



Soil moisture reduces egg mortality during wildfires in the Madeiran green bush-cricket

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Received: 24 January 2023 / Accepted: 17 August 2023 / Published online: 27 August 2023
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Abstract

The increasing frequency of fires is a major threat to biodiversity around the world, further facilitated by global warming. Fires usually affect insect populations directly, but insect eggs may partly be protected from wildfires when oviposited into the ground. Madeira belongs to the Macaronesian islands which experience wildfires annually. The Madeiran Green Bush-Cricket (*Psalmatophanes barretoii*) is endemic to the island and listed on the IUCN Red List as Vulnerable with wildfires being named as the major threat to the species. However, it remains unclear whether the eggs of *P. barretoii* may be partly protected from fires due to the oviposition substrate (soil). It also remains unknown whether increased temperature alone or increased drought are more important drivers of mortality when fires are approaching or surpassing an oviposition site. We hypothesized that drought might have a significant effect on mortality when heat levels remain slightly below or above mortal temperatures. Therefore, we tested the effects of temperature and drought on egg survival in two laboratory experiments by incubating eggs at different temperatures (49 °C, 55 °C) for six hours with and without water replacement. Our results show that the combination of drought and heat affected egg mortality significantly stronger than heat alone. As a result, we conclude that egg mortality is strongly mediated by soil desiccation and that eggs might be buffered from fire effects in moist habitats or after increased rainfall.

Implications for insect conservation

Our results suggest that soil moisture is a key variable to mitigate egg mortality from wildfires. This can be reached by protecting habitats with high soil moisture (e.g. laurel forests and many native bushes) or by prescribed burning during the winter months when soil moisture is higher than in summer.

Keywords Climate change · Bush-fires · Drought · Egg mortality · Madeira · Orthoptera

Introduction

Climate change is a significant threat to biodiversity (Omann et al. 2009; Mahl et al., 2020; Muluneh 2021). As a result of the changing climate, extreme weather events occur more

often, including storms, floods and droughts (Luber and McGeehin 2008; Clarke et al. 2022). The latter can facilitate various other stressors, such as wildfires, which increase in size and frequency globally, amplified by human carelessness and arson (Dale et al. 2001; Kelly et al. 2020). In Mediterranean areas, summer droughts have recently facilitated artificial wildfires (Guion et al., 2022). These fires may affect species differently based on their life histories and fire adaptations (Hochkirch and Adorf 2007; Moreno 2010). Many insects hibernate as eggs, and some have a diapause in the soil during the egg or larval stage (Ingrisch 1986; Unterweger et al. 2018; Branson 2020). Oviposition substrate and depth as well as egg development time are important factors mediating the effects of wildfires on insect populations (Hochkirch and Adorf 2007). Due to their short life cycles, insects are ideal organisms to study fire effects

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on their life stages. The effects of wildfires on Orthoptera have been studied by several authors (e.g. Bieringer 2002; Branson and Vermeire 2007; Hochkirch and Adorf 2007). The eggs of many Orthoptera species hibernate either in the ground or in plants (Bellmann et al. 2019). Fire survival of Orthoptera eggs is strongly related to oviposition depth as wildfires rarely lead to a critical temperature increase of the deeper soil (Bramson & Veimeire, 2007).

Madeira is one of the Macaronesian islands known for its large as Laurisilva forests, which are a global hotspot of biodiversity and inscribed on the UNESCO World Heritage List (Boeiro et al. 2015). Fires occur annually on Madeira (Institute of Forests and Nature Conservation in Madeira, Rhee et al. 2022). Summer in Madeira has lower precipitation than winter, but climate models suggest that Madeiran winters will suffer from lower precipitation in the future (Santos et al. 2004). Due to the summer droughts and higher temperatures, the summer period is more vulnerable to fires than winter (Couto et al. 2021). Most fires on the island are ignited by humans intentionally or unintentionally (Moreno 2010).

The Madeiran Green Bush-Cricket (*Psalmatophanes barretoii*) is endemic to Madeira (Pfau and Pfau 2005). The species is listed as Vulnerable on the IUCN Red List of Threatened Species (Hochkirch et al. 2016) with wildfires representing the main threat (Rhee et al. 2022). They inhabit in blackberry bushes and trees in laurel forests or at forest edges (Lange 1990; Pfau and Pfau 2005). The species is adult in summer and the eggs are laid in the ground. During pre-embryonic development, the species requires more than a year for hatching due to an obligatory diapause (personal observation). Therefore, the eggs may experience increased heat and drought during fires at any time of the year. Hence, the species is an ideal model species for testing the relationship between fire parameters and egg mortality.

The effects of fires on egg development are mediated via two factors, which are difficult to disentangle under natural conditions: drought and temperature. Each fire desiccates the soil but also increases soil temperature. While the effects of temperature on insect eggs is well understood, the effects of drought caused by the increased water evaporation from heating has not received a lot of attention. Therefore, experimental approaches are required to better understand the role of drought during fires. We conducted a laboratory experiment, in which we increased soil temperature to critical levels and measured the effects on the eggs of *P. barretoii*. The behaviour and intensity of fires can vary substantially. In many cases, temperatures in the soil (2 cm below the surface) do not increase as dramatically as above the ground (Beadle 1940; Niemeyer 2004; Carrington 2010). Therefore, we exposed eggs to increased temperatures just below and above lethal conditions (49 °C, 55 °C), following

the maximum threshold of animals (50 °C) (Whelan 1995, Branson & Vermire, 2007). In one treatment, we kept the soil water-saturated to exclude mortality from drought (“heated with moisture”). In a second treatment, we did not refill water to measure the drought effects (“heated without moisture”). Egg mortality of both treatments was compared to a control without any temperature increase. In addition, we hypothesised that egg mortality by fires may be lower in years with more variable climatic conditions compared to constantly cool winters. Therefore, both experiments were conducted on eggs kept under constantly cool (10 °C) and staggered warmer (14 °C – 5 °C – 14 °C) conditions following roughly the winter temperature conditions at higher elevations of the island (IPMA 2023).

Methods

Sampling

To obtain eggs for the experiments, fourteen females of *P. barretoii* were sampled between 12 July and 5 September 2021 on Madeira. These females were reared individually or with males in plastic terraria in the climate chamber of the Department of Biogeography at Trier University (Germany) at 23 °C and 13-hour dark/11-hour light conditions. Most females mated in the terraria or were sampled with spermatophores in the field, which indicates that they had been fertilised. Individuals were fed *ad libitum* on other Orthoptera species, caterpillars of wax moths, leaves and flowers of *Taraxacum spp.* and berries (*Rubus spp.* and *Vaccinium spp.*). Because females of *P. barretoii* oviposit in the soil, a plastic cup (192 ml) filled with commercial quartz sand was placed in each terrarium. All cups were initially watered until the sand was saturated. Afterwards, water was added to the cups with an automatic pipette every day *ad-lib*. All cups were placed into separate terraria after oviposition was observed or eggs were found in the cups.

Rearing

Until the second week of December 2021, all eggs were reared in the climate chamber at 23 °C and 13-hour dark/11-hour light conditions. Afterwards, we split the eggs and raised them under two different climate conditions. About half of the eggs were incubated constantly at 10 °C until the start of the experiment (n=596). The other half (n=598) were reared at 14 °C for one week, followed by 5 °C for one month. Afterwards, these eggs were incubated at 14 °C again until the fire experiment started. We subjected eggs from both climate conditions to light cycles of 12-hour dark/12-hour light and moistened them once per day with

2–5 mL of water using an automatic pipette. The temperatures chosen roughly correspond to Madeiran winter temperatures at higher elevations.

Heating experiments

As the maximum temperature threshold for animals is ca. 50 °C (Whelan 1995, Branson and Vermeire 2007), we performed two experiments, in which we heated the cups with the eggs at two different temperatures (49 °C: $n = 507$ eggs and 55 °C: $n = 473$ eggs) for six hours using an oven (Binder GmbH, Germany) (Online Resource S1). We have chosen a six hour treatment, as fires usually do not heat the soil for a long period when approaching or crossing an oviposition site. To be able to measure the effect of drought, we randomly assigned the cups to three treatments (i.e. heated without moisture, heated with moisture, unheated moisture) for the two different rearing conditions (i.e. 10 and 14 °C). In the first treatment, we did not add any water during heating (“heated without moisture”). In the second treatment, we controlled soil moisture based on the weight of the cups before starting the experiment. We added water using an automatic pipette if the weight of the cups was lower than



Fig. 1 Dead eggs of *Psalmatophanes barretoii* (above); alive eggs of *P. barretoii* (below)

before heating (“heated with moisture”). The third treatment (“unheated with moisture as control”) was similar to the second treatment but without any heating; the cups remained in the climate chamber. To examine whether eggs were alive before the experiment, we transferred all eggs into Petri dishes with dry filter papers and left them in the climate chambers for 12–24 h. After this period, we treated collapsed eggs as dead (Ingrisch per. comm.) (Fig. 1). For the experiment, only turgescient eggs were used. We assigned each egg randomly to one of the three treatments and placed them horizontally at 30 mm depth in the sand one by one in each cup as much as possible (which corresponds roughly to the natural oviposition depth; personal observation). All cups were filled with the same amount of sand (308 g dry weight). Afterwards, the cups were watered with the same amount (26 ml) with a pipette and then each cup was weighed before the experiment. The moisture was checked each hour during heating based on the weight before the experiment and refilled in the “heated with moisture” and “non-heated with moisture” (i.e. control) treatment. After the six-hour experiment, all eggs were kept at room temperature for 30 min before placing them back into the climate chambers. To account for the stark difference between heated with and without moisture after the experiment, we added ca. 30 ml water only to the eggs with the moisture treatments one day after heating. Two days after the experiment, the eggs from “heated without moisture” were moistened with the same amount of water. To determine the mortality of eggs, all eggs were moved into Petri dishes on dry filter paper three or four days after heating to quantify mortality (see method described above).

Statistical analysis

To test for differences in egg mortality between the three treatments, we used Generalized Linear Models (GLM) with binomial data distribution (i.e. logistic regression). The conditions of eggs (alive or dead) were treated as the response variable, and the three treatments (heating with drought, heating with moisture and control) were used as the predictor variable. To avoid pseudoreplication, the two experiments (49 or 55 °C) were tested with independent models (i.e. non-comparative statistics for testing the two heating temperatures). To test for differences in egg mortality between rearing conditions, we tested the relationship between the different rearing temperatures (predictor variable) and egg mortality (response variable), regardless of the three treatments for each experiment. In addition, we tested the interaction between the three treatments and the different rearing temperatures on egg mortality (response variable) using a GLM with binomial data distribution. All

Fig. 2 Mean egg mortality in the three treatments burnt at 49 °C (above) and at 55 °C (below), error bars are standard errors

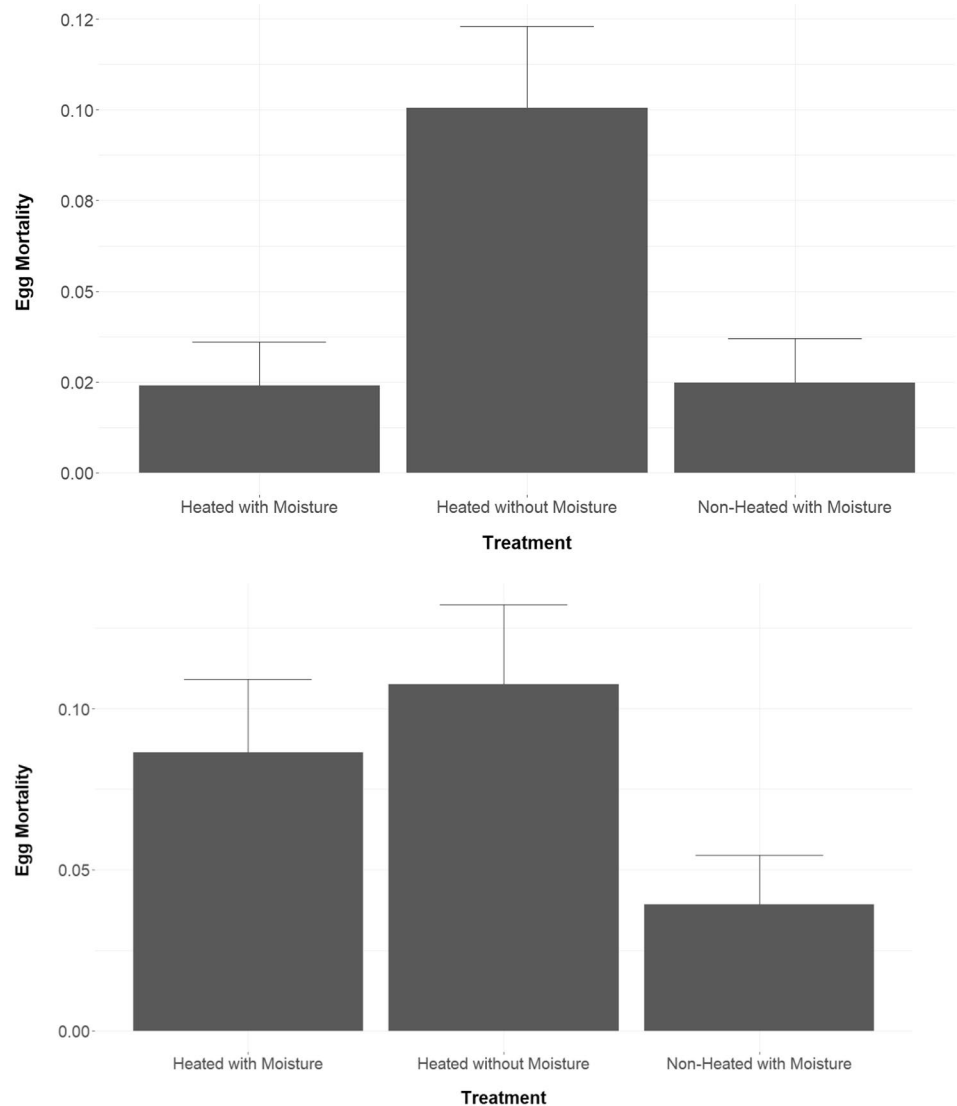


Table 1 Results of Generalized Linear Models (GLM) with binomial distribution of the relationship between egg mortality and the three treatments at 49 and 55 °C. All predictors in the two models were compared with the non-heated moisture (control)

Predictors	Burnt at 49°C		Burnt at 55°C	
	<i>z</i> value	<i>p</i> value	<i>z</i> value	<i>p</i> value
Heating with Drought	-2.62	0.009*	-2.21	0.03*
Heating with Moisture	0.05	0.96	-1.68	0.09

(The symbol * indicates the significance)

statistical and graphical analyses were conducted in R. 3.5.1 (R Core Team 2021).

Results

In experiment 1 (49 °C heating temperature), eggs from the “heated without moisture” treatment had significantly higher mortality than the non-heated with moisture (GLM, $df=504$, $z = -2.622$, $p=0.009$, Fig. 2; Table 1). However, the “heated with moisture” treatment did not differ significantly in egg mortality from the “non-heated with moisture” (GLM, $df=504$, $z=0.05$, $p=0.96$, Fig. 2; Table 1). This trend did not change when the experimental temperature was increased to 55 °C in experiment 2 (heated without moisture vs. non-heated with moisture: GLM, $df=470$, $z = -2.21$, $p=0.03$; heated with moisture vs. non-heated with moisture: GLM, $df=470$, $z = -1.98$, $p=0.09$, Fig. 2; Table 1). Egg

Fig. 3 Mean mortality of eggs reared at two different temperatures after heating of 49 °C (above) and 55 °C (below), error bars are standard errors

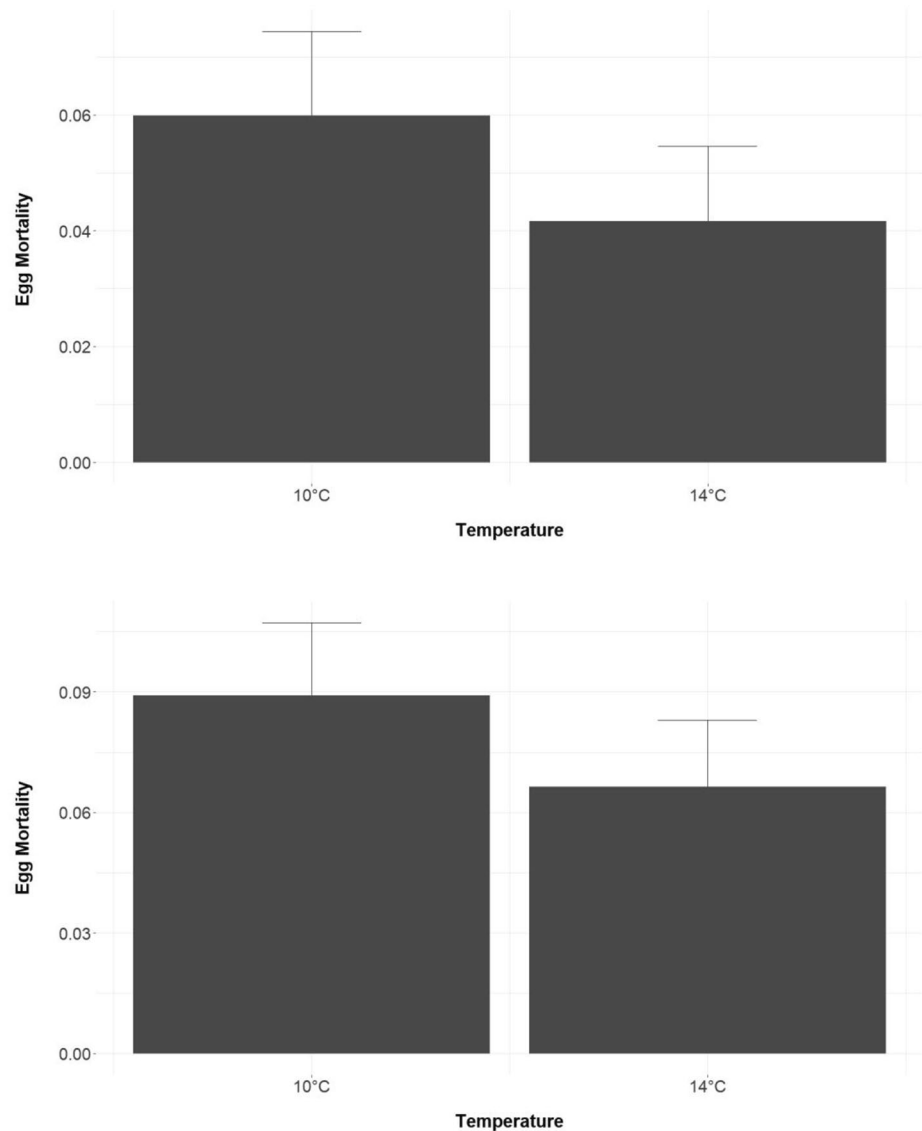


Table 2 Results of Generalized Linear Models (GLM) with binormal distribution of the relationship between the mortality of eggs and the three treatments with rearing temperature at 49 and 55 °C. All predictors in the two models were compared with the control treatment

Predictors	Burnt at 49°C		Burnt at 55°C	
	z value	p value	z value	p value
Rearing Temperature	-0.08	0.93	-0.93	0.35
Heating with Drought	-0.94	0.35	-2.34	0.02*
Heating with Moisture	-0.06	0.95	-0.72	0.47
Heating with Drought with Rearing Temperature	0.052	0.6	2.1	0.04*
Heating with Moisture with Rearing Temperature	0.07	0.94	0.48	0.63

(The symbol * indicates the significance)

mortality did not differ significantly between the two different rearing temperatures (10 °C/14°C) in both experiment 1 (GLM, df= 505, z=0.76, p=0.45, Fig. 3) and experiment 2 (GLM, df=469, z=0.9, p=0.37, Fig. 3). The two different rearing temperatures also did not affect egg mortality among the three treatments in experiment 1 (Heated without moisture vs. non-heated with moisture: GLM, df= 501, z=0.52, p=0.6, Table 2; Heated with moisture vs. non-heated with moisture: GLM, df= 501, z=0.07, p=0.94, Table 2). However, in experiment 2, we found a significant interaction between rearing temperature and heating treatment on egg mortality. Eggs reared at constantly cooler temperature and treated with “heated without moisture” had significantly higher mortality than those of the non-heated with moisture treatment (GLM, df=467, z=2.1, p=0.04, Table 2), while those reared at staggered warmer temperatures showed no

significant effect of the heating treatment (GLM, $df=467$, $z=0.48$, $p=0.63$, Table 2).

Discussion

Our study shows that egg mortality of *P. barretoii* is stronger when increased temperature is accompanied by drought than by high temperature alone. This means that even when soil temperature might not exceed fatal thresholds, drought may substantially increase mortality. Increased rearing temperature alone had no significant effects on egg mortality, regardless of the treatments. However, eggs raised at constantly cooler temperature were more sensitive to the “heated without moisture” treatment (experiment 2) than those raised at variable temperature. Branson & Velmeire (2007) have shown that mortality of insects from fires during hibernation or aestivation is reduced if eggs are placed below ground. Soil, therefore, acts as a buffer towards increased temperature and desiccation. The reduced egg mortality in our treatment “heated with moisture” suggests that soil moisture is a major factor mitigating negative effects from wildfires on insect eggs. This can be caused by both, the buffered temperature in moist soil compared to dry soil (Campbell et al. 1995), but also by direct desiccation of the eggs during fires. Desiccation can reduce the fitness of many insect species, not only by increasing egg mortality but also by slowing down embryonic development (Holmstrup 2019; Salgado et al., 2020; Wang et al. 2022). In insects, the desiccation tolerance of eggs may be due to the different physiological mechanisms of each species during pre-embryonic development, relating to degrees of water uptake (Ingrisch 1986, 1988; Le Hesran et al. 2019). Hence, species with higher drought resistance might also be less prone to wildfires than those with higher water requirements during egg development.

In insects, oviposition substrates buffer eggs against many environmental disturbances (e.g. cold weather, heat and drought) (Branson & Velmeire, 2007; Stauffer and Whitman 2007). Orthoptera species mainly vary in oviposition depth and site selection (Stauffer and Whitman 2007; Hermann et al., 2010; Fieding, 2011; Wünsch et al. 2012). The deeper they lay eggs, the better their eggs can be protected from ambient temperatures above the ground and maintain moisture (Stauffer & Whiteman, 2007; Herrmann et al. 2010). However, even if female Orthoptera lay eggs as deep as possible, desiccation above the soil caused by fires and/or climate change can lead to increased egg mortality. To avoid such negative effects, females may preferably oviposit in moist soil, but it is also known that eggs may mould under too wet conditions (Hartley 1967). Therefore, there is a trade-off between potential effects of drought and

moisture. Under global climate change and with increasing wildfire frequencies, natural selection may favor females ovipositing in moister soil and eggs with better physiological adaptations to desiccation. *P. barretoii* inhabits bushes or trees near streams or edges of Laurel forests (Lange 1990; Pfau and Pfau 2005), where soil moisture is generally higher than in pine forests (e.g. *Pinus pinaster*, *Pinus halepensis*, *Pinus radiata*, *Pinus nigra* and *Pinus sylvestris*) (Cerny et al. 2002; Guimarães and Olmeda 2008; Savill 2015). Consequently, oviposition site selection of females should be studied in the future.

Depending on the ontogenetic stages of the species, fires may affect the mortality of eggs differently. In insects, eggs exposed to heat showed either a slower growth of the embryos or a lower hatching rate compared to eggs that did not experience heat (Klockman & Fischer, 2017). Many Tettigoniidae require water during ontogeny to terminate the obligatory initial diapause (Ingrisch 1986). Older embryos demand higher oxygen than younger embryos to survive (Ingrisch 1987). Fires can decrease both the oxygen and moisture level of the soil (Bryant et al. 2005; Alkin and Kinoshita 2020). Hence, fires and drought may hamper oxygen consumption and water absorption of eggs compared to unburned areas. The different ontogenetic stages of *P. barretoii* may have variable responses to increased temperature and drought. In this study, we used eggs from a single year and conducted the experiment at a short period of time after hibernation. It would be important to also understand the effects of summer fires on egg development, as eggs are permanently laid as soon as the bush-crickets reach adulthood.

Implication for conservation management

An appropriate wildfire management is crucial to preserve fire-sensitive species. Prescribed burning of small areas during moist conditions may help to mitigate the negative effects of wildfires. Maintaining soil humidity is crucial to preserve the eggs of *P. barretoii*, and possibly many other species ovipositing in soil. A conservation management aiming at habitat protection or restoration of moister forest types (e.g. laurel forests) will better benefit such species compared to dry pine forests, not only because of the better soil moisture but also due to the less fire proneness of such forests. To restore natural laurel forests, planting or facilitating native bushes and trees will be necessary, which will also restore the soil conditions (Bell et al. 2009). Laurel forests are characterized by a dense bush layer and many ecotones (Guimarães and Olmeda 2008). This ecosystem does not only reduce fire risk and egg mortality from droughts, but also benefits nymphs and adults by providing habitats for both stages. Hence, restoring laurel forests in post-burnt

areas will help to recover the full habitat spectrum required by the species.

Conclusion

The relationship between fires and the life cycle of animals is relatively little understood (Pausas 2019). Our study shows that eggs of *Psalmatophanes barretoii* may suffer from increased temperatures of approaching or surpassing wildfires, but viability is higher in moist soil. Animals spending parts of their life cycle under ground can have reduced mortality from fires (Nowark et al., 2017, Matthew et al., 2017). Many insect species can survive fires well using this strategy, but our results suggest that survival depends upon the soil conditions, such as moisture or oxygen availability (Smith 2000; Coleman and Rieske 2006; Vincent et al. 2009). To avoid negative effects of fires on the population trend of *Psalmatophanes barretoii* several aspects should be considered: (1) Keeping the size of wildfires small will help to reduce mortality and increase recolonization probability (Rhee et al. 2022); (2) Restoring natural laurel forests will help to reduce the risk of wildfires and increase survival probability due to higher soil moisture; (3) Monitoring biodiversity inside and outside burnt areas will help to document changes and facilitate the implementation of conservation action (e.g. assisted colonization).

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10841-023-00508-5>.

Acknowledgements We would like to thank the Institute of Forests and Nature Conservation in Madeira (IFCN) for permitting us to sample animals on the island. We also thank Sigfrid Ingrisch and Klaus-Gerhard Heller for intensive discussions. We sincerely thank Susan Kennedy, Svenja Ellwart and Caroline Eichert for useful comments on the manuscript. We are also grateful for the help of Sophie Ogan, Lisa Reiss, Nico Fuhrmann and Ortwin Elle. Finally, we would like to thank Philipp Böning and Amadeus Plewnia for sharing a climate chamber for rearing eggs. This study was funded by Mohamed bin Zayed Species Conservation Fund and a Short-term Scholarship of Trier University.

Author contributions Conceptualization: Howon Rhee, Axel Hochkirch; Methodology: Howon Rhee, Axel Hochkirch; Formal analysis and investigation: Howon Rhee; Writing – original draft preparation: Howon Rhee, Axel Hochkirch; Writing – review and editing: Howon Rhee, Axel Hochkirch; Funding acquisition: Howon Rhee; Resources: Axel Hochkirch; Supervision: Axel Hochkirch.

Funding Open Access funding enabled and organized by Projekt DEAL.

Data Availability The data that support the findings of this study are available on request from the corresponding author (Howon Rhee).

Declarations

Compliance with Ethical Standards The Institute of Forests and Nature Conservation in Madeira (IFCN) provided the permit to sample *P. barretoii* on the island. No permits were required for the lab experiments.

Competing interests None.

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