







Evolutionary Implications of Trait-Fire Mismatches for Animals

Luke T. Kelly¹ 📵 | Ary A. Hoffmann² 🗈 | Craig R. Nitschke¹ | Juli G. Pausas³ | Olivia V. Sanderfoot^{4,5} | Morgan W. Tingley⁴

¹School of Agriculture, Food and Ecosystem Sciences, The University of Melbourne, Parkville, Victoria, Australia | ²School of BioSciences, Bio21 Institute, The University of Melbourne, Parkville, Victoria, Australia | ³Desertification Research Center, Consejo Superior de Investigaciones Científicas (CIDE, CSIC-UV-GV), Moncada, Valencia, Spain | ⁴Department of Ecology and Evolutionary Biology, University of California, Los Angeles, California, USA | ⁵Department of Ornithology, Natural History Museum of Los Angeles County, Los Angeles, California, USA

Correspondence: Luke T. Kelly (ltkelly@unimelb.edu.au)

Received: 8 July 2025 | Revised: 8 July 2025 | Accepted: 14 July 2025

Keywords: biodiversity | intraspecific variation | maladaptation | phenotype-environment mismatch | rapid evolution | wildfire

Human activity is changing when, where, and how fires burn, contributing to population declines of many species (Kelly et al. 2025). Animal populations can respond to modified fire regimes by dispersing to suitable areas, adjusting traits through plastic responses such as behavioral or reproductive shifts, and adapting through evolutionary changes in their genetic make-up (Jones et al. 2023). Evolutionary adaptation may be required when environmental conditions no longer match the traits animals have evolved, and this warrants specific attention in fire and global change research (Nimmo et al. 2021).

In this Perspective, we build on a plant-focused application of the phenotype-environment mismatch concept, extending it to animals to understand the evolutionary and ecological consequences of altered fire regimes. Mismatches are primarily studied in the context of climate-driven changes (e.g., Petrullo et al. 2023), but trait-fire mismatches require dedicated investigation given fire's global reach, rapid and difficult-to-predict shifts, and extensive direct and indirect impacts on animals. Our framing brings into focus the role of fitness, variation in traits within species, and selection in shaping evolutionary responses to fire. By applying this phenotypic approach to

animals, we provide a framework for investigating fire-related changes across a wide range of taxa and traits.

1 | Fire-Related Traits Vary Among and Within Animal Species

Fire regimes have temporal and spatial attributes, including the frequency and size of recurrent fires, as well as attributes that characterize the magnitude of fires such as their intensity (Figure 1). Many animal species thrive under particular fire patterns, so changes to fire attributes can affect fitness. Fires directly influence survival and reproduction: exposure to heat and smoke can cause mortality (Santos et al. 2025) or disrupt breeding (Krieg 2025). Other effects on survival and reproduction are indirect, developing through post-fire shifts in biotic interactions, microclimate, and resource availability (Jones et al. 2023).

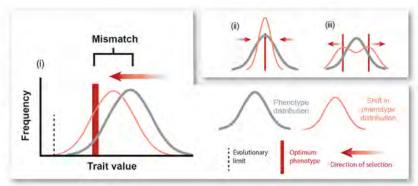
Ecological studies have generated important insights into firerelated traits, including behavioral, life-history, morphological, and physiological characteristics that influence fitness in fireprone environments. A common focus is interspecific variation

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2025 The Author(s). Global Change Biology published by John Wiley & Sons Ltd.

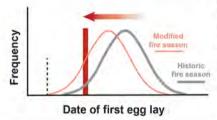
Panel A

Trait—fire mismatch is a form of maladaptation that occurs when a population's trait distribution differs from that best suited to a fire regime. One way to measure mismatch is the distance between the trait mean and the trait value that maximizes fitness—an intuitive measure when mismatch involves a single optimum, as in directional selection (i). Mismatches may also reflect excess variation around the optimum or clustering in a low fitness valley, consistent with stabilizing (ii) and disruptive selection (iii), respectively. In such cases, we propose that mismatch may be more generally assessed by comparing the population's average fitness across its full trait distribution, capturing spread and shape, to that of an of an optimally structured trait distribution.







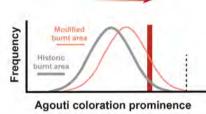


House wren (*Troglodytes aedon*) nestlings exposed to smoke pollution from Canadian wildfires were smaller than usual, likely reducing their fitness (Krieg 2025). Earlier wildfire seasons may harm songbirds during critical life stages. One hypothesis is that earlier breeding allows individuals to avoid smoke exposure, increasing reproductive success and potentially driving evolution of heritable traits such as egg-laying date.

Other temporal attributes: fire frequency, fire interval

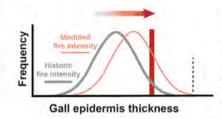
Other spatial attributes: fire patchiness, fire size





Eastern fox squirrels (Sciurus niger) with agouti-colored pelage—characterized by banded, multi-toned hair—are positively associated with a greater proportion of burnt area, whereas lighter-colored individuals are more common in cropland-dominated landscapes which are more visually uniform. Pelage color in fox squirrels is likely adaptive, with agouti coloration offering improved camouflage in the heterogeneous environments shaped by fire (Potash et al. 2020)





The Boheman weevil (Collabismus clitellae) induces galls in plant tissues, creating a protective structure for its developing larvae. In recently burnt areas, survival of immature weevils increases with thicker gall epidermis, possibly because thicker tissue reduces exposure to heat and flames. Intraspecific variation in gall structure is only beginning to be understood. One hypothesis is that intense fires may drive directional selection for thicker galls, if gall traits are heritable. Alternatively, if the relationship between gall thickness and survival differs between burnt and unburnt areas, or at sites burnt at different intensities, this could lead to disruptive selection (Santos et al. 2025).

Other magnitude attributes: fire severity, fire type

FIGURE 1 | Trait–fire mismatching. Panel A: Conceptual overview of how trait–fire mismatches are defined and measured. Panel B: Illustrative examples where changes in fire patterns may reduce animal fitness (See: Krieg 2025; Potash et al. 2020; Santos et al. 2025). In each case, modified fire regimes—shifts in the timing, spatial attributes, or magnitude of fire—are hypothesized to impose selection pressures. The evolutionary potential of fire-related traits is represented by idealized phenotypes in transition and signals the possibility of adaptive change. Photo credits: House wren: Cephas, CC BY-SA 4.0, via Wikimedia Commons; Eastern fox squirrel: U.S. Fish and Wildlife Service - Midwest Region, Public domain, via Wikimedia Commons; Gall of the Boheman weevil: Jean Carlos Santos.

(between species) in fire-related traits. For example, traits such as diet, foraging location, and nesting habits help explain bird species' distributions across stages of post-fire vegetation succession (Rainsford et al. 2023). Yet, understanding how animals are affected by shifting fire regimes requires moving beyond static trait-fire associations and considering how relevant traits themselves may evolve.

Intraspecific trait variation (within species) provides the raw material for contemporary adaptive evolution, with growing evidence of fire-related differences among individuals of the same species. In Sweden, melanistic (black) pygmy grasshoppers (*Tetrix subulata*) are more common in burnt forests than unburnt areas, likely because melanism enhances camouflage in recently burnt vegetation (Forsman et al. 2011). A laboratory common garden experiment indicates that color variation in pygmy grasshoppers has a heritable component, suggesting rapid evolutionary adaptation (Forsman et al. 2011). A Mediterranean lizard (*Psammodromus algirus*) in fire-prone habitats reacts more frequently and intensely to smoke than conspecifics from rarely burnt areas, likely an adaptive behavior that enhances survival during fire (Álvarez-Ruiz

et al. 2021). In Brazil, Boheman weevils (*Collabismus clitellae*) induce galls by manipulating plant growth, and within a recently burnt area thicker gall walls improved larval survival, potentially by reducing exposure to heat and flames (Santos et al. 2025).

Key insights from this concise selection of studies are that firerelated traits can vary within species, enhance fitness, and be heritable. These are preconditions for adaptive evolution.

2 | Mismatches Between Animal Traits and Emerging Fire Regimes

To examine the consequences of shifting fire patterns on animal life, we develop a "trait-fire mismatch" framework that focuses on how selection acts on phenotypes and highlights within-species trait variation as central to adaptation (Figure 1). This builds on the concept of phenotype-environment mismatch, which describes misalignment between organisms and altered environments, and has recently been applied to plant-fire dynamics (Kelly et al. 2025). While existing ecological frameworks often focus on a narrow set of traits to assess fire-related vulnerability, trait-fire mismatch enables examination of a wide range of traits and fire regime characteristics within a single framework. This is particularly useful given the diversity of animal traits that influence fitness in fire-prone systems (Figure 1). Trait-fire mismatch thus provides a common phenotypic currency for comparing the effects of modified fire regimes across traits, populations, and species.

Trait-fire mismatch occurs when a population's trait distribution diverges from that best suited to a given fire regime (Figure 1). Such mismatches can be driven by shifts in fire timing, spatial pattern, or magnitude. Large mismatches create evolutionary crossroads: reduction in survival and reproduction to the point of local extinction or selection that promotes persistence. We suggest that strong selection may not be enough to counter fire regime changes if intraspecific variation is low, few individuals have advantageous traits, realized heritability is limited, or fire regime changes are abrupt. Few studies have tested whether fire patterns drive rapid animal evolution, but focus on intraspecific variation and selection opens new opportunities for research. For example, P. algirus from fire-prone habitats reacted to smoke more frequently (93% of individuals) than those from non-fire-prone areas (71%), but to what extent is recognition of smoke heritable? And how close are populations to "hard" evolutionary limits—such as insufficient genetic variation—or to "soft" limits imposed by lack of gene flow? Addressing such questions requires methods that quantify links between ecological and evolutionary processes.

3 | Investigating Trait-Fire Mismatches

Quantitative genetics offers methods to estimate how fire-driven selection shapes phenotypes. The breeder's equation provides a starting point, predicting evolutionary change based on heritability and selection strength, with extensions incorporating multiple traits, phenotypic plasticity, gene flow, and demographic constraints (Kelly et al. 2025). Field studies, manipulative experiments, and laboratory experiments can generate the phenotypic and fitness data needed to parameterize these models. Genome-wide association studies (GWAS) and genotype-environment associations (GEAs) can identify loci linked to trait variation and fire exposure (Kelly et al. 2025). Coupled with empirical or simulated fire and environmental data, these approaches help determine whether populations can adapt as fire regimes shift.

While quantitative methods deepen our understanding of fire-driven evolution, studying animals presents distinct challenges. First, trait-fire mismatches can develop indirectly through post-fire changes in habitat structure, microclimate, or resource availability (Figure 1). Direct and indirect effects may be examined by comparing trait distributions to optima, but interpreting mismatches requires understanding how fire mediates resources such as food and shelter. Clarifying these pathways helps identify how ecological conditions shaped by fire translate to selection on phenotypes. Second, species interactions—including antagonisms, commensalisms, and mutualisms—can shape evolutionary responses to fire (Nimmo et al. 2021). Investigating how interactions between taxa are shaped by modified fire patterns, such as insect pollination of plants, will improve understanding of co-evolutionary dynamics and disruptions to biotic relationships. Third, covariation among traits may constrain or facilitate adaptation, including when fire modifies other selection processes like predation (Forsman et al. 2011). Quantitative genetic models provide insights into these linkages but are challenging to parameterize. Finally, fire-related traits span molecular to whole-organism levels. While traits such as diet, foraging behavior, and shelter selection are well-studied across species, examining their variation within species will clarify their role in fire-driven adaptation. Simultaneously, expanding research to underexplored traits—including those involved in fire detection, survival, and post-fire reproduction—is essential to uncover the breadth of adaptive responses.

4 | Animal Conservation in a Fast-Changing World

Conservation can be improved by examining how mismatches between animal traits and fire regimes arise, whether through larger, more intense wildfires or reduced fire frequency. One strategy is to manage fires to better align animal traits with environmental conditions. For example, knowing how interactions between bird traits and fire-generated patterns vary across biogeographic regions can inform where and when fire should be applied or moderated (Rainsford et al. 2023). A second strategy fosters adaptation by managing phenotypes. For instance, boosting population sizes, connectivity, and gene flow will likely enhance adaptive potential in response to changing fire patterns. While mismatches typically reduce fitness, maintaining some mismatched phenotypes can promote persistence in unpredictable environments by supporting adaptive potential (Petrullo et al. 2023). A cornerstone of effective management will be conserving conspecific animal populations across the range of their fire-related trait variation.

5 | Conclusion and Future Directions for Trait-Fire Research

Recognizing variation within species opens opportunities to understand evolutionary adaptation. Nevertheless, evolution is no guarantee of persistence—many animal species may not adapt fast enough to keep pace with emerging fire regimes. A phenotypic perspective helps assess how trait distributions match—or mismatch—with changing fire regimes. To advance this approach, we suggest four key questions:

- How much intraspecific variation exists in fire-related animal traits?
- 2. What is the likely heritability of these traits?
- 3. How does trait covariation shape adaptation under interacting fire, climate, and biotic pressures?
- 4. Can the tempo of evolutionary adaptation match the rate of fire regime changes?

More broadly, our perspective is that global change and evolutionary research will benefit from recognizing fire as an important process that interacts with other global drivers to shape animal diversity and adaptation.

Acknowledgments

Kelly was supported by a sabbatical from the Faculty of Science at The University of Melbourne and gratefully acknowledges the Department of Ecology and Evolutionary Biology at University of California, Los Angeles, and the Department of Plant Sciences, University of Cambridge, UK, for hosting his research. Open access publishing facilitated by The University of Melbourne, as part of the Wiley - The University of Melbourne agreement via the Council of Australian University Librarians.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The authors have nothing to report.

References

Álvarez-Ruiz, L., J. Belliure, and J. G. Pausas. 2021. "Fire-Driven Behavioral Response to Smoke in a Mediterranean Lizard." *Behavioral Ecology* 32: 662–667. https://doi.org/10.1093/beheco/arab010.

Forsman, A., M. Karlsson, L. Wennersten, J. Johansson, and E. Karpestam. 2011. "Rapid Evolution of Fire Melanism in Replicated Populations of Pygmy Grasshoppers." *Evolution* 65: 2530–2540. https://doi.org/10.1111/j.1558-5646.2011.01324.x.

Jones, G. M., J. F. Goldberg, T. M. Wilcox, et al. 2023. "Fire-Driven Animal Evolution in the Pyrocene." *Trends in Ecology & Evolution* 38: 1072–1084. https://doi.org/10.1016/j.tree.2023.06.003.

Kelly, L. T., A. A. Hoffmann, C. R. Nitschke, and J. G. Pausas. 2025. "Can Plants Keep Up With Fire Regime Changes Through Evolution?" *Trends in Ecology & Evolution* 40: 663–672. https://doi.org/10.1016/j.tree.2025.04.009.

Krieg, C. A. 2025. "Depressed Nestling Growth During Exposure to Smoke From Distant Wildfires." *Scientific Reports* 15: 8200. https://doi.org/10.1038/s41598-025-93101-6.

Nimmo, D. G., A. J. Carthey, C. J. Jolly, and D. T. Blumstein. 2021. "Welcome to the Pyrocene: Animal Survival in the Age of Megafire." *Global Change Biology* 27: 5684–5693. https://doi.org/10.1111/gcb. 15834.

Petrullo, L., S. Boutin, J. E. Lane, A. G. McAdam, and B. Dantzer. 2023. "Phenotype–Environment Mismatch Errors Enhance Lifetime Fitness in Wild Red Squirrels." *Science* 379: 269–272. https://doi.org/10.1126/science.abn0665.

Potash, A. D., D. U. Greene, V. L. Mathis, B. Baiser, L. M. Conner, and R. A. McCleery. 2020. "Ecological Drivers of Eastern Fox Squirrel Pelage Polymorphism." *Frontiers in Ecology and Evolution* 8: 119. https://doi.org/10.3389/fevo.2020.00119.

Rainsford, F. W., K. M. Giljohann, A. F. Bennett, et al. 2023. "Ecosystem Type and Species' Traits Help Explain Bird Responses to Spatial Patterns of Fire." *Fire Ecology* 19: 59. https://doi.org/10.1186/s42408-023-00221-3.

Santos, J. C., H. Venâncio, G. R. Demetrio, W. R. de Almeida, W. S. de Araújo, and P. Cuevas-Reyes. 2025. "Set Fire to the Gall: Can the Gall Protect the Galling Weevil From Fire?" *Ecology* 106: e70083. https://doi.org/10.1002/ecy.70083.

4 of 4 Global Change Biology, 2025