Trends in
Ecology & Evolution

CellPress

Letter

Fire-adapted traits in animals

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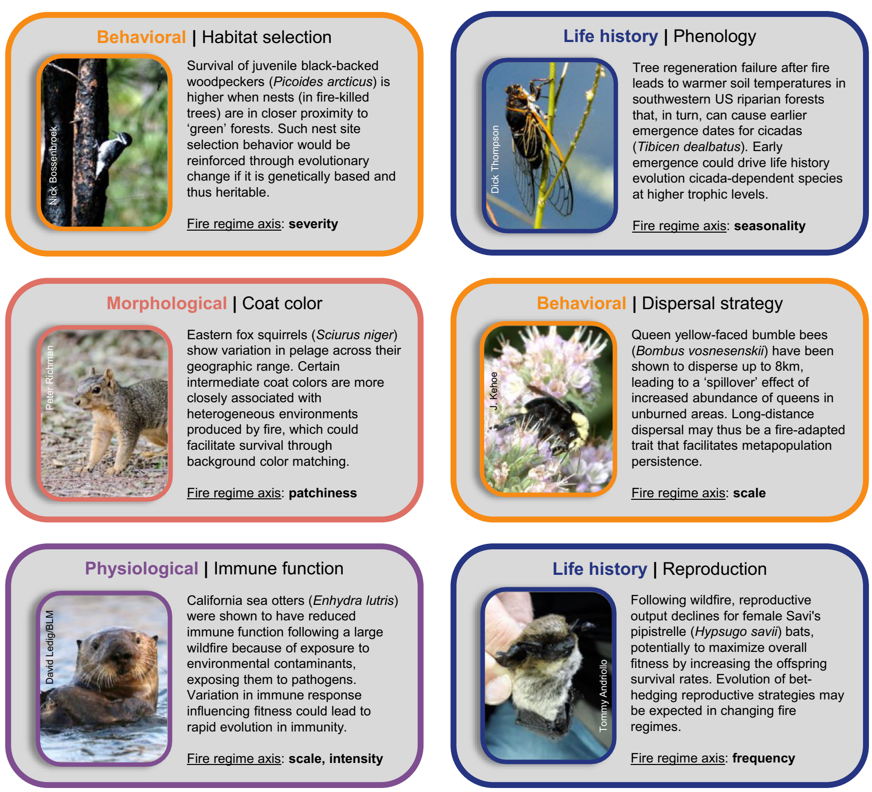
Fire is a pervasive driver of trait evolution in animals and its importance may be magnified as fire regimes rapidly change in the coming decades. This was the thesis of our paper published recently in *Trends in Ecology and Evolution* [1]. In their response letter, Nimmo *et al*. [2] reinforce our thesis and suggest expansion of some of our conceptual models.

Specifically, Nimmo *et al*. [2] outline two possible additions. First, they argue that a broader range of traits should be considered as potentially being responsive to fire and draw particular attention to reproductive and phenological traits. This expanded range of traits is likely to experience selective pressure in response to different axes of a fire regime, for example, selection on breeding strategies may be closely linked to fire seasonality. Second, Nimmo *et al*. [2] suggest an expansion of the definition of 'fire-adapted' fauna to include a broader swath of taxa that may not have obvious traits to facilitate fire survival or persistence, but instead may have evolved movement or dispersal strategies that enhance their persistence in fire-prone landscapes.

Traits can be difficult to characterize since they aggregate in complex ways to determine organismal performance in dynamic environments, particularly fire-prone environments. We agree some expansion is beneficial beyond the categories we included: behavioral, physiological, and morphological traits, which were originally proposed by Pausas and Parr [3] (Figure 1). Yet many traits related to phenology and reproduction fall within existing categories. Both phenology and reproduction are often set by developmental rates and other physiological traits, and sometimes phenological and reproductive traits involve behavioral responses to environmental cues related to the seasonal timing of events. One productive strategy aligned with what Nimmo *et al*. [2] suggest is to consider fire-driven life history evolution, which relates to pace-of-life syndromes, age-dependent strategies, juvenile development, lifespan, and similar traits. A comprehensive consideration of linkages between fire and life history can illuminate evolutionary responses to fire [4].

We appreciate the emphasis by Nimmo *et al*. [2] on animal movement strategies and we agree they should be considered fire-adapted traits. Fire-associated movement and dispersal strategies may represent a promising avenue for future fire-driven evolution research given they are relatively easy to study, for example, using GPS or satellite transmitters. The potential evolutionary importance of movement strategies was noted by Pausas and Parr [3], where they give 'ability to move long-distance' as an example of a trait that



Trends in Ecology & Evolution

Figure 1. Examples of potential fire-driven trait evolution in animals and possible fire regime axis that may drive selection. We identify four classes of traits: behavioral, morphological, physiological, and life history traits, indicated by different box colors. Note that we have included 'dispersal strategy' as a type of behavioral trait and 'phenology' and 'reproduction' as types of life history traits. From upper left to lower right, the studies corresponding with the examples are Stillman *et al*. [7] (top left), Mola *et al*. [8] (top right), Potash *et al*. [9] (middle left), Bowen *et al*. [10] (middle right), Smith *et al*. [11] (bottom left), Ancillotto *et al*. [12] (bottom right). All photos are used under a CC-BY license or are in the public domain.

could be adaptive for animals living in fire-prone landscapes. Similarly, in our paper, we wrote: 'Whether fire facilitates or inhibits gene flow likely depends on the scale of the fire relative to animal dispersal capabilities…' and 'If the trait(s) related to fire are heritable, vary within the population, and create a fitness differential (i.e., different phenotypes show variance in survival), selection will act upon the distribution of trait values within a population'. Thus, we think that fire-adapted fauna should be defined as those with any type of genetically based traits that increase the fitness of animal populations in response to fire regimes, which could include movement, dispersal, life-history strategies, and any others.

We concur with the need for a broad view of traits subject to selection. Responses to novel selection pressures associated with changed fire regimes will involve many traits, even beyond those that have so far been proposed by us and by Nimmo *et al*. [2] (e.g., Figure 1). Combinations of traits may be selected for that are novel across evolutionary history [5]. Evolution can be slowed substantially when novel selection acts against existing trait correlations [6]. Thus, we must think broadly and synthetically about the many types of traits mediating ecological and evolutionary responses to fire in a changing world, how they may interact, and to which components of fire regime they may be linked (Figure 1). At the same time, we need researchers to add case studies to understand how selection of multiple traits actually unfolds in laboratory and natural systems.

Our hope is that, like Nimmo *et al*. [2], more researchers will attempt to downscale and adapt the broad recommendations we made in our paper to meet their needs and their deep understanding of the systems they work on. We did not intend our brief list of the types of traits (morphological, behavioral, physiological) to be exhaustive or all-encompassing and we suspect there are classes of traits still not included after our dialogue with Nimmo *et al*. [2].

Declaration of interests

No interests are declared.

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https://doi.org/10.1016/j.tree.2023.09.016

Published by Elsevier Ltd.

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