Animal movements in fire-prone landscapes

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ABSTRACT

Movement is a trait of fundamental importance in ecosystems subject to frequent
disturbances, such as fire-prone ecosystems. Despite this, the role of movement in facilitating
responses to fire has received little attention. Herein, we consider how animal movement
interacts with fire history to shape species distributions. We consider how fire affects
movement between habitat patches of differing fire histories that occur across a range of
spatial and temporal scales, from daily foraging bouts to infrequent dispersal events, and
annual migrations. We review animal movements in response to the immediate and abrupt
impacts of fire, and the longer-term successional changes that fires set in train. We discuss
how the novel threats of altered fire regimes, landscape fragmentation, and invasive species

result in suboptimal movements that drive populations downwards. We then outline the types of data needed to study animal movements in relation to fire and novel threats, to hasten the integration of movement ecology and fire ecology. We conclude by outlining a research agenda for the integration of movement ecology and fire ecology by identifying key research questions that emerge from our synthesis of animal movements in fire-prone ecosystems.

I. INTRODUCTION

Movement is of fundamental importance to animals: it shapes their ability to access resources, maintain homeostasis, find mates, and respond to predators, parasites and competitors, thus influencing growth, survival, reproduction and hence fitness (Nathan *et al.*, 2008; Weinstein, Buck & Young, 2018). The types and patterns of movements that animals undertake depend on a species' ecological traits, life-history stage, and their external environment, including both biotic and abiotic factors (Holyoak *et al.*, 2008; Nathan *et al.*, 2008). Movement – motivated by different goals – occurs over a variety of spatial and temporal scales, from daily foraging within a home range to long-distance dispersal and migration (Jeltsch *et al.*, 2013).

Movement is particularly important in environments that are subject to periodic changes (Hanski, 1999; Roshier, Doerr & Doerr, 2008), such as those experiencing regular fire. By incinerating plant matter, fire resets successional processes, altering the composition and structure of vegetation (Fox, 1982). As vegetation structure and composition change during post-fire succession, so too does the type, abundance and distribution of resources available to animals, including shelter, food, and foraging microhabitats (Nimmo *et al.*, 2014; Valentine *et al.*, 2014; van Mantgem, Keeley & Witter, 2015). The dynamic nature of fire-prone landscapes thus places a premium on strategies of mobility that improve the chances of individual survival and the persistence of populations. In the short term, animals may move to avoid being burnt during fire (Geluso & Bragg, 1986; Grafe, Döbler & Linsenmair, 2002; Pausas & Parr, 2018), but in the longer term may need to track shifts in resources that emerge during post-fire vegetation succession. The ease and risk of movement will be affected by the landscape patterns brought about by fires (Bradstock *et al.*, 2005), specifically, the composition, areal extent and spatial configuration of patches of different fire histories and intensities across the landscape (Parr & Andersen, 2006; Nimmo *et al.*, 2013).

Here, we consider how animal movement interacts with the fire regime to influence species distributions. Our focus is on fire-dependent animal species (Pausas & Parr, 2018), i.e. species that are acutely affected either by direct mortality during fire events or by the longer-term effects of fire, such as post-fire changes in resource availability. Because fire-dependent species depend on resources affected by fire, their distributions are closely linked to one or more aspects of the fire history of an area – the time since fire, the severity and season of fires, and the average interval between or frequency of fires, collectively termed the 'fire regime' (Gill, 1975; Gill & Allan, 2009) – that characterises a particular patch.

We consider movements in relation to two broad classes of fire-induced change: (*i*) abrupt changes that occur during and immediately following a fire, in which large amounts of biomass are incinerated, often resulting in radical changes in vegetation structure (Section II), and (*ii*) the longer-term successional changes that occur in the period following fire (Sections III and IV), in which vegetation gradually returns in a process that can continue for decades or even centuries (Haslem *et al.*, 2011; Davis *et al.*, 2018). We consider how fire affects movement among habitat patches of differing fire histories that occur across a range of spatial

and temporal scales (Fig. 1): infrequent dispersal events (Section II), daily foraging bouts (Section III) and large-scale, opportunistic movements and annual migrations (Section IV). We identify novel factors that might result in suboptimal movements of animals in a fire-prone landscape (Section V). We conclude by highlighting data needs (Section VI) and key questions (Section VII) that will help clarify the role of animal movements in affecting the responses of species to fire-induced vegetation change.
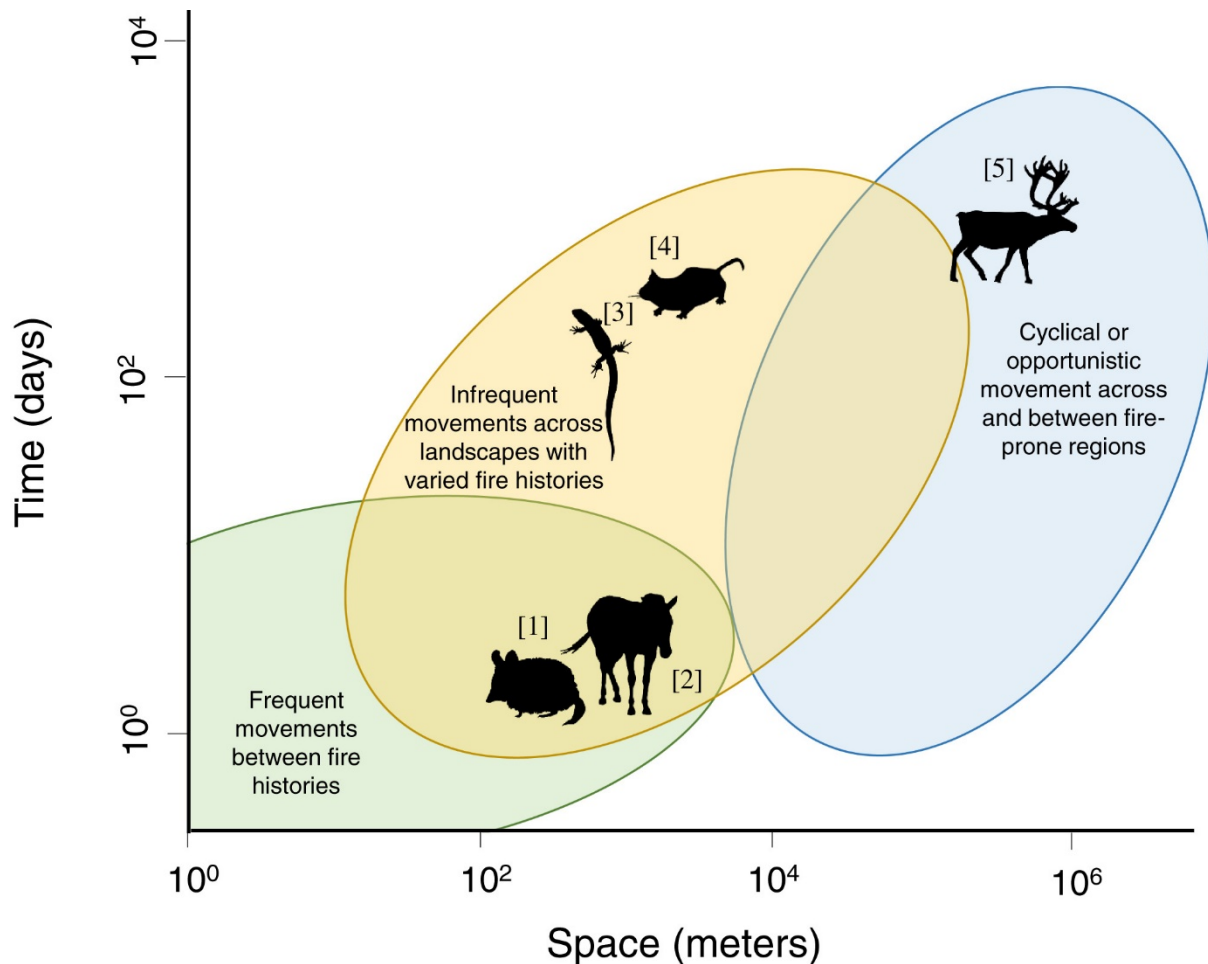

Figure 1, Overview of the spatial and temporal scales of animal movements (adapted from Jeltsch *et al*. (2013) and how they relate to types of movements in fire-prone landscapes. Animal silhouettes indicate the following examples from the literature: [1], Letnic & Dickman (2005); [2], Burkepile *et al*. (2013); [3], Templeton, Brazeal & Neuwald (2011); [4], Pereoglou *et al*. (2013); [5], Skatter *et al*. (2017).

II. INFREQUENT MOVEMENTS ACROSS NON-PREFFERED FIRE HISTORIES

(1) Movements in response to abrupt, fire-induced changes

The immediate effects of a fire trigger a range of movements, both within, away from, and towards the burned (or burning) area. Movements towards fires and recently burned patches are well documented for predators, which take advantage of increased detection of prey exposed to a simplified post-fire landscape (McGregor *et al*., 2015; Leahy *et al*., 2016). Hovick *et al*. (2017) showed that raptors are strongly drawn towards fires, with maximum abundances increasing sevenfold during (*cf*. before) fire. There have been similar observations of rock kestrels (*Falco tinnunculus*) and jackal buzzard (*Buteo rufofuscus*) selectively hovering above recently burned areas (Barnard, 1987). Indeed, Bonta *et al*. (2017) report evidence of black kites (*Milvus migrans*), whistling kites (*Haliastur sphenurus*), and

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brown falcons (*Falco berigora*) deliberately spreading fire by transporting burning sticks in tropical Australian savannas. The scale of directional movements towards fires by such predators remains largely unknown, but, given the mobility of many large predators and the strong olfactory and visual cues of fire (e.g. smoke plumes), directional movements could be triggered tens to hundreds of kilometres from the fire boundary (depending on fire size and intensity). For example, in arid and tropical Australia, feral cats (*Felis catus*) have been recorded making >10 km directional movements to locate recently burned areas (McGregor *et al*., 2016; McGregor, Cliff & Kanowski, 2017).

Early successional species other than predators are also attracted to fire or to recently burned areas (Nappi *et al*., 2010; Saracco, Siegel & Wilkerson, 2011). A prime example is fire beetles (genus *Melanophila*), which are highly dependent on recent fire for reproduction, as their larvae develop only in the wood of trees recently killed by fire (Schütz *et al*., 1999). These beetles have chemoreceptors that can detect the olfactory cues of fire at very low concentrations (a few parts per billion), facilitating the detection of distant fire (Schütz *et al*., 1999; Schmitz *et al*., 2008). *Melanophila* species also possess thermoreceptors that can detect infrared radiation from fires, with one species (*Melanophila acuminata*) able to detect a 50 acre fire from 5 km away (Evans, 1966), and one study suggesting that individuals of some species can detect fire from 130 km (Schmitz & Bousack, 2012). Some animal species depend on pyrophillic invertebrates as food sources, and so are drawn into burned areas in turn; the black-backed woodpecker (*Picoides articus*) is an early successional species that prefers severely burned areas partly due to high abundances of their wood-boring beetle prey (Hutto, 1995, 2008; Smucker, Hutto & Steele, 2005; Saracco *et al*., 2011). As with predators, an important question is what distances early successional species like the black-backed woodpecker travel to access recently burned areas. Such knowledge could help explain variation in post-fire assemblages based on dispersal limitations (Brotons, Pons & Herrando, 2005; Watson *et al*., 2012a).

The period during and immediately following a fire is a particularly critical time for species dependent on resources that have been consumed by fire, as it requires either rapid dispersal away from the burned area in search of more suitable habitat, or seeking refuge to buffer individuals from the altered resource base and heightened predation risk that characterises recently burned areas (Leahy *et al*., 2016; Hovick *et al*., 2017). Some fire-dependent species possess adaptations that allow them to weather these immediate impacts of fire by avoiding movement (Stawski *et al*., 2015a). For instance, some mammals use torpor to reduce their energetic requirements and remain within their natal home range despite fire-induced changes (Tannenbaum & Pivorun, 1989; Körtner, Pavey & Geiser, 2007). Short-beaked echidnas (*Tachyglossus aculeatus*) seek refuge and use torpor during fire to maintain lower average body temperatures and reduce activity, thereby reducing energetic demands (Nowack, Cooper & Geiser, 2016). Similarly, brown antechinus (*Antechinus stuartii*) and yellow-footed antechinus (*Antechinus flavipes*) increase the frequency and duration of torpor and decrease their daily activity after a fire and therefore avoid risky foraging bouts within the simplified post-fire landscape (Stawski *et al*., 2015a*;* Matthews *et al*., 2017).

For species that cannot draw on these or similar adaptations, rapid refuge-seeking will be undertaken both within and beyond the fire boundary (Grafe *et al*., 2002; Garvey *et al*., 2010). The behavioural response of many species to fire cues points to the importance of a rapid reaction to incipient fire. For instance, eastern red bats (*Lasiurus borealis*), which hibernate beneath leaf litter, rewarmed from torpor in response to smoke and the sound of flames (Scesny, 2006), while smoke exposure initiated rapid rewarming in Gould's long-

eared bats (*Nyctophilus gouldi*) and fat-tailed dunnarts (*Sminthopsis crassicaudata*) (Stawski *et al*., 2015b*;* Doty *et al*., 2018). These flight responses are presumably due to the flammability of their retreat sites. Similarly, Grafe *et al*. (2002) showed that juvenile reed frogs (*Hyperolius nitidulus*) fled towards protective cover in response to the sounds of fire.

(2) Tracking fire histories across space and time

Some fire-dependent species that are small in size or have low mobility relative to the spatial grain of the landscape are likely to gain all or most of their resources from a single patch of a given fire history. For these species, the majority of 'maintenance movements' (i.e. movements aimed at meeting an individual's immediate and short-term needs, *sensu* Roshier & Reid, 2003) occur at a finer scale than the average fire-patch size. While these species can avoid regular movements (e.g. for foraging, shelter or mate-searching) into patches of non-preferred fire histories, the distribution and abundance of resources they require within a fire history – such as food or shelter (Higgins *et al*., 2007; Haslem *et al*., 2011) – changes with the time since the last fire. Therefore, such species must find ways of tracking their preferred habitat across space, as the changes that occur during post-fire succession render an occupied site unsuitable (i.e. as it transitions from a preferred to an unpreferred fire history). Movements of such species between patches of different fire histories are infrequent and undertaken primarily for the purposes of dispersal, motivated by the need to leave a site that has become unsuitable. Dispersal is likely to be a major determinant of population persistence for such species because if individuals do not disperse they risk reduced fitness or increased mortality (Amarasekare & Possingham, 2001; Brotons *et al*., 2012).

When there is an element of predictability in how environments change, condition-dependent dispersal strategies can evolve in response (Bowler & Benton, 2005; Bonte & de la Pena, 2009). Given that successional changes that occur following fire are relatively predictable (Haslem *et al*., 2011), species in fire-prone ecosystems should display condition-dependent dispersal, with dispersal probabilities varying according to (among other things) temporal variation in habitat quality (Bowler & Benton, 2005). Condition-dependent dispersal can be triggered by prenatal or postnatal cues that affect the probability of natal dispersal (Massot *et al*., 2002; Matthysen, 2005), or environmental cues affecting breeding dispersal (Robertson, Fletcher & Austin, 2017). Dispersal cues could act indirectly, if the body condition of breeding adults deteriorates in low-quality habitat and leads to increases in natal dispersal, or directly if adult animals emigrate from an area as it progresses into unsuitable habitat.

The decision to disperse will be influenced by a number of other factors affecting the costs and benefits of dispersal, including the habitat an animal will be moving through (as this may contribute to the risk of mortality during transit), the likelihood of finding an appropriate site elsewhere, and the costs and benefits of knowledge acquisition about nearby habitats. The first of these factors relates to a species' 'boundary response' (Fahrig, 2007): how a species responds when it encounters a boundary between an occupied patch and a different patch type. In ecosystems where fire history is a major determinant of vegetation structure, the contrast between patches will be influenced by fire history. For instance, in some ecosystems, patches that are close in fire-age are more structurally similar than patches that are far apart in age (Haslem *et al*., 2011). In those instances, the structural contrast between adjacent fire-ages determines how 'hard' or 'soft' the boundary is between fire-ages.

The contrast between patch types can influence a species' boundary response. For instance, eastern collared lizards (*Crotaphytus collaris*) do not disperse into unburned forests

surrounding occupied patches, but move readily through recently burned areas that more closely resemble the glades they prefer to occupy (Templeton *et al.*, 2011). Similarly, the eastern chestnut mouse (*Pseudomys gracilicaudatus*), an early successional species, disperses readily through recently burned vegetation (Pereoglou *et al.*, 2013). Movements of the bush rat (*Rattus fuscipes*) display sharper turning angles following fire compared with before fire (Fordyce *et al.*, 2015). The latter authors hypothesised that this was due to animals within unburned vegetation (their preferred fire history) moving sharply away from the boundary between unburned and recently burned areas (Fordyce *et al.*, 2015). Studies of modified landscapes also demonstrate that the matrix between preferred cover types strongly affects dispersal probability (Ricketts, 2001).

Knowledge is a key constraint in optimal decision-making and movement is often a component of strategies animals use to gain information about environmental variability (Stephens, 1987). Such information-gathering strategies may include exploratory movements away from an occupied patch, prior to dispersal, to help ascertain conditions in the more-distant habitat and thereby assess the risk of transfer (Vangen *et al.*, 2001; Haughland & Larsen, 2004). Some of these exploratory movements could involve searching for signs of predators or distant cues of potentially suitable habitat. For example, caribou (*Rangifer tarandus groenlandicus*) will enter severely burned boreal forests but rapidly retreat towards unburned areas (Rickbeil *et al.*, 2017). Such behaviours could indicate exploratory movements into an unpreferred fire history to briefly assess risk or search for distant cues of suitable habitat. Exploratory movements and distant cues may be particularly important for individuals with maintenance movements confined to a single patch. Aside from memories acquired during exploratory movements, memory-based movements – either acquired or genetic – are unlikely to contribute substantially to an individual's navigation capacity during dispersal due to the lack of direct experience (Fagan *et al.*, 2013).

The extent and configuration of fire histories may affect a species' ability to gain information about potential distant habitat, and therefore to orient their movement towards it. Vegetation structure has a major impact on the perceptual range of animals (Forero-Medina & Vieira, 2009; Prevedello, Forero-Medina & Vieira, 2010), i.e. the distance within which an animal can detect a feature in the landscape (Lima & Zollner, 1996). Some studies have shown that species' perceptual ranges can be higher in areas that have simple or low-stature vegetation compared with tall or complex vegetation (Prevedello, Forero-Medina & Vieira, 2011; Kay *et al.*, 2016). For instance, Prevedello *et al.* (2011) showed that movement paths of forest-dependent marsupials were strongly affected by matrix type, with more oriented movements (i.e. targeted towards forest patches) observed in vegetation types that had fewer visual obstructions. Similarly, Kay *et al.* (2016) showed that the perceptual range of arboreal geckos was influenced by vegetation height, with more oriented movements towards trees when travelling through shorter vegetation. Both Prevedello *et al.* (2010) and Kay *et al.* (2016) showed that animals exhibited tortuous movements (i.e. with many turns) when their preferred habitat was beyond their perceptual range, and more linear, oriented movements when it was within their perceptual range.

The simplified nature of recently burned areas may enhance the perceptual range of individuals dispersing through burned areas while attempting to locate mid- or late-successional vegetation. However, if high-intensity fires burn large areas well beyond the perceptual range of individuals, it will hamper their ability to locate appropriate habitat because of a lack of distant cues to orient their movements (Fig. 2) (Doherty & Driscoll, 2018). Failure to detect a cue would lead to non-oriented movements (Fig. 2), increasing

travelling time and therefore increasing energetic costs and predation risk (Awade *et al.*, 2017), an effect that could be heightened in highly simplified post-fire environments where visual detection of prey by predators is likely enhanced (McGregor *et al.*, 2015). For example, Johnson *et al.* (2009) found that mortality risk in American martens (*Martes americana*) increased with the distance travelled by dispersing juveniles, and that this effect was greater in regenerating compared with mature forests. By contrast, Spear & Storfer (2010) found that fire had little effect on gene flow in the Rocky Mountain tailed frog (*Ascaphus montanus*), a species usually associated with an intact forest canopy. They speculated that biological legacies characteristic of less-intense fires, such as fallen trees, may have permitted movement through the burned forest.
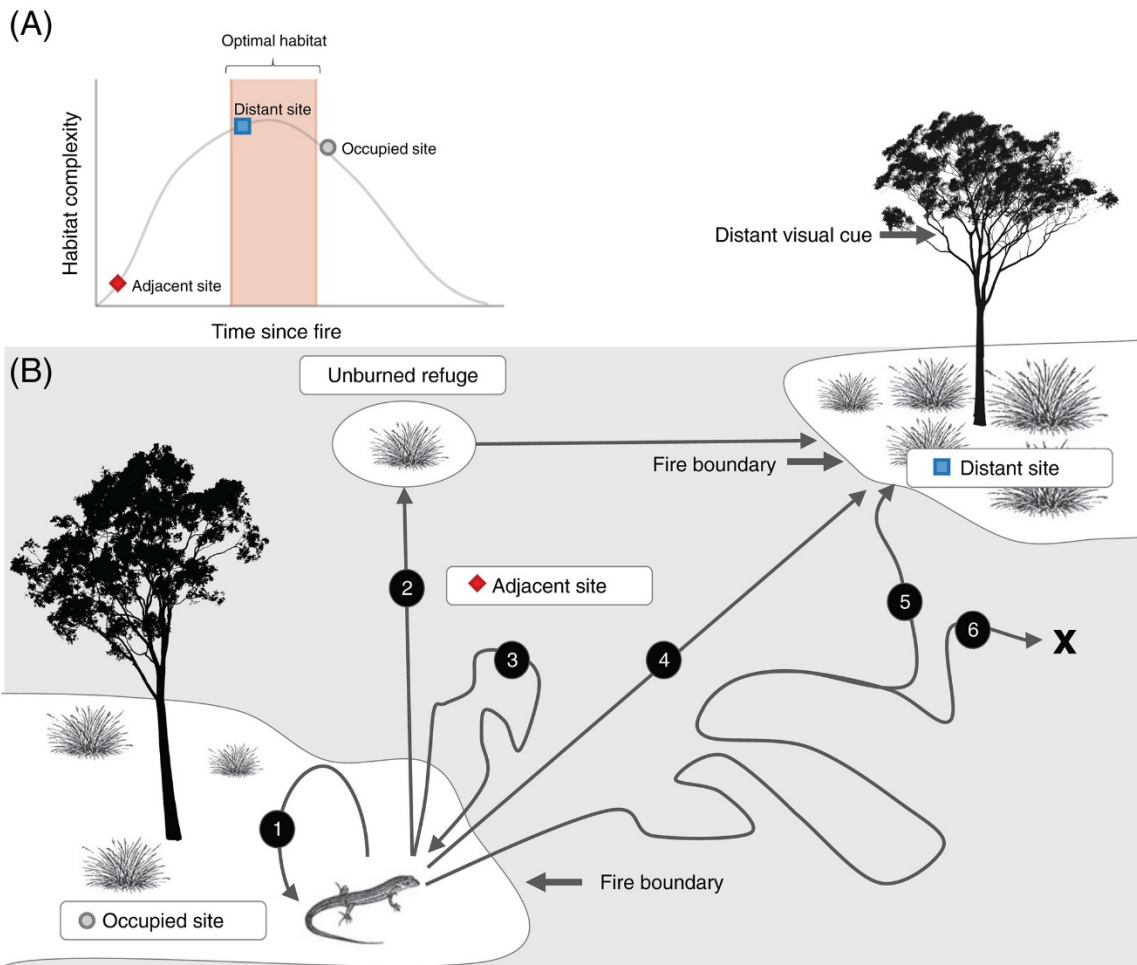

Figure 2. Movement across landscapes with varied fire histories of a fire-dependent species. (A) The optimal habitat for this species is mid-successional vegetation due to its high habitat complexity. The occupied site has aged beyond the species' preferred fire history (due to a reduction in habitat complexity), triggering possible movement away from the site. This involves the individual moving through an adjacent patch with a non-preferred fire history, which is recently burned and has low habitat complexity, towards an unoccupied distant site that is that is of the species' optimal fire history. (B) Possible movement pathways: 1, a strong boundary response to the contrast between the occupied site and the adjacent site may prohibit the species from moving beyond the suboptimal patch, and therefore face reduced fitness or increased risk of mortality. 2, an unburned refuge is within the perceptual range of the animal, allowing it to use the refuge as a stepping stone until a larger visual cue is within its perceptual range. 3, exploratory movements into the adjacent patch type to evaluate risk of transit and search for distant cues of suitable habitat. 4, the distant visual cue is within the perceptual range of the individual, allowing rapid, oriented movement towards the unoccupied site. 5, the distant visual cue is beyond the perceptual range of the animal, leading to tortuous, non-oriented movements that eventually result in successful transit and immigration. 6, the distant visual cue is beyond the perceptual range of the animal, leading to tortuous, non-oriented movements that result in unsuccessful transit (x = mortality event). Sketches by A. Foster.
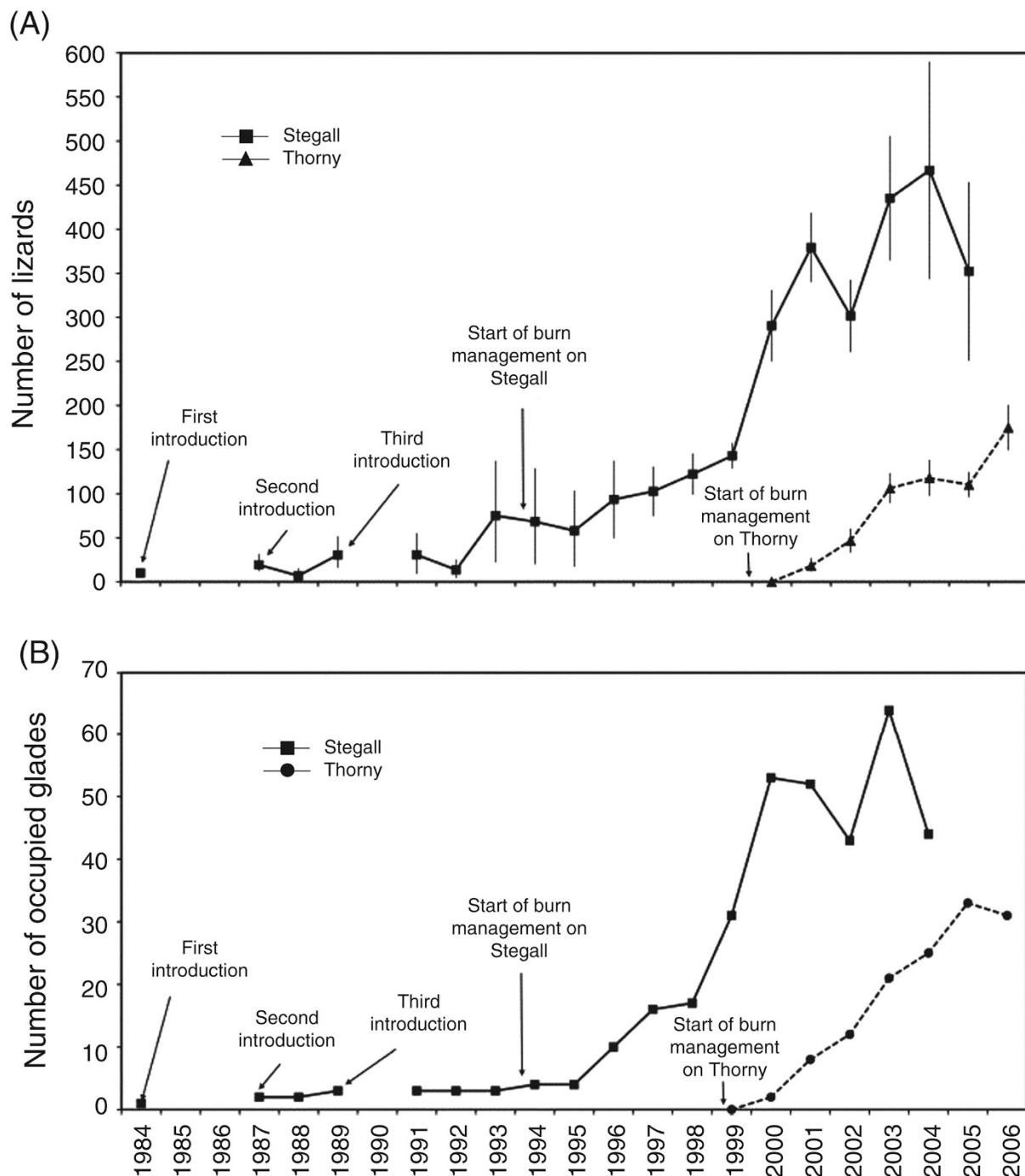
Figure 3. The response of the Collared Lizard to fire management at two locations (Stegall and Thorny) within the Missouri Ozarks: (A) total population size; (B) number of occupied glades. Reproduced with permission from Templeton *et al.* (2011).

An outstanding example of the effects of fire on animal dispersal, and how such effects can flow through to populations, comes from the Missouri Ozarks (Templeton *et al.*, 2011). Here, a 22-year study has monitored populations of the eastern collared lizard, a species limited in distribution within the region to desert-like glades on ridge tops. Management of the region promoted fire suppression for several decades, leading to the growth of dense forests between the glades. This growth limited the movement of collared lizards, almost eliminating dispersal between populations, and 75% of populations became extinct. Glades separated by as little as 50 m by fire-suppressed forests experienced no dispersal of individuals, despite efforts to restore the glades themselves through burning to reduce woody invasion. After a

decade of glade restoration, from 1984 to 1993, mark–recapture data revealed that no individuals had been observed colonising new glades, although subsequent genetic analyses revealed a small number of dispersal events (Neuwald & Templeton, 2013). In 1994, management changed and prescribed burning was applied to the forest surrounding the glades. The response by the collared lizard was rapid, with increases in the number of occupied glades and population size (including all glades) increasing over the following decade (Fig. 3). After prescribed burning between glades, the percentage of dispersing individuals increased from 1.5% to 14.1%; a >9-fold increase (Templeton *et al*., 2011), with genetic diversity increasing in turn (Neuwald & Templeton, 2013).

III. FREQUENT MOVEMENTS BETWEEN FIRE HISTORIES

While individuals of some species may meet their needs within a patch of a given fire history, others must range across multiple patches with differing fire histories to obtain sufficient food resources, mates or shelter or to reduce predation risk. That is, maintenance movements of individuals typically occur at a coarser scale than the average fire-patch size. Animals that move frequently between or across fire histories to obtain resources (e.g. on a daily or seasonal basis) can be classified into two groups: (*i*) species that draw upon resources from habitats in multiple fire histories (e.g. food in recently burned areas, shelter in long-unburned areas) and (*ii*) species that draw upon resources within a specific fire history (e.g. long-unburned areas), but have resource requirements that necessitate regular movement among multiple patches of that fire history, including movement through non-preferred fire-ages. These two movement patterns are known as landscape complementation and landscape supplementation, respectively (Dunning, Danielson & Pulliam, 1992).

(1) Landscape complementation and supplementation

Landscape complementation occurs when species require multiple habitats to meet their needs because resources or conditions associated with each habitat are non-substitutable (Dunning *et al*., 1992; Law & Dickman, 1998; Pope, Fahrig & Merriam, 2000). For individuals to engage in landscape complementation, the complementary resources must be distributed at a scale that matches, or is finer than, the activity range of the individual animal. Examples include when individuals take refuge in one fire history, such as older areas with more complex vegetation, and forage in another fire history, such as recently burned areas. The mala (*Lagorchestes hirsutus*), for instance, is thought to shelter in unburned areas of dense hummock grass and forage in recently burned areas (Bolton & Latz, 1978; Lundie-Jenkins, 1993). Zebras (*Equus quagga*) exploit sites with different fire-ages by day and night, selecting more frequently burned, open sites at night when lions (*Panthera leo*) – an ambush predator – are active, and foraging more in less frequently burned and more vegetatively complex sites during the day, when lions are less active and the risk of ambush is reduced (Burkepile *et al*., 2013). Bird *et al*. (2013) found that the sand goanna (*Varanus gouldii*) was more common near transitions between recently burned and long-unburned spinifex grasslands, speculating that recently burned areas provide superior foraging opportunities, while unburned areas provide greater cover from predators. Consequently, sand goannas are more likely to occur in landscapes comprising a mix of fire histories, including recently burned and long unburned patches (Bird *et al*., 2018).

Landscape supplementation occurs when an animal requires resources from multiple patches of a similar fire history. For instance, some fire-dependent species might forage across several patches of a given fire history to access sufficient food resources to meet their

energetic demands, moving between such patches on a regular basis. This is likely for larger-bodied species or those that occupy a high trophic position (i.e. top predators), as they require a larger area to access sufficient food resources (McNab, 1963; Tucker, Ord & Rogers, 2014). However, small animals may also need to engage in landscape supplementation when their favoured resource is patchily distributed or their preferred patch types are too small to meet their needs: bush rats normally prefer long-unburnt habitat, but move through recently burned areas to access residual patches of unburned vegetation when unburned patches are small (Fordyce *et al.*, 2015).

Whether individuals are engaging in landscape complementation or supplementation (or neither) should be evident in their movement patterns. Animals moving through fire histories within their home range that are perceived as risky or of low benefit will generally move more rapidly and linearly (Fahrig, 2007). Therefore, the tortuosity of movement should indicate whether individuals are using, or simply moving through, a patch of a particular fire-age (Fig. 4); the more slow and tortuous the movement, the more likely the animal is within a preferred patch. For instance, Rickbeil *et al.* (2017) found that barren-ground caribou moved more slowly through areas burned at low compared with high severity, indicating that they were using the former more for foraging and the latter primarily as movement pathways. Whereas tortuous movements can arise when animals are dispersing through unknown areas (resulting in non-oriented movements; Prevedello *et al.*, 2010; Clark *et al.*, 2017), such movements are less likely for individuals making maintenance movements within their home range. This is because these individuals should have acquired spatial memory to assist them in navigation within their home range (Fagan *et al.*, 2013).
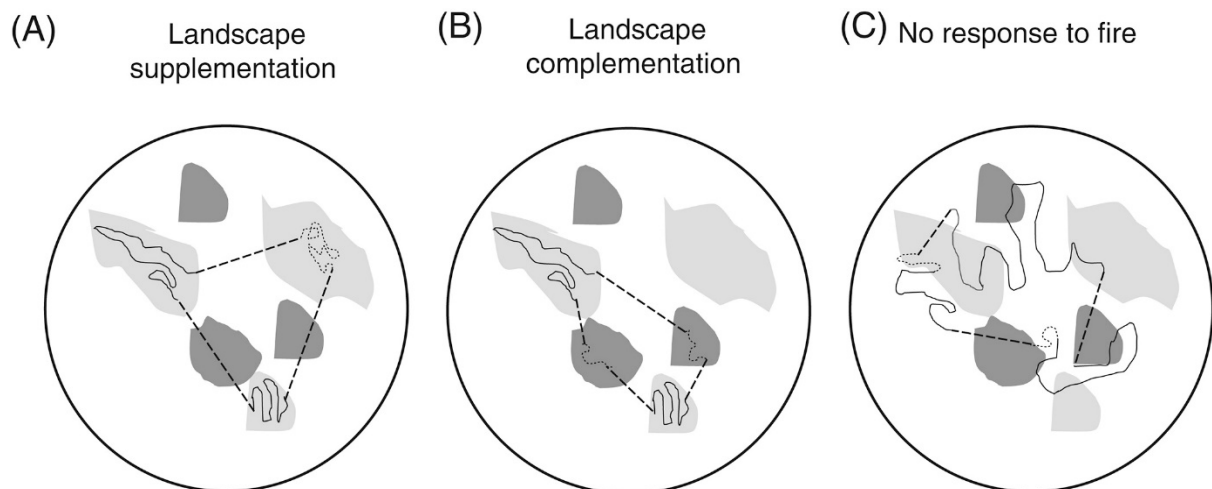

Figure 4. Hypothesised movement patterns of animals in different fire mosaics. (A) An individual displaying landscape supplementation, such that it requires resources from multiple patches of a similar fire-age (light grey patches), and will move linearly and rapidly through other, non-preferred fire-ages (white and dark grey). (B) An individual displaying landscape complementation, such that it requires resources from patches of different fire-ages (light and dark grey), and will move linearly and rapidly through a non-preferred fire-age (white). (C) An individual unaffected by fire, such that it uses a variety of fire-ages but movements are similar in each. Lines indicate different behavioural states inferred from accelerometer data (black solid line = foraging, dashed line = running, dotted line = denning).

Given uncertainty in relating movement patterns to behaviours, measurements of behavioural states (Nams, 2014; Mahoney & Young, 2017) or residence time (Torres *et al.*, 2017) can complement movement data to distinguish better between the use of different fire histories by

broad-ranging species. Evidence of landscape complementation would include at least two behavioural states (e.g. foraging, sheltering) being linked with at least two fire histories, potentially with rapid, linear movements through other, non-preferred fire histories (Fig. 4A). By contrast, evidence for landscape supplementation would include a specific behavioural state being expressed in multiple patches of a preferred fire history, combined with linear and rapid movements through non-preferred fire-ages (Fig. 4B). Finally, some animals may move through multiple fire-ages, but the behavioural states being expressed may not relate to fire history, meaning the animal is engaging in neither landscape supplementation nor complementation (Fig. 4C).

The properties of fire mosaics will also likely shape foraging movement patterns (Fig. 5). In terms of landscape complementation, the composition of fire-ages within a landscape determines if the right mix of fire histories is present, whereas the configuration of fire-ages determines their accessibility (Fig. 5). If the composition of a fire mosaic does not include all fire-ages required within close enough proximity (dictated by the species' movement capacity and perceptual range), this may prevent an individual from establishing a home range and persisting in the mosaic (Fig. 5). Even if all required fire-ages are present, some species may not be able to persist if the configuration of required fire histories is not suitable. For instance, suitable patches may be too far apart for individuals to meet the energetic costs of regularly moving between them (Fig. 5), or such movements may result in excessive predation risk. However, to our knowledge no studies have definitively demonstrated that a particular configuration of fire histories is necessary for population persistence.
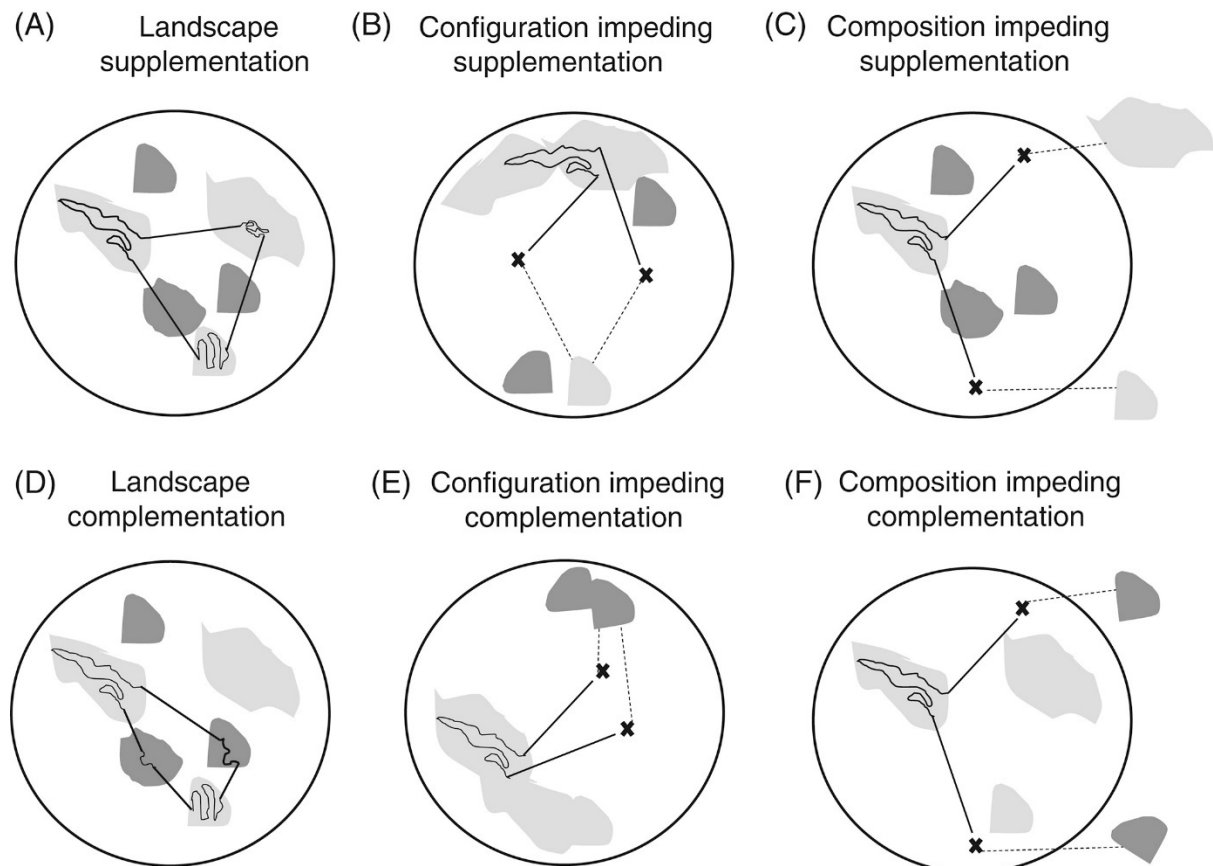

Figure 5. Examples of how the configuration and composition of fire mosaics can influence the ability of species to employ landscape supplementation (A–C) or complementation (D–F). Solid lines are movement pathways; x = mortality event; dotted lines indicate the target habitat patch that the animal was required to travel to in order to supplement (B, C) or complement (E, F) their resources.

An important distinction for species that make use of landscape complementation is whether species are entirely reliant on the resources located in different fire histories (which we term 'obligate' landscape complementation), or whether they simply benefit from accessing resources in multiple fire histories ('facultative' landscape complementation). This distinction determines how each species responds to an absence of the ideal composition and configuration of fire histories; facultative species may be negatively affected, such as through reduced reproductive output, whereas obligate species may become locally extirpated.

IV. CYCLICAL OR OPPORTUNISTIC MOVEMENT ACROSS AND WITHIN FIRE-PRONE REGIONS

The final type of movement that we consider is long-distance movements from outside a fire-prone region to a preferred fire-age within it. Multiple maintenance movements of such species, measured over time, encompass at least one fire-prone vegetation type in addition to other vegetation types that may or may not be fire prone. This includes the movement of migrants along predictable migratory routes that encompass fire-prone ecosystems, and more unpredictable and sporadic movements of nomadic or boom-and-bust species that opportunistically enter a fire-prone ecosystem when conditions are favourable.

A well-documented example of the former involves caribou, which live primarily in alpine and arctic tundra during warmer months and migrate to boreal forests during winter (Klein, 1982). In these forests, fire affects their primary food source, fruticose lichens, which are more abundant in older successional stages (Morneau & Payette, 1989). Caribou thus show a preference for forest areas that have not recently burned (Joly *et al*., 2003), selecting long-unburned areas (>40 years since fire) during and shortly after calving (Skatter *et al*., 2017). In areas that are predominantly burned, caribou make use of small unburned islands (Skatter *et al*., 2017). When caribou do venture into recently burned areas, they remain in close proximity (within 500 m) to unburned areas (Joly *et al*., 2003). Thus, the fire history of caribou winter habitat is an important determinant of their breeding success and population size (Rupp *et al*., 2006).

Migratory bird species may also show clear preferences for patches with specific fire histories. Two closely related, partially migratory species, the golden whistler (*Pachycephala pectoralis*) and rufous whistler (*Pachycephala rufiventris*), prefer patches of longer-unburned vegetation in mallee and forest ecosystems of southern Australia (Watson *et al*., 2012b*;* Berry, Lindenmayer & Driscoll, 2015). Ground-and-shrub-nesting migratory birds are less abundant and experience lower nest success in recently burned oak forests of the eastern U.S.A., selecting unburned areas with greater vegetation complexity for nesting (Aquilani, LeBlanc & Morrell, 2000). The migratory American robin (*Turdus migratorius*) responds positively to prescribed fire in ponderosa pine forests of the western U.S.A. Thus, the presence or abundance of habitat of a given fire history may be important to migratory species when fire alters the availability of food or shelter.

Examples of sporadic movements into highly fire-prone regions from areas that seldom burn can be found in some Australian desert rodents. During prolonged dry periods, species such as the long-haired rat (*Rattus villosissimus*) and sandy inland mouse (*Pseudomys hermannsburgensis*) are confined to mesic woodland or riparian habitats that rarely burn (Dickman *et al*., 2011; Greenville, Wardle & Dickman, 2013), but after rains migrate to sites that may be more than 10 km away in fire-prone spinifex grassland (Dickman, Predavec & Downey, 1995). Both species maintain high rates of survival, and body and reproductive

condition in spinifex patches, with sandy inland mice foraging preferentially in spinifex patches of varied fire histories (Letnic, 2001; D'Souza *et al*., 2013). Animals retreat again to unburned refuges when conditions dry and productivity declines in the spinifex mosaics, probably due to a reduction in resources within spinifex patches.

V. EMERGING ISSUES FOR ANIMAL MOVEMENT IN FIRE-PRONE REGIONS

Although species in fire-prone landscapes have evolved to cope with fire, several factors make fire an important conservation issue for the 21st century (Kelly & Brotons, 2017). First, fire regimes in many regions have departed from those regimes under which species evolved (Pausas & Keeley, 2014; Trauernicht *et al*., 2015). This means that the properties of fire mosaics have changed (Burrows *et al*., 2006; Andela & Van Der Werf, 2014; Liebmann *et al*., 2016), and are predicted to change further due to climate change (Moritz *et al*., 2012). Second, landscapes are increasingly being fragmented by land clearing, including in many fire-prone ecosystems (Cochrane, 2003; Parsons & Gosper, 2011). Third, the spread of non-native species throughout the world has resulted in novel communities, such that the biotic context of communities – including competition, disease, and predation – has changed (Hobbs *et al*., 2006; Doherty *et al*., 2016). Each of these factors can contribute towards non-optimal movements in fire-prone landscapes, with potential negative outcomes for individual fitness and population persistence.

(1) Altered fire regimes

The changing properties of fire mosaics may threaten species with movement parameters that evolved under a particular fire regime. When movement parameters are under natural selection, they may evolve to match the scale of patchiness in the landscape (Fahrig, 2007), including those shaped by fire history. For fire-dependent species that move infrequently between fire-ages (i.e. for dispersal), increases in the size, frequency, severity and intensity of fires could: (*i*) alter the probability of an animal emigrating, due to increasingly sharp boundaries between occupied and adjacent sites eliciting strong boundary responses, and the loss of distant cues of suitable habitat that might trigger dispersal; (*ii*) alter the risk of mortality during transfer, due to the loss of stepping stones – small unburned patches and biological legacies – whose presence can help diminish the risk of predation by offering refuge (Leahy *et al*., 2016); and (*iii*) increase travel time, as animals are forced to move longer distances in search of unburned areas, or are confounded by a lack of visual cues leading to non-oriented, tortuous movement patterns, which further increase predation risk. Each of these could have population-level consequences for species by reducing reproductive output or increasing mortality, and may result in suitable habitat being unoccupied due to a reduction in colonisation probabilities and rescue effects.

Changes in the properties of fire mosaics will also affect species that rely on landscape complementation or supplementation. The costs of regular movements between patches may be altered if the distance between suitable patches increases due to the rescaling of fire mosaics. This would increase the energetic costs of movement while also potentially increasing predation risk by increasing the time individuals must spend in unpreferred patches. In some cases, obligate species may not be able to persist if the distance between complementary or supplementary resources becomes too great. This is what is hypothesised to have occurred to the mala, which declined rapidly due to the loss of fine-grained mosaics following the cessation of Aboriginal burning practices in arid Australia (Bolton & Latz, 1978; Burbidge *et al*., 1988).

Altered fire regimes could also have a substantial impact on species that make cyclical or opportunistic use of fire-prone ecosystems. For example, increases in the annual area burned due to climate change is predicted to threaten caribou populations by limiting the availability of high-quality winter habitat (Rupp *et al*., 2006). Resources associated with particular fire histories might be critical to compensate for the energetic demands of migration, for facilitating successful breeding, or for providing resources required for return journeys.

(2) Fragmentation

Besides reducing the amount of available habitat, fragmentation represents a significant threat to fire-dependent species as it can disrupt the ability of animals to reach sites of a suitable successional stage. Large distances between fragments, typical of increasingly modified landscapes, means that such movements are less likely to result in successful emigration to a new site, and a lack of cover between patches means that such land may have an elevated risk of predation. Movement through vast agricultural landscapes may have similar hazards to moving through intensely burnt areas due to the lack of stepping stones and visual cues to orient movement (Doherty & Driscoll, 2018). In addition, modified land uses bring with them another suite of potential hazards, from the risks of trampling by livestock to encountering heavy machinery, fertilisers and pesticides. These hazards may further raise the risk of mortality for native species in search of habitat.

Remaining within a fragment as it ages beyond a preferred fire history also poses risks to fire-dependent animals. Fire is often excluded from isolated habitat fragments (e.g. Parsons & Gosper, 2011); if early-successional specialists are confined to such isolated patches then as they become unsuitable, reduced population size and local extinctions may occur (Driscoll, Whitehead & Lazzari, 2012). Driscoll *et al*. (2012) found that remnant isolated patches separated by >1–2 km were unlikely to be occupied by the early-successional knob-tailed gecko (*Nephrurus stellatus*), likely due to the exclusion of fire. For species that depend on mid- or late-successional vegetation, fires that do occur in small, fragmented patches may leave few (or no) fire refuges for individuals to persist *in situ*, therefore requiring recolonisation from outside the fragment. Due to the distance between fragments and the risks associated with moving through human-disturbed landscapes outlined above, the probability of recolonisation and rescue effects will often be low, leading to permanent local extinction. The fragmentation of vegetation also poses a challenge for species that rely on landscape complementation or supplementation: unless such species can draw upon resources from human land uses (e.g. crops for grazing mammals), the likelihood of having the necessary area or complement of fire-ages within a single isolated fragment is low.

(3) Invasive species

The role of invasive predators in fire-prone ecosystems has received particular attention due to interactions between fire and predation (Woinarski *et al*., 2011; Doherty *et al*., 2015; Ziembicki *et al*., 2015). There is growing evidence that fire exposes prey to heightened predation risk by invasive predators, benefiting predators due to increased detection of prey (McGregor *et al*., 2014; McGregor *et al*., 2015; Leahy *et al*., 2016). Predation risk may be particularly high near the edge of burnt areas, where exploratory movements of potential prey will be most common. Feral cats in Australia are known to travel >10 km to locate recently burned areas, exploiting the edges of fire scars presumably to capitalise on exposed prey (McGregor *et al*., 2016, 2017). Pastro (2013) showed that two invasive predators, red fox (*Vulpes vulpes*) and feral cat, specialised on ecotones between burned and unburned

vegetation in arid Australia. She speculated that this was to enhance foraging efficiency in burned areas by using the camouflage afforded by unburned vegetation while capitalising on the exposure of prey in the adjacent burned areas. A key consideration is the distances invasive predators travel to fire scars, as this could influence the scale at which predator-control programmes are employed in concert with fire management (Doherty *et al*., 2015; Baker & Bode, 2016; Geary *et al*., 2018).

Invasive predators may fundamentally change the relationship between cover types and predation risk, thereby leading to increased prey mortality as animals move to locate sites of a suitable fire age. Prey are often naïve to the olfactory and visual cues of invasive predators with which they have not co-evolved (Salo *et al*., 2007), leading them to fail to deploy anti-predator responses and enhancing their risks of predation (Sih *et al*., 2010). Exploratory movements aimed at assessing the risk of predation may fail to recognise the cues of invasive predators, and therefore fail to assess the risk of dispersal accurately.

VI. DATA NEEDS RELATING TO ANIMAL MOVEMENT IN FIRE-PRONE LANDSCAPES

Hastening the integration of movement ecology and fire ecology to grapple with the threats outlined above could be achieved by: (*i*) effective use of existing data to test movement-related questions; and (*ii*) rapid adoption of both current and emerging technologies to monitor animal movements directly or indirectly. Below, we summarise the types of data needed to enhance our understanding of movement ecology in fire-prone landscapes.

(1) High-resolution spatial fire data sets

Remotely sensed spatial data are often large in extent, but lack detail at small spatial (pixel) scales (Kerr & Ostrovsky, 2003; Neumann *et al*., 2015). Hence, there is often a mismatch between the spatial scale of an animal's response and the scale at which the fire data are collected. Satellite imagery is usually employed to map wildfire extent, leading to the difference in spatial scales arising for two reasons. Firstly, the area burnt may be mapped as one continuous area that assumes that wildfire intensity and patchiness are the same. However, changes in weather and landscape patterns (e.g. vegetation and topography) can result in variations in the intensity and patchiness of vegetation burnt within the larger wildfire area (Hammill & Bradstock, 2006). Secondly, the resolution of commonly used satellite sensors ranges from 15 to 4000 m (Kerr & Ostrovsky, 2003; Avitabile *et al*., 2013). Commercially operated sensors offer higher spatial resolution (1–5 m), but can be prohibitively expensive ($20/km) for researchers (Marvin *et al*., 2016). For small animals, unburnt habitat patches within a larger burnt area may not be identified and thus important movement patterns between them will be missed. Ideally, researchers need access to high-resolution (1–5 m) imagery and spatial fire data sets. Advances in technology, such as drones for high-resolution airborne mapping and new free web-based platforms, such as *Google Earth* and *Google Earth Engine* are increasingly allowing researchers to gain access to such high-resolution spatial data (Neumann *et al*., 2015; Marvin *et al*., 2016). High-resolution imagery and fire data sets will not only help to elucidate patterns of animal movement in fire-prone environments, but can also be used to identify more-subtle fire-history differences among habitats, identify refuges within burnt areas or determine minimum patch-size requirements for different species.

(2) Small-scale movement data

Well-established methods of directly tracking fine-scale animal movements have led to substantial insights in movement ecology in modified landscapes, and may well do likewise in fire-prone landscapes. For example, Tingley *et al.* (2014) used radio-tracking to determine variation in the home-range size of black-backed woodpeckers nesting in mixed-fire-severity forests in North America. Data from spool-and-line devices helped demonstrate the effects of vegetation type on path tortuosity of didelphid marsupials in the Atlantic Forest of Brazil (Moura *et al.*, 2005), while Kay *et al.* (2016) used fluorescent pigment to track fine-scale gecko movements and quantify the influence of grass height on their perceptual range, a technique that has also been applied to study the daily movements of the kangaroo rat (*Dipodomys merriami*) following fire in Joshua Tree National Park, U.S.A. (Hulton VanTassel & Anderson, 2018). Quantifying perceptual ranges using these methods could be particularly important for gaining insights into infrequent movements across fire histories, including assessing cues for emigration. Spool-and-line devices allowed Fordyce *et al.* (2015) to show that bush rats used more convoluted pathways following fire and made infrequent movements through burned areas to reach their preferred unburned areas, thus providing evidence of landscape supplementation. Studies that provide incentives for boundary-crossing, such as gap-crossing studies (Robertson & Radford, 2009), could also help quantify how boundary responses are affected by fire. Cost-efficient luminescent tags or 'mini chemi-lights' (~0.05 g) have been used to assess small-mammal foraging and habitat selection in fire-prone ecosystems of southern and inland Australia (Bos & Carthew, 2003; Potter, Greenville & Dickman, 2018). Such tags could be used to monitor the movements of animals in the period immediately following fire, or to assess if an individual's maintenance movements are confined to a single patch, as opposed to engaging in landscape complementation or supplementation.

(3) Occurrence data

The main type of biodiversity data available in fire-prone regions is that describing the occurrence of species: either presence data derived from wildlife atlases (Reside *et al.*, 2012; Connell *et al.*, 2017), or presence/absence or abundance data derived from research or monitoring programmes (Hale *et al.*, 2016; Prowse *et al.*, 2017). Occurrence data can allow researchers to examine questions relating to animal movement indirectly by assessing occurrence in relation to fire history. Long-term monitoring programs in fire-prone regions are rare, but could be particularly informative when coupled with dynamic occupancy modelling. Dynamic occupancy modelling uses repeated surveys conducted over multiple 'seasons' (e.g. consecutive years) to model initial occupancy, and the subsequent probability of extinction and colonisation at sites, while accounting for imperfect species detection (Tingley *et al.*, 2018). Relating extinction and colonisation probabilities to the fire history of a site can provide insight into the post-fire timing of infrequent (dispersal) movements. Long-term monitoring of habitat fragments in fire-prone landscapes could reveal how fire history and fragmentation interact to influence extinction and colonisation probabilities. Occurrence data could also be used to explore evidence of landscape complementation or supplementation by relating occurrence probabilities to site context, such as the extent, configuration and composition of fire-ages surrounding the site. For instance, if an animal species is consistently more likely to occur, or is more abundant, where two fire-ages are in close proximity, this suggests that the species may be moving between fire-ages and potentially engaging in landscape complementation.

Modern faunal sampling techniques, such as remotely triggered cameras and automated acoustic devices, could provide further information to complement occurrence data, such as the timing of records. As camera traps record a timestamp indicating when an animal is observed, this provides data on when animals are using habitats both diurnally and seasonally (Borchert, 2012). If occurrence within fire-ages is temporally partitioned (i.e. species use particular fire histories at certain times of the day or in particular seasons), this suggests that animals may be using fire histories for different purposes (i.e. landscape complementation), as different behaviours (e.g. denning, foraging) are often temporally segregated.

(4) Mark–recapture data

Data sets where individual animals are tagged and released to allow subsequent identification (or have natural markings that allow individual recognition) have proved effective in describing animal movements in fire-prone landscapes. Mark–recapture data are well suited to detecting relatively infrequent movement events across fire histories, such as dispersal away from an occupied site ('movement probability'), where many individuals need to be monitored in order to detect enough events for analysis. Tagging individuals allowed Templeton *et al*. (2011) to identify movements of eastern collared lizards between glades, and therefore to examine how the frequency of movements (e.g. dispersal events) changed in relation to different fire regimes. Part of the success of their study was due to the focal species forming relatively discrete populations within specific habitats (glades within forests). Use of this approach will not be as straightforward for more-dispersed populations.

(5) Satellite and GPS telemetry

Data that capture the actual movements of animals, such as satellite and GPS telemetry data, will be pivotal in enhancing understanding of animal movements in fire-prone landscapes. Satellite and global positioning system (GPS) tracking devices are increasingly becoming more affordable, including off-the-shelf GPS devices that can be modified to become inexpensive GPS wildlife trackers (Cain & Cross, 2018). Satellite and GPS tracking data can be used to calculate a range of movement parameters (Thiebault & Tremblay, 2013), which can be quantitatively assigned to 'movement states' (Van Moorter *et al*., 2010). For instance, Van Moorter *et al*. (2010) used cluster analysis to categorise elk (*Cervus canadensis*) movements into four types: inter-patch movements, intra-patch foraging, rest, and inter-patch foraging. Relating the locations of movement types to the distribution of fire histories would allow researchers to assess whether animals are engaging in different kinds of movement in different fire histories, and therefore to assess evidence of landscape complementation or supplementation (Allred *et al*., 2011). A recent example of such research is the use of GPS telemetry to document spatial and temporal changes in foraging movement behaviour of the mountain brushtail possum (*Trichosurus cunninghamii*) inhabiting cool-temperate rainforest gullies in unburnt, patchily burnt and severely burnt landscape contexts in SE Australia (Berry *et al*., 2016), and GPS tracking of feral cats showing extraterritorial hunting expeditions towards recent fires (McGregor *et al*., 2016).

Satellite and GPS tracking devices could also provide insights into how migratory or nomadic species use fire-prone ecosystems, including the regularity of visits to such ecosystems, and whether visits result in predictable associations with fire histories. For instance, Joly *et al*. (2003) used GPS telemetry to demonstrate that caribou avoided recently burned areas in their winter habitat.

The cost involved in satellite and GPS tracking places a limit on how many individuals can be monitored, and therefore infrequent movement events may be overlooked. Furthermore, despite tracking devices becoming increasingly miniaturized, now including devices weighing less than 1 g (Bridge *et al*., 2011), such small devices collect few fixes and operate over a short time frame. Satellite and GPS tracking remains difficult and costly for small animals (Kissling, Pattemore & Hagen, 2014). However, these obstacles may be overcome given rapid advances in GPS technology, and for larger species there is now growing interest in combining GPS collars with camera (video) collars to capture fine-scale behaviour and movement data.

(6) Biologging

Recent miniaturisation of electronic loggers has facilitated the development of miniature accelerometers (a device that measures an object's acceleration along three axes). Accelerometers provide a different type of data to GPS telemetry, as they provide an index of output of mechanical movement measured in terms of acceleration, and at high resolution, measured at a frequency of up to 200 Hz. Accelerometer data do not provide information on distance travelled or directionality. In contrast to satellite and GPS telemetry that provides information on changes in an animal's location, accelerometers can differentiate between high- and low-activity behaviours for a given distance moved. For example, intense foraging or sleeping could result in little movement between locations, but differ markedly in terms of energy expenditure (Elliott *et al*., 2013). Accelerometer data can thus be used to characterise 'behavioural states' of individuals, often at very fine temporal resolution, based on patterns of movement. For instance, Gerencsér *et al*. (2013) used accelerometer data to categorise dog behaviours accurately into one of seven behavioural states (sitting, laying, walking, standing, trotting, galloping, and cantering). Behavioural-state analysis could thus permit researchers to distinguish animal behaviours in fire-prone landscapes.

Accelerometer data and GPS data are most useful when combined (Nams, 2014), permitting an assessment of the types of behaviours animals engage in within particular habitats. For instance, Nams (2014) used accelerometer data in combination with GPS data to show different behavioural states expressed in the movement paths of the fisher (*Martes pennanti*). This approach could be used to examine changes in animal movement behaviour to reveal whether specific behaviours are displayed in specific fire-ages: for instance, individuals making use of some fire histories for foraging, and others for sheltering, which would provide compelling evidence for landscape complementation. Combining accelerometer and GPS data can also provide insights into behaviours of migratory species within fire-prone regions, for instance revealing if specific behaviours are associated with particular fire histories while breeding, at stopovers, or at wintering grounds (Bouten *et al*., 2013).

(7) Genetic data

Genetic data contain information about the history of dispersal events and can provide information on dispersal in situations where other data types are not feasible to collect (Driscoll *et al*., 2014), and can identify dispersal events that other sampling techniques might overlook (Neuwald & Templeton, 2013). With appropriate sampling, genetic information can identify dispersal by individuals (Banks & Lindenmayer, 2014). Landscape genetic approaches can be used to rank alternative ecological hypotheses about connectivity against genetic-distance data that reflect relative dispersal rates (Storfer *et al*., 2007). For instance, studies have used fire history as a land cover metric to identify recently burned areas as

having greater permeability to movement by early successional-stage specialist eastern chestnut mice (Pereoglou *et al*., 2013). The developing application of network models in landscape-genetic studies of dispersal increases the scope of this approach to allow consideration of hypotheses about patch characteristics and connectivity patterns in the same framework (Storfer *et al*., 2007), which should offer improvements in the insights we can obtain from genetic data.

It is important to recognise that population responses to fire other than dispersal can have genetic consequences (Davies *et al*., 2016). For instance, genetic differentiation among locations is commonly used as an indicator of gene flow (genetically effective dispersal) but can also be influenced by differences in effective population size (Prunier *et al*., 2017), which can occur in landscapes with spatially heterogeneous fire regimes (Banks *et al*., 2017). While this might pose a problem for drawing conclusions about dispersal from genetic data, we can refine our hypotheses by pairing empirical genetic data with simulation modelling of population processes. Banks *et al*. (2017) simulated alternative recovery mechanisms for small mammals that suffered major population declines associated with a wildfire in south-eastern Australia. The observed ecological and genetic patterns during population recovery were inconsistent with simulation predictions from models of recovery by immigration from outside the fire-affected area, but consistent with nucleated recovery from local fine-scale refuges for one species (the bush rat) and with a model of *in situ* recovery within burnt forest for another species (the agile antechinus, *Antechinus agilis*). Likewise, Smith *et al*. (2016) used simulations and empirical data to separate the effects of post-fire successional changes in dispersal and density on genetic patterns.

Genetic data can also fill an obvious gap in our knowledge of invertebrate movement in the context of fire. The small size of most invertebrates limits the approaches that we can use to track individuals, yet their (often) high abundance makes them ideal candidates for genetic analysis. Few studies have yet taken this approach to invertebrate movement ecology in fire-prone landscapes, although Menz, Gibb & Murphy (2016) used genetic data to conclude that population recovery of detritivorous amphipods following a major wildfire was due to *in situ* population recovery rather than recolonisation. Due to the ability to generate large-scale genetic data rapidly from non-model species, genetic approaches to movement ecology are increasingly accessible to ecological entomologists studying the impacts of fire.

VII. FUTURE QUESTIONS

Stemming from our review we can identify a series of key questions that, if addressed, will enhance our understanding of the importance of animal movement in fire-prone landscapes. (*i*) What cues do animals use to detect fire at different distances (e.g. nearby *versus* distant fires), and what are the behavioural responses associated with cue detection? (*ii*) What distances do early successional species travel to reach fires or recently burned areas? (*iii*) What are the cues that trigger emigration from a patch as it ages beyond a species' preferred fire history? (*iv*) How do species detect and navigate towards a preferred fire-age, and how is this influenced by the spatial pattern of fire history in the landscape? (*v*) What cues do animals use to identify the suitability of patches for successful immigration? How do they weigh the costs and benefits of moving? (*vi*) How common is facultative *versus* obligate complementation in fire-prone ecosystems? (*vii*) How does re-scaling of fire mosaics due to altered fire regimes influence the emigration and immigration of species, and regular movements of individuals that underpin landscape complementation and supplementation? (*viii*) How does fragmentation of fire-prone ecosystems affect the probability of emigration

and immigration, and the energetic costs and predation risks during transfer? (*ix*) What distances do predators, and invasive predators in particular, travel to fires, and what (visual, auditory, olfactory) cues do they use to detect distant fire? (*x*) In what ways do species alter their use of, and movements between, fire histories when exposed to the cues of invasive predators or competitors?

VIII. CONCLUSIONS

(1) This review highlights the many aspects of animal movement that may be fundamental to the persistence of fire-dependent species in fire-prone ecosystems. The potential importance of movement is somewhat inconsistent with the prevailing view of species' responses to fire history as being driven solely by local habitat conditions. The Fox (1982) habitat accommodation model, which has been the predominant framework for predicting the responses of fire-dependent animals to fire (Lindenmayer *et al*., 2008; Nimmo *et al*., 2012; Smith, Bull & Driscoll, 2013; Santos, Badiane & Matos, 2016), does not incorporate animal movement, instead assuming that species' responses to fire are a product of each species' habitat requirements and how they change along the post-fire successional axis. Incorporating movement into this conceptual model could help improve its predictive capacity, which has generally been poor (Nimmo *et al*., 2014).

(2) Our review highlights that sites with an appropriate fire history could remain unoccupied for several reasons: strong boundary responses as a result of sharp boundaries between fire histories leading to a lack of emigration; increased travel time during transfer leading to increased probability of mortality and thus reduced probability of successful immigration; and reduced cues of appropriate habitat leading to non-oriented movements and increased probability of mortality.

(3) We consider the use of fire mosaics by animals within a landscape-ecology framework by drawing on concepts of landscape complementation and supplementation, and note the importance of distinguishing between obligate and facultative forms of landscape complementation. We draw attention to the potential importance of fire to migratory and nomadic species, which has rarely been considered previously.

(4) By considering how movement interacts with novel threats, this review identifies movement as a key mechanism helping to explain why over 1400 animal species are threatened by altered fire regimes (IUCN, 2015). Suboptimal movements due to altered fire regimes, landscape fragmentation and introduced predators highlight the importance of managing landscapes to restore movement and help conserve species in fire-prone ecosystems. Our review draws attention to facets of animal movement that may make species particularly prone to novel threats; these involve both increases in movement leading to increased mortality, and reduced movement due to strong boundary responses leading to reduced fitness and local extinction. Understanding which, if any, of these mechanisms are affecting species of conservation concern in fire-prone landscape could help guide management. Watson & Watson (2015) introduced the idea of 'mainstreaming' animal reintroductions to overcome dispersal limitations in agricultural landscapes. Such an approach might be required in fragmented fire-prone landscapes to assist species in accessing patches with an appropriate fire history that are unoccupied due to a lack of dispersal.

(5) Recent approaches to fire management emphasise the diversity of fire-ages required to support the needs of particular ecosystems and species (Di Stefano *et al*., 2013; Kelly *et al*.,

2015; Hale *et al*., 2016), but give less attention to how fire histories should be configured to enhance the probability of species being able to track particular fire histories through time. Movement ecology can help fill this gap, by identifying configurations of fire histories that facilitate dispersal of fire-dependent fauna or allow species access to multiple fire histories within their activity range. Our review points to the potential benefits of low-intensity, patchy fires to facilitate movement through fire-prone landscapes, due to the retention of stepping stones (unburned refuges) and nearby visual cues of suitable habitat that could help overcome boundary responses and promote dispersal.

(6) While there remain serious challenges to collecting the types of data needed to integrate movement ecology and fire ecology further, promisingly, we may be at the beginning of a revolution in the acquisition of movement data due to the miniaturisation and cost reduction of several movement technologies (Allan *et al*., 2018; Berger-Tal & Lahoz-Monfort, 2018), which could help hasten progress in this field when applied to fire-dependent species.

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