranean ecosystem show resilience to the occurrence of fire, yet many species show negative short-term responses by altering their spatial behaviour and decreasing their investment in reproduction. Future increases in fire occurrence and intensity due to climate change may alter bat assemblages and impair population viability in the long term, hampering the fundamental ecosystem services provided by structured bat communities.

Introduction

Fire is a powerful driving force of ecosystem changes, playing a critical role in shaping wildlife assemblages worldwide (Bowman *et al*., 2009). Besides natural ignitions, anthropogenic fire has also a role in influencing the dynamics and functioning of landscapes across the globe (Bowman & Haberle, 2010), drastically changing environmental conditions and eliciting a range of responses by different organisms.

A limited number of biological communities are favoured by the occurrence and passage of fire (Cissel, Swanson, & Weisberg, 1999), whereas the survival of many others is jeopardized by this type of disturbance, implying habitat loss and altered environmental conditions to which organisms fail to respond (McKenzie, Miller, & Falk, 2011). Moreover, even communities that are adapted to wildfires may be threatened should fire be too frequent or affect especially large areas (Pastro, Dickman, & Letnic, 2011). Such effects, besides affecting people's safety and economy, make wildfire a prime global conservation issue (Hardesty, Myers, & Fulks, 2005).

Ecosystem responses to both natural and prescribed fire have attracted researchers' attention worldwide (Fernandes *et al*., 2013), nonetheless little is still known on the effects of fire on faunal assemblages (Pastro *et al*., 2011). The response of animal species to wildfires is usually complex and non-consistent across case studies, resulting from the interaction of landscape composition, habitat types, wildfire extent, frequency and intensity, wind direction and speed, local climate, and species' ecological and biological traits (Griffiths, Garnett, & Brook, 2015; Kelly *et al*., 2017). Responses by vertebrates even differ according to whether prescribed fire or wildfires are taken into account, and recorded reactions are highly taxon-specific (Pastro *et al.*, 2011).

Bats make an interesting model to explore vertebrate responses to environmental stressors, being sensitive and reactive to even subtle habitat changes (Jones *et al.*, 2001). Bats are, therefore, deemed promising indicators of environmental conditions and trends (Jones *et al.*, 2009; Russo & Ancillotto, 2015; De Conno *et al.*, 2018). Bats are potentially put at risk by wildfires because of direct mortality and loss of key resources such as roost trees and foraging sites, yet studies on prescribed fire indicate that bats show high plasticity in exploiting post-fire availability of roosts and insect prey (Lacki *et al.*, 2009; Buchalski *et al.*, 2013; Law *et al.*, 2018, 2019). In fact, wildfire may be beneficial in the long run, for example by opening up spaces that are used for foraging by edge- or open-habitat specialists, or by killing trees which turn into snags suitable for roosting (Loeb & O'Keefe, 2014). Overall, the effects of prescribed fire on bats are more studied (Boyles & Aubrey, 2006; Lacki *et al.*, 2009; Loeb *et al.*, 2014; Cox *et al.*, 2016), while still little research addressed the reaction of bat assemblages to wildfires, especially over long periods of time.

Traits such as mobility (Bader *et al.*, 2015), longevity (Wilkinson & Adams, 2019) and behavioural plasticity (Salinas-Ramos *et al.*, 2019) may allow bats to cope with habitat modifications following wildfire through flexibility in spatial behaviour, or by compensating reduced resource availability through a temporarily reduction in reproductive investment (Adams & Hayes, 2008; Adams, 2010; Lučan, Weiser, & Hanák, 2013; Amorim *et al.*, 2015).

Ecomorphology of bats is strongly linked to habitat preferences, as traits such as wing loading and aspect ratio (Bininda-Emonds & Russell, 1994) strongly differ between species foraging in cluttered (e.g. forest) and open (e.g. pastures) habitats, respectively, and confer bats' different abilities in terms of manoeuvrability, dispersal and long-distance traveling (Norberg & Rayner, 1987).

The bat species that occur in Europe reproduce once a year, with births occurring in late spring to early summer (Dietz *et al.*, 2009). The period of time between June and August is, therefore, fundamental to raise offspring and store fat reserves needed to overwinter, when such species reduce active foraging and largely rely on energy reserves to hibernate. In many bat species, weather conditions during such crucial months represent an important predictor of body condition and in turn short-term reproductive success (Heideman, 2000; Adams & Hayes, 2008; Lučan *et al.*, 2013; Amorim *et al.*, 2015). In this study, we measure the effects of a severe wildfire on insectivorous bats by assessing variation in species occurrence, community structure, activity levels and reproductive output before and after the event took place. We adopted a before-after control-impact (BACI) design, respectively, 1 year before the occurrence of the wildfire and in 2 subsequent post-fire years. Specifically, we formulate the following hypotheses and predictions:

1. Wildfire effects on bats are trait-biased (e.g. Blakey *et al.*, 2019). Fire in forest habitats creates open areas at the expense of clutter by burning underwood vegetation, shrubs and tree crowns, thus, favouring activity of bat species whose wing morphology, flight style and echolocation call design best-fit flight in open spaces (Russo, Ancillotto, & Jones, 2017). These open- or edge-habitat specialists are usually species that may move over long distances and cope with strongly modified habitats (Ancillotto *et al.*, 2019; Santini *et al.*, 2019), both potentially key features in responding to an extensive wildfire like the one that occurred at the Vesuvius National Park. Building up on previous work (Bosso *et al.*, 2018), we predict that a) species adapted to dwell in dense vegetation ("clutter" specialists) such as forest will be affected adversely by the wildfire, while open-space or edge-foraging species will either show no response or increase their activity and occupancy in burnt areas. Moreover, we predict that b) such effects will alter bat assemblages, that is, burnt sites will feature modified species composition in terms of activity levels.
2. Because bats may compensate for a decline in food resources due to sudden habitat modifications by reducing their reproductive output (Amorim *et al.*, 2015), we hypothesize that this will also hold true after the disappearance of foraging habitat caused by a wildfire. We therefore predict that fewer females will be pregnant or lactating and that fewer males will be sexually active following the wildfire.

Materials and methods

Study area

We did our study at the Vesuvius National Park (hereafter: VNP) and surrounding areas (40°49′ N, 14°26 E). The VNP covers an area of 84.82 km^2: the main habitat types found within the VNP are represented by mesophilic or thermophilic forests of broadleaved tree species (*Castanea sativa; Ostrya carpinifolia, Fraxinus ornus, Arbutus unedo, Laurus nobilis, Alnus cordata, Quercus ilex* and *Q. pubescens*), interspersed within large patches of typical Mediterranean scrubland (*Cytisus scoparius, Spartium junceum and Genista aetnensis*), non-native pine plantations (*Pinus pinea, P. pinaster, P. halepensis and P. nigra*) and black locust standings (*Robinia pseudoacacia*). The VNP is also characterized by the massive presence of urban and agricultural areas, falling within 13 municipalities and home to *c.* 352 000 people, and is surrounded by an extensive conurbation which makes it a biodiversity "island" (Bosso *et al.*, 2018; www.parconazionaledelvesuvio.it).

The area has a typical Mediterranean climate with mild winters and hot and dry summers, a mean annual precipitation of *c.* 1100 mm and mean minimum temperature of the coldest month and mean maximum temperature of the warmest month, respectively, of 5.7°C (January) and 21.7°C (July) (Ducci & Tranfaglia, 2008). The bat species present at the VNP show diverse foraging and roosting preferences, ranging from forest specialists to extremely generalist taxa (Table 1).

Wildfires occur on a regular basis within the VNP, yet those affecting >100 ha are relatively rare and occur on

Table 1 Environmental variables used to predict associations with bat activity levels at 21 sites in the Vesuvius National Park (S Italy) between 2016 and 2019

PCA	Variable name	Description	Unit/ type	Mean %; Range
PC1	Scrubland2016	Amount of scrubland habitat in a 200 m radius around recording station, before the wildfire	%/ Continuous	42.4: 0–100
	Forest2016	Amount of forest habitat in a 200 m radius around recording station, before the wildfire	%/ Continuous	58.8; 0–100
PC2	Scrubland2018	Amount of scrubland habitat in a 200 m radius around recording station, after the wildfire	%/ Continuous	5.33; 0–42
	Forest2018	Amount of forest habitat in a 200 m radius around recording station, after the wildfire	%/ Continuous	13.0; 0–87
PC3	Dist firefront	Distance to the closest unburnt area	km/ Continuous	1.9; 0.0–4.4
	Dist water	Distance to the closest permanent water site	km/ Continuous	1.9; 0.1–5.3
NA	Fire control	Sampling in a site that did not burn	NA/ Categorical	NA
	Fire pre	Sampling in a site that did burn, before the wildfire	NA/ Categorical	NA
	Fire burn1	Sampling in a site that did burn, 1 year after the wildfire	NA/ Categorical	NA
	Fire burn2	Sampling in a site that did burn, 2 years after the wildfire	NA/ Categorical	NA

PCA indicates how variables were ordered following a Principal Component Analysis; NA, non-applicable.

average every 5–6 years (Ministero dell'Ambiente e della Tutela del Territorio e del Mare, 2016). In July 2017, a severe wildfire occurred in the Park, affecting *c*. 40% of its surface (*c*. 4000 ha), burning tree canopies and underwood on a ring-shaped continuous area around Mount Vesuvius (i.e. leaving no patch of untouched vegetation within the burnt area); Fig. 1) and affecting extended portions of forest and scrubland, as well as farmland and urban areas (Bosso *et al*., 2018). The VNP hosts at least 12 species of bats (Bosso *et al*., 2018), that is, 34.3% of the Italian bat species richness (Loy *et al*., 2019), and thus represents a stronghold for the conservation of bats on a wider geographic scale.

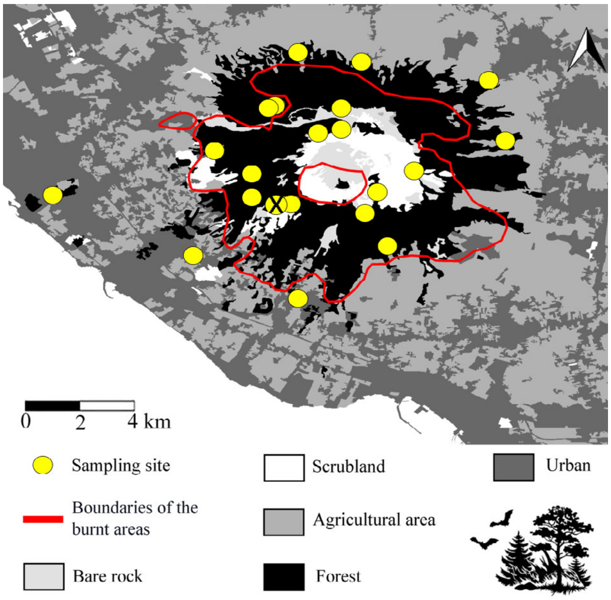

Figure 1 Map of study area, illustrating the Vesuvius National Park and its immediate surroundings, habitat types and sampling site locations, and the boundaries of the area that burnt in 2017; *X* = location of mistnetting site.

Bat acoustic sampling

We recorded bat activity through acoustic surveys in June–August 2016, that is, 1 year before the wildfire, and repeated sampling in the same months of 2018 and 2019, respectively, 1 and 2 years following the event. In 2017, when the wildfire took place, we could not sample bat activity because the area was inaccessible for safety reasons. Sampling was initiated before the wildfire as part of a VNP's project on bat monitoring, and the replications that followed the wildfire were done with a BACI design.

The sampling resulted in a total of 21 sites covering all major habitat types represented in the park; consecutive sites were at least 250 m apart to reduce the risk of recording the same individuals at nearby sites. Albeit such distance is relatively small in relation to bat movement abilities, it is usually longer than the mean foraging core areas within individual bats' nightly home ranges (e.g. Rainho & Palmeirim, 2011), which makes consecutive points relatively independent. Each recording site consisted of a geo-referenced point location, which was selected to provide a complete coverage of the Park's area, at the same time representing the habitat types in proportion to their extension within the study area (Fig. 1). Each site was classified in 2017 as burnt or unburnt by assessing the presence of wildfire signs on ground, such as extensive amounts of ash and carbonized or blackened tree trunks in 50 m around each location. The entire campaign led to a total of 63 (21 sites × 3 visits) recording nights during 3 sampling years (2016, 2018 and 2019); as each recording session lasted *c*. 4 h, totalling 252 h of recordings.

We placed automatically triggered bat detectors (D500x, Pettersson Elektronik, Uppsala, Sweden) at each site and set them to record continuously for 4 h since sunset, between

June and August each year. Bat detectors were secured to the vegetation or other structures 1.5 m above the ground pointing towards likely flight corridors or foraging spots, with an upward 45° angle. The recordings were then stored automatically as *.wav files onto CF memory cards. We made recordings consistently on the same day across sampling years, and in all cases, recording nights had clear sky and no precipitation. We identified echolocation calls manually by measuring frequency and time variables as in Russo & Jones (2002) and identifying to species all calls for which this procedure was unambiguous, which was the case for all recordings except a few *Myotis* passes that we classified to genus level. At each site we measured bat species richness and both overall and single-species activity (Russo & Jones, 2003).

Mapping habitats and wildfire

Of 21 sampling sites, 12 burned in 2017: these lost 35–100% of forest cover, and between 38% and 100% of scrubland cover, respectively, as assessed in 200 m circular plots surrounding each site. The nine unburnt sites underwent no significant change in habitat composition between 2016 and 2018. To date, no Corine Land Cover map is available for 2019, but a visual assessment of burnt sites indicated a significant vegetation regrowth, especially Mediterranean scrubland, holm oaks *Quercus ilex* and black locust *Robinia pseudacacia*.

Effects of wildfire on bat activity

We built a set of generalized linear mixed models (GLMM) with negative binomial error distribution and log-link function for the total bat activity and for each species separately. We limited single-species analyses to those species for which we recorded 30 or more passes and occurring in >20% of recording sites in each sampling year. For each response variable, we built a model including the following fixed effects:

a Sampling year, comprising three levels: pre-fire (2016); 1 year after fire (2018) and 2 years after fire (2019);
b Treatment, comprising two levels: sites that burnt in 2017 and those that did not;
c Interaction term between year and treatment, which we used to test whether any activity change occurred at a burn site was a response to fire rather than an effect of the year when activity was sampled.

We first checked all models for data overdispersion, and site identity was used as a random factor to account for inter-site variability.

To test the association between bat activity and several environmental variables potentially shaping bat responses to fire, we also calculated the distance to the closest water site, distance to fire front (i.e. to the closest unburnt area, with unburnt sites = 0 km) and the per cent amount of scrub and tree cover, respectively, before (2016) and after (2018) the wildfire. The latter, which may also be interpreted as an inverse proxy of site-specific fire severity, was assessed within 200-m-radius circular areas surrounding each recording point, and such areas were overlaid to the Corine Land Cover IV level map (available from http://www.sinanet.isprambiente.it/it/sia-ispra/download-mais/corine-land-cover). We used the ArcGis software programme (rel. 10.2.2) to clip the Corine Land Cover within the boundaries of the VNP and quantified habitat composition by extracting the per cent occurrence of each habitat type within the above-mentioned circular plots (e.g. Ancillotto *et al*., 2019). All variables were first tested for collinearity by running a Variance Inflation Analysis (VIF), which showed that none had VIF values >10. We then ordered environmental variables by running a Principal Component Analysis (PCA) and used the resulting components as predictors in a Canonical Correspondence Analysis (CCA) to visually assess the effects of environmental variables to bat activity (Table 1). We assessed the proportion of explained variance by selected predictors in the CCA by running the "ANOVA" function on the CCA model.

Effects of wildfire on bats' occupancy dynamics and assemblage structure

We calculated the observed naïf occupancy for each bat species, separately for each year, as the ratio between the numbers of sites where one or more passes of a given species was recorded and the total number of sampled sites (n = 21). We did not conduct occupancy/detection modelling as our sampling protocol (one visit per site/year) allowed to account for an assessment of species' detectability under stable environmental conditions. Instead, we assumed that species' detectability remained constant throughout each session, an assumption justified by the short duration of each sampling season (Bader *et al*., 2015). Yet, the consistent protocol, as well as the temporal replication and the BACI design, all contribute to make the use of naïf occupancy acceptable.

Overall changes in bat occupancy were tested by running a paired Student's t-test on the numbers of occupied sites between 2016 and 2018, as well as between 2018 and 2019, using species as the pairing factor. The effect of the wildfire on occupancy was then tested by comparing occupancy rates, expressed as changes in the ratio of occupied sites, between burnt and unburnt sites in 2016–2018 and 2018–2019. For this analysis, we employed chi-square or Fisher's exact tests according to sample size, and considered significant only results for which $P < 0.05$.

To detect changes in the composition of local bat assemblages due to the wildfire, we also ran analyses of similarity (ANOSIM) with 999 permutations on bat activity levels using the interaction term between treatment and year as the grouping factor, which thus led to six groups. ANOSIM tests the ranked distances of assemblages among samples based on a Bray-Curtis Dissimilarity matrix, as calculated from the numbers of bat passes per species. The latter were first log transformed to reduce the effect of rare or very abundant species, as well as reduce issue due to mean-variance relationships (Warton *et al.*, 2012; Duchet *et al.*, 2019). When assemblages were assessed as significantly different, we ran an analysis of similarity percentage (SIMPER) to quantify the contribution of each bat species to such differences (Clarke & Warwick, 2001).

Effects of wildfire on body condition and reproduction

We mist-netted bats four times during each sampling year at the main bat drinking site, that is, an artificial circular pond of *c.* 5.5 m diameter, located at *c.* 200 m from the closest burnt area. This pond is the only permanent water source within the boundaries of the Park, thus, it is likely to genuinely represent a sample of bats from a broader landscape surrounding its location (e.g. *H. savii* captured at this site were found roosting up to 5.5 km away; Ancillotto *et al.*, 2018). Numbers (n = 2) and size (6 and 12 m long × 3 m high) of mist nets used, their position and session duration (*c.* 4 h per night) were consistent across all sessions. Captured bats were identified to species (Dietz *et al.* 2009), forearm length and body mass were recorded, and each bat was assigned to an age class (considering juveniles all bats with evident epiphyseal cartilages on wing bones), and to a reproductive status class. Specifically, following Kunz & Parsons (2009), males were considered reproductive when they had enlarged epididymes and evident buccal glands, while females were considered as reproductive when they were diagnosed as pregnant by palpation, as well as lactating or post-lactating based on examination of the area of the mammary glands (Kunz & Parsons, 2009). Species identity of bats belonging to cryptic complexes was assessed by collecting a - mm round wing tissue for molecular identification (Galimberti *et al.*, 2012).

We concentrated our analysis on the most abundant species (*Hypsugo savii*), which was constantly present across years with sample sizes suitable for analyses.

The effect of wildfire on *H. savii* body condition was tested by running a LMM, using the scaled mass index to express body condition (Peig & Green, 2009) as the response variable, year as the explaining variable and sex as the random effect. We did not calculate the Scale Mass Index for pregnant females and juveniles.

We ran Chi-square tests to make comparisons between the proportions of reproductive *H. savii* in different sampling years. We ran paired comparisons between all years for which data were available (2014, 2015, 2016, 2018 and 2019) to see whether reproductive rates in post-fire years differed from those observed in the remaining years (total capture occasions: n = 20). As for the acoustic sampling, capture sessions (ordinally numbered from 1 to 4) were conducted each year on the same date (±5 days); as pairing factor, we used the ordinal number assigned to each capture session each year.

We ran all tests in R 2.1.14 (R Core Team 2016), using the vegan package (Oksanen *et al.*, 2013) for CCA, SIMPER and ANOSIM tests, and lme4 (Bates *et al.*, 2007) for GLMMs and GLMs.

Results

In 2016–2019, we recorded 4156 bat passes assigned to 12 species and one species group (*Myotis* spp.; Table 2). Total bat activity was apparently only influenced by sampling year, with a slight increase from 2016 to 2019 (Tables 2 and 3), with no visible effect of treatment or wildfire.

We obtained sufficient recordings to model bat activity separately for six species (Table 3; Fig. 2): *H. savii*, *P. kuhlii*, *P. pipistrellus*, *Tadarida teniotis*, *Plecotus austriacus* and *Rhinolophus ferrumequinum*. Three of them (*H. savii*, *P. kuhlii* and *P. pipistrellus*) were all more active in control sites, independently from the year considered. Three species increased their activity across the years, namely, *H. savii*, *P. austriacus* and *R. ferrumequinum,* while that of *P. pipistrellus* decreased. *Pipistrellus kuhlii*, *T. teniotis*, *R. ferrumequinum* and *P. austriacus* also showed a significant interaction between treatment and year, meaning that they were affected by the wildfire. Among these, *P. kuhlii* and *T. teniotis* showed a significant increase in activity in burnt sites post-fire, while R. *ferrumequinum* and *P. austriacus* showed a significant decrease after 1 year since the wildfire and a strong increase 2 years after the wildfire, at burnt sites. For example, *P. austriacus* at burnt sites showed almost no activity in 2018, but showed an over twofold increase in the subsequent year. Finally, both *R. ferrumequinum* and *P. austriacus* showed a slight increase at control sites 1 year after the wildfire (Fig. 2).

The PCA identified three main components which summarize the effect of environmental variables. Such components

Table 2 Numbers of passes and occupancy levels of 12 bat species and one species group before (2016) and after (2018, 2019) a severe wildfire, as recorded at 21 sites within the Vesuvius National Park (S Italy)

	Activity			Occupancy		
Species	2016	2018	2019	2016	2018	2019
Hypsugo savii	440	436	554	90.5	95.2	95.8
Pipistrellus kuhlii	316	299	468	100.0	95.2	100.0
Pipistrellus pipistrellus	191	150	141	85.7	76.2	79.2
Tadarida teniotis	98	109	121	57.1	62.5	66.6
Plecotus austriacus	50	29	59	47.6	19.0	41.7
Rhinolophus hipposideros	45	33	49	19.0	12.7	14.3
Rhinolophus ferrumequinum	23	20	39	33.3	23.8	38.1
Myotis emarginatus	28	9	20	28.6	19.0	20.8
Myotis crypticus	16	6	17	23.8	14.3	16.7
Nyctalus leisleri	14	4	10	38.1	14.3	20.8
Pipistrellus pygmaeus	4	4	3	9.5	9.5	9.5
Miniopterus schreibersii	2	3	3	4.8	4.8	9.5
Myotis spp.	15	18	11	–	–	–
Total	1,242	1,110	1,495			

Activity, total number of passes across recording sites; Occupancy, per cent of recording sites with calls from the species.

Table 3 Generalized linear mixed models (GLMM) for seven bat species by sampling year (Year), fire treatment (Fire) and their interaction

Species/Group	Variable	Estimate (Error)	*P*
All species pooled	Year	0.111 (0.034)	**
	Treatment	0.095 (0.061)	n.s.
	Year:treatment	−0.234 (0.143)	n.s.
Hypsugo savii	Year	0.258 (0.057)	**
	Treatment	0.114 (0.012)	*
	Year:treatment	−0.012 (0.021)	n.s.
Pipistrellus kuhlii	Year	0.023 (0.038)	n.s.
	Treatment	0.134 (0.031)	*
	Year:treatment	0.282 (0.054)	***
Pipistrellus pipistrellus	Year	−0.110 (0.041)	**
	Treatment	0.451 (0.091)	*
	Year:treatment	0.640 (0.145)	n.s.
Tadarida teniotis	Year	0.010 (0.032)	n.s.
	Treatment	0.192 (0.089)	n.s.
	Year:treatment	−0.541 (0.098)	*
Rhinolophus ferrumequinum	Year	0.788 (0.035)	**
	Treatment	−0.201 (0.079)	n.s.
	Year:treatment	0.139 (0.010)	*
Plecotus austriacus	Year	0.871 (0.034)	*
	Treatment	0.173 (0.550)	n.s.
	Year:treatment	−0.325 (0.056)	**

n.s., not significant.

* $P < 0.05$.

** $P < 0.01$.

represent variation in landscape composition, in terms of amount of remnant vegetation, before (PCA1) and after (PC2) the wildfire, as well as distance from unburnt areas and water sources areas (PC3), explaining 74.6, 15.2 and 9.4% of variance in bat activity levels respectively. A visual assessment of the CCA biplot (Supporting Information Figure S1) also revealed species-specific associations with environmental variables. *P. austriacus* activity was associated with both PC1 and PC2; that of *N. leisleri* with PC1; while activity levels of *M. emarginatus* and *R. hipposideros* were mainly related to PC2 only; all other species did not show any particular association. *Hypsugo savii* and *T. teniotis* showed a weak relationship with PC3 too (Supporting Information Figure S1.

Overall, species occupancy changed significantly from 2016 to 2018 ($t = -2.63$, $P < 0.05$) and from 2018 to 2019 ($t = 3.14$, $P < 0.05$). In the first year after the wildfire, 8 out of 12 species showed a decrease in the proportion of occupied sites, whereas 2 (*H. savii* and *T. teniotis*) showed an increase. Between 2018 and 2019, ten species showed an increase in occupancy, but only one (*R. ferrumequinum*) showed an increase in comparison to pre-fire conditions. Occupancy between 2016 and 2018 changed significantly between burnt and unburnt sites for all species in the *Rhinolophus* and *Myotis* genera, as well as for *Plecotus austriacus*, with a higher proportion of disappearance from burnt sites than from control ones (all $P < 0.05$; see Supporting Information Table S1). Between 2018 and 2019, a significant change in occupancy between burnt and unburnt sites was evident only for *R. ferrumequinum* and *P. austriacus*, with a higher proportion of burnt sites being re-colonized.

Bat species composition in the VNP as a whole did not change across the study years, yet the ANOSIM showed significant differences in the assemblages' structure at sites under different treatment*year conditions ($R = 0.08$, $P < 0.01$). Such differences were mainly driven by contrasts

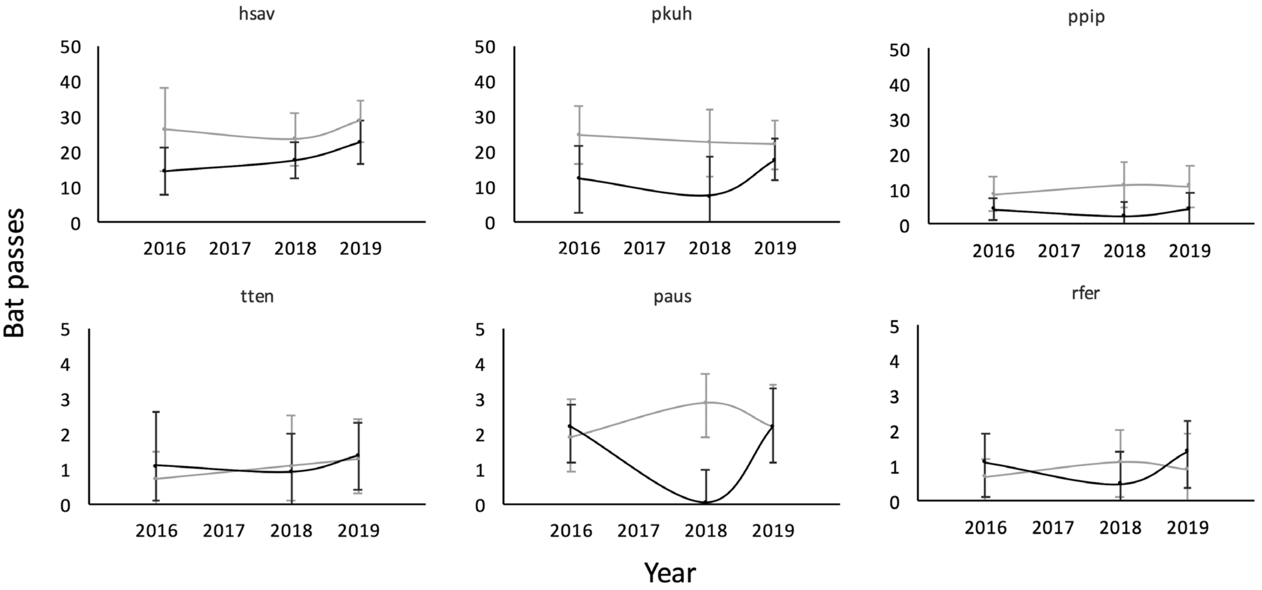

Figure 2 Bat activity trends (mean numbers of bat passes per site/night ±standard deviation) in burnt (black lines) and unburnt (grey lines) sites (n tot = 21) at three time intervals (pre: 2016; post 1: 2018; post 2: 2019), in the Vesuvius National Park (S Italy). Species: hsav: *Hypsugo savii*; pkuh: *Pipistrellus kuhlii*; ppip: *Pipistrellus pipistrellus*; tten: *Tadarida teniotis*; rfer: *Rhinolophus ferrumequinum*; paus: *Plecotus austriacus*. Dashed lines indicate the year when the wildfire occurred.

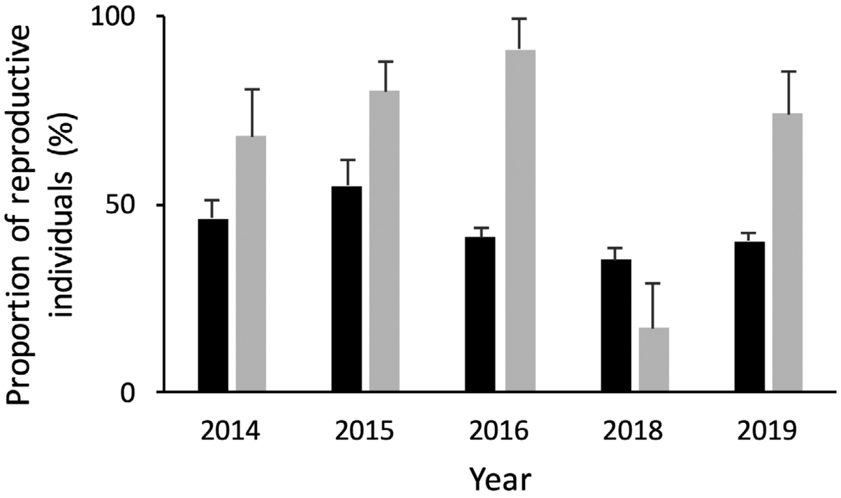

Figure 3 Proportion (mean±D) of reproductive males (black bars) and females (grey bars) of Savi's pipistrelles *Hypsugo savii* before (2014–2016) and after (2018–2019) the occurrence of a wildfire at the Vesuvius National Park (S Italy); error bars indicate standard deviation.

between burnt sites before and 1 year after the wildfire, between control sites before and 1 year after the wildfire, as well as between burnt sites in the first and in the second year after the fire (all $P < 0.025$). Again, the differences in question were mostly due to changes in the activity levels of *Rhinolophus* spp., *Myotis* spp. and *Plecotus*, which cumulatively accounted for 83.1% of total dissimilarity (Table 4); namely, the latter was mainly driven by relatively uncommon species such as *R. hipposideros* and *M. emarginatus*, cumulatively accounting for 59.3% of sample dissimilarity.

Reproduction and body condition

We captured 208 bats of five species between 2016 and 2019, 182 of which were *H. savii* (72 males, 110 females); all other species were not captured in sufficient numbers for quantitative analyses (*P. kuhlii*: n = 13; *M. crypticus*: n = 6; *P. austriacus*: n = 5; *N. leisleri*: n = 1; *M. schreibersii*: n = 1). Mean species richness at each capture session increased (n = 12, ANOVA: $F_{1,11} = 2.35$, $P < 0.01$) between pre-fire (1.17 ± 0.41) and post-fire years (3.25±0.96). The mean numbers of captured *H. savii* did not vary between paired sessions across years (n = 12, ANOVA: $F_{1,11} = 1.34$, P = n.s.), yet their scaled mass index decreased from 2016 to 2018 (estimate: −0.01, $P < 0.05$). The same variable increased significantly between 2018 and 2019 (estimate: 0.01; $P < 0.05$), and reached values comparable to those recorded in the years before the wildfire (estimate: 0.00; P = n.s.). The per cent of *H. savii* reproductive females decreased ($P < 0.001$) from 92%–95% in pre-fire years to 17%–35% in 2018 (first year post-fire). The percentage of reproductive males did not change significantly across years (pre-fire: 46%–55%; post-fire 35%–40%). The proportions of reproductive males and females (Fig. 3), respectively, did not differ significantly between pairs of pre-fire years (all P = n.s.). We observed a significant increase in the proportion of reproductive females (Chi-square: 11.65, $P < 0.01$) from 2018 to 2019, while in 2019 (2 years after the wildfire), this proportion recovered to the values recorded in pre-fire years (see Supporting Information Table S2).

Table 4 SIMPER per cent dissimilarity of bat assemblages in burnt and unburnt sites at 21 sites in the Vesuvius National Park (S Italy), across 1 pre- and 2 post-fire years

Species	Av. Dissimilarity	Contribution (%)	Cumulative (%)
Rhinolophus hipposideros	27.50	39.02	39.02
Myotis emarginatus	14.31	20.31	59.33
Rhinolophus ferrumequinum	12.23	17.35	76.68
Plecotus austriacus	4.51	6.40	83.08
Myotis crypticus	4.49	6.37	89.44
Hypsugo savii	4.03	5.72	95.16
Pipistrellus pipistrellus	3.41	4.84	100.00
Nyctalus leisleri	0.00	0.00	100.00
Pipistrellus kuhlii	0.00	0.00	100.00
Tadarida teniotis	0.00	0.00	100.00

Discussion

The severe wildfire that occurred at the VNP in 2017 affected significantly the use of space by bats, their occupancy patterns and reproductive output. Such effects were species-specific in intensity and direction, yet in most cases led to a fast recovery to the pre-fire conditions, suggesting that at least some bat species are resilient to environmental alteration by fire.

Bat activity in response to wildfire

Bat activity showed different responses depending on the time elapsed since the occurrence of fire. Edge specialists (genera *Pipistrellus* and *Hypsugo*) were not apparently affected by fire, or were even favoured in the long term, showing higher levels of activity at burnt sites after 2 years than before the wildfire. Bats adapted to clutter habitats instead showed a strong decrease at burnt sites 1 year since the fire, and a subsequent significant increase after 2 years. Noticeably, clutter-adapted species also increased activity at unburnt sites 1 year after the wildfire, respectively, confirming their higher susceptibility to environmental changes when compared to open habitats' species (Safi & Kerth, 2004), and suggesting a relevant role of areas untouched by fire as alternative foraging sites when favoured ones were not available. In fact, the amount of untouched vegetation played a major role in determining bat activity levels after the wildfire. Moreover, the positive effect of water accessibility is well documented for bats (Adams, 2010; Ancillotto, Tomassini & Russo, 2016; Amorim *et al*., 2018), while that of the distance into the burnt areas from the fire front is likely a proxy of disturbance intensity (Buchalski *et al*., 2013).

Bat assemblages differ between burnt and unburnt sites

The responses of bat activity in terms of species composition mainly consisted of modified assemblages occurring at burnt sites, with differences mostly due to clutter-adapted species such as the five bat species from the genera *Rhinolophus*, *Plecotus* and *Myotis*. Clutter-adapted species are potentially more exposed to habitat loss and local extinction risk (Safi & Kerth, 2004; Bosso *et al*., 2018). Although we did not test any effect of species-specific roost preferences on bat responses to the wildfire, these likely played a minor role, probably because most species found in the study area are not strictly dependent from single roost types, that is, they use both buildings, underground sites (*Rhinolophus* spp.) and tree cavities (all other species). We could not test the effects of fire on rare species, yet a visual assessment of their trends indicates that the rarest species, such as *Myotis crypticus*, *M. emarginatus* and *R. hipposideros* may have not fully recovered after the wildfire, as also suggested by the fact that these species were those that most influenced the differences among years. Namely, *Myotis* spp. and *R. hipposideros* were also the species out of those we recorded that rely more on cluttered habitats for foraging, and may thus take longer to recolonize burnt sites following forest regrowth (Bontadina, Schofield, & Naef-Daenzer, 2002; Flaquer *et al*., 2008; Smith & Racey, 2008). Further studies applying integrated methods (e.g. long-term roost survey schemes and radiotracking: Van der Meij *et al*., 2015; Ancillotto *et al*., 2018) may be needed to assess the response of rarer species to wildfire; yet, extensive or repeated wildfires may destabilize bat communities and, thus, jeopardize the ecosystem services that the latter provide (Russo, Bosso, & Ancillotto, 2018).

Bat occupancy in response to wildfire

Bat response in terms of species' occupancy reflected that of activity levels, with two clutter specialists avoiding using burnt sites after 1 year and apparently re-colonizing 2 years from the wildfire respectively. Shrubs appear only few years after wildfires that affect Mediterranean forests (Ubeda, Outeiro, & Sala, 2006), and plant communities gradually show a trend towards pre-fire productivity levels, as quantified by an increase in the Normalized Difference Vegetation Index, which is linked with insect biomass (Sweet *et al*., 2015). This means that bat food availability in such ecosystems should recover relatively quickly, albeit the relationship among bat activity, vegetation regrowth and insect abundance in forest habitats subjected to wildfires is not yet clear, and probably not consistent among different habitats (Malison & Baxter, 2010; Cox *et al*., 2016; Lacki *et al*., 2017; Austin *et al*., 2018; Moreira *et al*., 2019).

Wildfires affect bat reproduction

Capture data on *H. savii* showed that body condition declined following the wildfire, and that some responses were sex specific. In particular, fewer females were reproductive 1 year after the wildfire. *H. savii* is small (body mass: 4–9 g) and an open-space/edge habitat specialist, yet the habitat loss these bats faced probably did not allow them to acquire sufficient energy reserves to cope with pregnancy. This is also in line with a radiotracking study conducted in the VNP, highlighting the importance of forests as foraging habitat for this species (Ancillotto *et al*., 2018). Similar responses were recorded in other bat species under different adverse conditions such as prolonged water scarcity (Adams, 2010; Amorim *et al*., 2015) and weather unpredictability due to climate change (Adams, 2010; Lučan *et al*., 2013). In our study area, summer monthly precipitation (June-August) showed a minimum in 2017, that is, the year when the wildfire occurred (6.7 ± 5.9 mm, vs. 20.7 ± 18.9 and 36.1 ± 23.1 mm in 2016 and 2018 respectively; http://agricoltura.regione.campania.it/home.htm). Under physiological stress such as overheating, *H. savii* may make more frequent use of daytime torpor (Russo *et al*., 2017; Ancillotto *et al*., 2018), and the same strategy might be used by bats that cope with food shortage following wildfires (Doty *et al*., 2016), at the expense of gametogenesis (McAllan & Geiser, 2014). Skipping a reproductive event may be an effective energy-saving strategy for long-lived species to cope with adverse environmental conditions (Pilastro, Tavecchia, & Marin, 2003; Rivalan *et al*., 2005). Noticeably, female *H. savii* recovered their average reproductive status as soon as 2 years after the wildfire, once again most likely reflecting a quick return to sufficient insect food availability associated with fast vegetation regrowth at burnt sites.

Conclusions

Our study shows that Mediterranean bat communities respond to wildfires and may alter their use of space and reproductive output to compensate for the transient loss of food or foraging habitat, re-establishing their pre-fire patterns as soon as favourable environmental conditions are restored. The picture provided by the modelling assessment of the same wildfire we dealt with in this study (Bosso *et al*.,

2018) was less optimistic because it could not account for dynamic changes such as bat behavioural plasticity and quick vegetation regrowth, nor could it unveil patterns at smaller spatial scales than those typically covered in spatial modelling exercises. Bosso *et al*. (2018) assessed species-specific habitat losses due to wildfire as irreversible, which led to predictions of more adverse long-term effects on local bat populations.

Our results on bat activity and reproductive success rest upon a relatively small sampling effort in terms of survey hours and numbers of sites; yet, the sampling design we followed and the fact that the capture site we investigated is a very important drinking and foraging site attracting bats from several kilometres (see Ancillotto *et al*., 2018) compensate for such limitations, and may genuinely reflect a more general, broad-scale trend of bat populations.

The resilience to fire shown by the bat community we examined reflects long-term preferences of different bat guilds found in other Mediterranean biomes, that is, Western US (Blakey *et al*., 2019), where clutter-adapted species favoured areas with less severe and less frequent wildfires. Nonetheless, such results should not be taken incautiously as a “general reaction” of bats to such events. First, the unpredictable nature of exceptional wildfires and the lack of information on bat activity on longer time scales in the past make it difficult to assess whether the resilience we found actually represents a recovery to a “baseline” level. Secondly, numerous variables such as wildfire size, frequency, post-fire dynamics of vegetation and insect prey assemblages, and bat species occurring in an area may all differ from case to case, potentially leading to very different outcomes.

Fire may act as a filter to bat assemblages according to species’ ecological preferences and traits such as wing morphology (as in Bosso *et al*., 2018). We cannot rule out that in other situations, responses would differ; for example, Starbuck *et al*. (2020) found that pyrodiversity was a poor predictor of bat habitat preferences in an heterogeneous landscape, while bats in mountainous conifer forests were mostly favoured by both pyrodiversity and fire severity, with few species-specific exceptions (Steel *et al*., 2019). Moreover, species naturally occurring at low population sizes or densities, and consequently more difficult to monitor and detect, may be less resilient, thus, how fire affects them may go unnoticed.

Our results highlight that remnants of untouched habitats thus represent a fundamental resource for bats to cope with critical environmental crises (Metcalf, Hampson & Koons, 2007), probably favouring prompt re-colonization of burnt areas once these become suitable again (Zielinski & Gellman, 1999), and are thus pivotal targets for conservation.

Acknowledgements

We thank Francesca Festa, Francesca Cosentino, Angelo Palmieri, Clarissa Canfora, Vincenzo Meola and Tommaso Notomista for their help during fieldwork, Vincenzo Longobardi for his support in planning and conducting fieldwork, and Luca Santini for providing useful suggestions on data analysis. We also thank Andrea Galimberti for the molecular identification of *Myotis* samples. The project was funded by the Vesuvius National Park (Azione di Sistema – Identificazione di hot spot di diversità della chirotterofauna e implicazioni per la gestione – Direttiva “Biodiversità” 2016, Prot. 0015956/GAB).

Authors’ contributions

DR, LA, LB and PC conceived and designed the study; LA performed fieldwork and acoustic identification of bat calls; LA and LB analysed the data; LA, LB and DR wrote the ms.

Data availability statement

Bat activity data are available on the authors’ ResearchGate profiles upon request.

References

Adams, R.A. (2010). Bat reproduction declines when conditions mimic climate change projections for western North America. *Ecology* **91**, 2437–2445.

Adams, R.A. & Hayes, M.A. (2008). Water availability and successful lactation by bats as related to climate change in arid regions of western North America. *J. Anim. Ecol.* **77**, 1115–1121.

Amorim, F., Jorge, I., Beja, P. & Rebelo, H. (2018). Following the water? Landscape-scale temporal changes in bat spatial distribution in relation to Mediterranean summer drought. *Ecol. Evol.* **8**, 5801–5814.

Amorim, F., Mata, V.A., Beja, P. & Rebelo, H. (2015). Effects of a drought episode on the reproductive success of European free-tailed bats (*Tadarida teniotis*). *Mammal. Biol.* **80**, 228–236.

Ancillotto, L., Bosso, L., Salinas-Ramos, V.B. & Russo, D. (2019). The importance of ponds for the conservation of bats in urban landscapes. *Landsc. Urb Plan.* **190**, 103607.

Ancillotto, L., Budinski, I., Nardone, V., Di Salvo, I., Della Corte, M., Bosso, L., Conte, P. & Russo, D. (2018). What is driving range expansion in a common bat? Hints from thermoregulation and habitat selection. *Behav. Process.* **157**, 540–546.

Ancillotto, L., Tomassini, A. & Russo, D. (2016). The fancy city life: Kuhl’s pipistrelle, *Pipistrellus kuhlii*, benefits from urbanisation. *Wildlife Res.* **42**, 598–606.

Austin, L.V., Silvis, A., Ford, W.M., Muthersbaugh, M. & Powers, K.E. (2018). Bat activity following restoration prescribed burning in the central Appalachian upland and riparian habitats. *Nat. Areas J.* **38**, 183–196.

Bader, E., Jung, K., Kalko, E.K., Page, R.A., Rodriguez, R. & Sattler, T. (2015). Mobility explains the response of aerial insectivorous bats to anthropogenic habitat change in the Neotropics. *Biol. Conserv.* **186**, 97–106.

Bates, D., Sarkar, D., Bates, M.D. & Matrix, L. (2007). *The lme4 package*. R package version, 2, 74.

Bininda-Emonds, O.R.P. & Russell, A.P. (1994). Flight style in bats as predicted from wing morphometry: the effects of specimen preservation. *J. Zool.* **234**, 275–287.

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.

Bontadina, F., Schofield, H. & Naef-Daenzer, B. (2002). Radio-tracking reveals that lesser horseshoe bats (*Rhinolophus hipposideros*) forage in woodland. *J. Zool.* **258**, 281–290.

Bosso, L., Ancillotto, L., Smeraldo, S., D'Arco, S., Migliozzi, A., Conti, P. & Russo, D. (2018). Loss of potential bat habitat following a severe wildfire: a model-based rapid assessment. *Int. J. Wildland Fire.* **27**, 756–769.

Bowman, D.M.J.S., 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.O., Johnston, F.H., Keeley, J.E., Krawchuk, M.A., Kull, C.A., Marston, J.B., Moritz, M.A., Prentice, I.C., Roos, C.I., Scott, A.C., Swetnam, T.W., van der Werf, G.R. & Pyne, S.J. (2009). Fire in the Earth system. *Science* **324**, 481–484.

Bowman, D. & Haberle, S.G. (2010). Paradise burnt: how colonizing humans transform landscapes with fire. *PNAS* **107**, 21234–21235.

Boyles, J.G. & Aubrey, D.P. (2006). Managing forests with prescribed fire: implications for a cavity-dwelling bat species. *For. Ecol. Manag.* **222**, 108–115.

Buchalski, M.R., Fontaine, J.B., Heady, P.A. III, Hayes, J.P. & Frick, W.F. (2013). Bat response to differing fire severity in mixed-conifer forest California, USA. *PLoS One* **8**, e57884.

Cissel, J.H., Swanson, F.J. & Weisberg, P.J. (1999). Landscape management using historical fire regimes: Blue River, Oregon. *Ecol. Appl.* **9**, 1217–1231.

Clarke, K.R. & Warwick, R.M. (2001). A further biodiversity index applicable to species lists: variation in taxonomic distinctness. *Mar. Ecol. Prog. Ser.* **216**, 265–278.

Cox, M.R., Willcox, E.V., Keyser, P.D. & Vander Yacht, A.L. (2016). Bat response to prescribed fire and overstory thinning in hardwood forest on the Cumberland Plateau, Tennessee. *For. Ecol. Manag.* **359**, 221–231.

De Conno, C., Nardone, V., Ancillotto, L., De Bonis, S., Guida, M., Jorge, I., Scarpa, U. & Russo, D. (2018). Testing the performance of bats as indicators of riverine ecosystem quality. *Ecol. Ind.* **95**, 741–750.

Dietz, C., Nill, D. & von Helversen, O. (2009). *Bats of Britain, Europe and Northwest Africa*. London: A & C Black.

Doty, A.C., Stawski, C., Law, B.S. & Geiser, F. (2016). Postwildfire physiological ecology of an Australian microbat. *J. Comp. Physiol. B.* **186**, 937–46.

Ducci, D. & Tranfaglia, G. (2008). Effects of climate change on groundwater resources in Campania (southern Italy). *Geol. Soc. Spec. Publ.* **288**, 25–38.

Duchet, C., Mukherjee, S., Stein, M., Spencer, M. & Blaustein, L. (2019). Effect of desiccation on mosquito oviposition site selection in Mediterranean temporary habitats. *Ecol. Entomol*. **45**(3), 498–513. https://doi.org/10.1111/een.12821

Fernandes, P.M., Davies, G.M., Ascoli, D., Fernández, C., Moreira, F., Rigolot, E., Stoof, C.R., Vega, J.A. & Molina, D. (2013). Prescribed burning in southern Europe: developing fire management in a dynamic landscape. *Front. Ecol. Environ.* **11**, e4–e14.

Flaquer, C., Puig-Montserrat, X., Burgas, A. & Russo, D. (2008). Habitat selection by Geoffroy's bats (*Myotis emarginatus*) in a rural Mediterranean landscape: implications for conservation. *Acta Chiropterol.* **10**, 61–67.

Galimberti, A., Spada, M., Russo, D., Mucedda, M., Agnelli, P., Crottini, A., Casiraghi, M. (2012). Integrated operational taxonomic units (IOTUs) in echolocating bats: a bridge between molecular and traditional taxonomy. *PLoS One* **7** (6), e40122.

Griffiths, A.D., Garnett, S.T. & Brook, B.W. (2015). Fire frequency matters more than fire size: testing the pyrodiversity–biodiversity paradigm for at-risk small mammals in an Australian tropical savanna. *Biol. Conserv.* **186**, 337–346.

Hardesty, J., Myers, R. & Fulks, W. (2005). Fire, ecosystems, and people: a preliminary assessment of fire as a global conservation issue. *The George Wright Forum.* **22**, 78–87.

Heideman, P.D. (2000). Environmental regulation of reproduction. In *The reproductive biology of bats*: 469–499. Chrichton, E.G. & Kutsch, P. (Eds.). New York: New York Academic Press.

Jones, K.E., Barlow, K.E., Vaughan, N., Rodríguez-Durán, A. & Gannon, M.R. (2001). Short-term impacts of extreme environmental disturbance on the bats of Puerto Rico. *Anim. Conserv. Forum.* **4**, 59–66.

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.

Kelly, L.T., Haslem, A., Holland, G.J., Leonard, S.W., MacHunter, J., Bassett, M., Bennet, A.F., Bruce, M.J., Chia, E.K., Christie, F.J., Clarke, M.F., Di Stefano, J., Loyn, R., McCarthy, M.A., Pung, A., Robinson, N., Sitters, H., Swan, M. & York, A. (2017). Fire regimes and environmental gradients shape vertebrate and plant distributions in temperate eucalypt forests. *Ecosphere* **8**, e01781.

Kunz, T.H. & Parsons, S. (2009). *Ecological and behavioral methods for the study of bats*. 2nd edn. Baltimore, MD: Johns Hopkins University Press.

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.

Lacki, M.J., Dodd, L.E., Skowronski, N.S., Dickinson, M.B. & Rieske, L.K. (2017). Relationships among burn severity, forest canopy structure and bat activity from spring burns in oak–hickory forests. *Int. J. Wildland Fire* **26**, 963–972.

Law, B., Doty, A., Chidel, M. & Brassil, T. (2018). Bat activity before and after a severe wildfire in Pilliga forests: resilience influenced by fire extent and landscape mobility? *Austral Ecol.* **43**, 706–718.

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**(6), 1013–1024. https://doi.org/10.1111/aec.12768.

Loeb, S. & O'Keefe, J. (2014). Indiana bats, northern long-eared bats, and prescribed fire in the Appalachians: challenges and considerations. Proceedings, Wildland Fire in the Appalachians: discussions among managers and scientists. General Technical Reports SRS-199. Asheville, NC: US Department of Agriculture Forest Service. *Southern Research Station.* **208**, 73–81.

Loy, A., Aloise, G., Ancillotto, L., Angelici, F.M., Bertolino, S., Capizzi, D., Castiglia, R., Colangelo, P., Contoli, L., Cozzi, B., Fontaneto, D., Lapini, L., Maio, N., Monaco, A., Mori, E., Nappi, A., Podestà, M., Russo, D., Sarà, M. & Scandura, M. (2019). Mammals of Italy: an annotated checklist. *Hystrix.* **30**, 87–106.

Lučan, R.K., Weiser, M. & Hanák, V. (2013). Contrasting effects of climate change on the timing of reproduction and reproductive success of a temperate insectivorous bat. *J. Zool.* **290**, 151–159.

Malison, R.L. & Baxter, C.V. (2010). The fire pulse: wildfire stimulates flux of aquatic prey to terrestrial habitats driving increases in riparian consumers. *Can. J. Fish. Aquat. Sci.* **67**, 570–579.

McAllan, B.M. & Geiser, F. (2014). Torpor during reproduction in mammals and birds: dealing with an energetic conundrum. *Am. Zool.* **54**, 516–532.

McKenzie, D., Miller, C. & Falk, D.A. (2011). *The landscape ecology of fire*. New York: Springer.

Metcalf, C.J.E., Hampson, K. & Koons, D.N. (2007). What happens if density increases? Conservation implications of population influx into refuges. *Anim. Conserv.* **10**, 478–486.

Ministero dell'Ambiente e della Tutela del Territorio e del Mare. (2016). *Statistiche incendi boschivi nei parchi nazionali (1997–2015).* Technical report available at: www.minambiente.it/pagina/statistiche-incendi-boschivi-nei-parchi-nazionali-1997-2015.

Moreira, F., Allsopp, N., Esler, K.J., Wardell-Johnson, G., Ancillotto, L., Arianoutsou, M., Clary, J., Brotons, L., Clavero, M., Dimitrakopoulos, P.G., Fagoaga, R., Fiedler, P., Filipe, A.F., Frankenberg, E., Holmgren, M., Marquet, P.A., Martinez-Harms, M.J., Martinoli, A., Miller, B.P., Olsvig-Whittaker, L., Pliscoff, P., Rundel, P., Russo, D., Slingsby, J.A., Thompson, J., Wardell-Johnson, A. & Beja, P. (2019). Priority questions for biodiversity conservation in the Mediterranean biome: heterogeneous perspectives across continents and stakeholders. *Conserv. Sci. Practice.* **1**, e118.

Norberg, U.M. & Rayner, J.M. (1987). Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philos. T. R. Soc. B.* **316**, 335–427.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E. & Wagner, H. (2013). *Package 'vegan'.* Community ecology package. Version 2.

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.

Peig, J. & Green, A.J. (2009). New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos* **118**, 1883–1891.

Pilastro, A., Tavecchia, G. & Marin, G. (2003). Long living and reproduction skipping in the fat dormouse. *Ecology* **84**, 1784–1792.

R Core Team (2016). R: A language and environment for statistical computing [Computer software manual]. Vienna, Austria.

Rainho, A. & Palmeirim, J.M. (2011). The importance of distance to resources in the spatial modelling of bat foraging habitat. *PLoS One* **6**(4), e19227.

Rivalan, P., Prevot-Julliard, A.C., Choquet, R., Pradel, R., Jacquemin, B. & Girondot, M. (2005). Trade-off between current reproductive effort and delay to next reproduction in the leatherback sea turtle. *Oecologia* **145**, 564–574.

Russo, D. & Ancillotto, L. (2015). Sensitivity of bats to urbanization: a review. *Mammal. Biol.* **80**, 205–212.

Russo, D., Ancillotto, L. & Jones, G. (2017). Bats are still not birds in the digital era: echolocation call variation and why it matters for bat species identification. *Can. J. Zool.* **96**, 63–78.

Russo, D., Bosso, L. & Ancillotto, L. (2018). Novel perspectives on bat insectivory highlight the value of this ecosystem service in farmland: research frontiers and management implications. *Agr. Ecosyst. Environ.* **266**, 31–38.

Russo, D., Cistrone, L., Budinski, I., Console, G., Della Corte, M., Milighetti, C., Di Salvo, I., Nardone, V., Brigham, R.M. & Ancillotto, L. (2017). Sociality influences thermoregulation and roost switching in a forest bat using ephemeral roosts. *Ecol. Evol.* **7**, 5310–5321.

Russo, D. & Jones, G. (2002). Identification of twenty-two bat species (Mammalia: Chiroptera) from Italy by analysis of time-expanded recordings of echolocation calls. *J. Zool.* **258**, 91–103.

Russo, D. & Jones, G. (2003). Use of foraging habitats by bats in a Mediterranean area determined by acoustic surveys: conservation implications. *Ecography* **26**, 197–209.

Safi, K. & Kerth, G. (2004). A comparative analysis of specialization and extinction risk in temperate-zone bats. *Conserv. Biol.* **18**, 1293–1303.

Salinas-Ramos, V.B., Ancillotto, L., Bosso, L., Sánchez-Cordero, V. & Russo, D. (2019). Interspecific competition in bats: state of knowledge and research challenges.

Mammal Rev. **50**, 68–81. https://doi.org/10.1111/mam.12180.

Santini, L., González-Suárez, M., Russo, D., Gonzalez-Voyer, A., von Hardenberg, A. & Ancillotto, L. (2019). One strategy does not fit all: determinants of urban adaptation in mammals. *Ecol. Lett.* **22**, 365–376.

Smith, P.G. & Racey, P. (2008). Natterer's bats prefer foraging in broad-leaved woodlands and river corridors. *J. Zool.* **275**, 314–322.

Starbuck, C.A., Considine, E.S. & Chambers, C.L. (2020). Water and elevation are more important than burn severity in predicting bat activity at multiple scales in a post-wildfire landscape. *PLoS One* **15**(4), e0231170.

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**, 1–11.

Sweet, S.K., Asmus, A., Rich, M.E., Wingfield, J., Gough, L. & Boelman, N.T. (2015). NDVI as a predictor of canopy arthropod biomass in the Alaskan arctic tundra. *Ecol. Appl.* **25**, 779–790.

Úbeda, X., Outeiro, L.R. & Sala, M. (2006). Vegetation regrowth after a differential intensity forest fire in a Mediterranean environment, northeast Spain. *Land Degrad. Dev.* **17**, 429–440.

Van der Meij, T., Van Strien, A.J., Haysom, K.A., Dekker, J., Russ, J., Biala, K., Limpens, H. (2015). Return of the bats? A prototype indicator of trends in European bat populations in underground hibernacula. *Mammal. Biol.* **80**, 170–177.

Warton, D.I., Wright, S.T. & Wang, Y. (2012). Distance-based multivariate analyses confound location and dispersion effects. *Methods Ecol. Evol.* **3**, 89–101.

Wilkinson, G.S. & Adams, D.M. (2019). Recurrent evolution of extreme longevity in bats. *Biol. Lett.* **15**, 20180860.

Zielinski, W.J. & Gellman, S.T. (1999). Bat use of remnant old-growth redwood stands. *Conserv. Biol.* **13**, 160–167.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Comparisons between burnt and unburnt sites (n = 21) of the occupancy rates by 11 bat species in the Vesuvius National Park (S Italy) before (2016) and after (2018, 2019) the occurrence of a severe wildfire

Table S2. Significance of Chi-squared tests on the proportions of reproductive males (orange) and females (green) Savi's bats (*Hypsugo savii*) caught in different years (n sessions per year = 4) at the Vesuvius National Park (S Italy)

Figure S1. Canonical correspondence analysis (CCA) ordination of the activity levels by ten bat species in relation to environmental variables ordered as Principal Components (following Table 1).