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REVIEW

Refuges for fauna in fire-prone landscapes: their ecological function and importance

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Summary

1. Rapid environmental change is placing increasing pressure on the survival of many species globally. Ecological refuges can mitigate the impacts of change by facilitating the survival or persistence of organisms in the face of disturbance events that would otherwise lead to their mortality, displacement or extinction. Refuges may have a critical influence on the successional trajectory and resilience of ecosystems, yet their function remains poorly understood.

2. We review and describe the role of refuges in faunal conservation in the context of fire, a globally important disturbance process.

3. Refuges have three main functions in relation to fire: they enhance immediate survival during a fire event, facilitate the persistence of individuals and populations after fire and assist in the re-establishment of populations in the longer term. Refuges may be of natural or anthropogenic origin, and in each case, their creation can arise from deterministic or stochastic processes. The specific attributes of refuges that determine their value are poorly known, but include within-patch attributes relating to vegetation composition and structure; patch-scale attributes associated with their size and shape; and the landscape context and spatial arrangement of the refuge in relation to fire patterns and land uses.

4. *Synthesis and applications*. Refuges are potentially of great importance in buffering the effects of wildfire on fauna. There is an urgent need for empirical data from a range of ecosystems to better understand what constitutes a refuge for different taxa, the spatial and temporal dynamics of species' use of refuges and the attributes that most influence their value to fauna. Complementary research is also required to evaluate threats to naturally occurring refuges and the potential for management actions to protect, create and enhance refuges. Knowledge of the spatial arrangement of refuges that enhance the persistence of fire-sensitive species will aid in making decisions concerning land and fire management in conservation reserves and large natural areas. Global change in the magnitude and extent of fire regimes means that refuges are likely to be increasingly important for the conservation of biodiversity in fire-prone environments.

Key-words: biodiversity, biological legacies, disturbance, prescribed fire, residual habitat, unburnt patch, wildfire

Introduction

Globally, the survival of many species is under mounting pressure from environmental change, including the impacts of habitat loss and modification, invasive species, overexploitation of resources and climate change (Lindenmayer & Fischer 2006; Brook, Sodhi & Bradshaw 2008). Such anthropogenic pressures can modify the temporal and spatial dynamics of natural disturbance regimes, placing the inherent resilience of ecosystems under greater stress (McKenzie *et al.* 2004; Brook, Sodhi & Bradshaw 2008). The ability of species to cope with change arising from disturbance will depend on their ecological and

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life-history attributes (Sousa 1984). Species with low dispersal capabilities are less able to directly avoid rapid shocks and will be at increased risk of mortality unless they possess other adaptations (e.g. behaviours or physiologies) that allow them to survive *in situ* (Whelan 1995). Specific components of a landscape that endure (or escape) change caused by a disturbance can lessen the impacts of environmental shocks on organisms and increase their likelihood of surviving: these components are commonly referred to as refuges (e.g. Lindenmayer *et al.* 2009; Brennan, Moir & Wittkuhn 2011). Refuges may have a critical influence on the successional trajectory and resilience of ecosystems to disturbance events. Consequently, if the specific properties of high-quality refuges can be successfully identified, then these areas can be located and managed to ameliorate against major environmental pressures.

Refuges are defined here as habitat features within a landscape that facilitate the survival or persistence of organisms (or species) in the face of a disturbance event that would otherwise result in their mortality, displacement or extinction (see also Mackey *et al.* 2002). We review the concept and role of refuges in faunal conservation in the context of fire. Fire profoundly influences the structure and composition of ecosystems, and the distribution and abundance of organisms globally (Bond, Woodward & Midgley 2005). The impact of fire is inherently heterogeneous (Burton *et al.* 2008). This reflects variation in fire regimes (i.e. fire intensity, time since fire, interfire interval, season of burning: Gill 1975) and in the spatial pattern of fires (e.g. their size, shape and context of unburnt vegetation). The occurrence of refuges is an element of this heterogeneity. Thus, the relationship between refuges, disturbance regimes and the environment involves complex interactions that are both spatially and temporally dynamic.

In the context of fire, refuges typically occur at relatively small spatial scales (e.g. forest patches, logs, burrows) within the fire boundary. They may occur as isolated patches or as peninsulas surrounded by the burnt matrix (Perera, Buse & Routledge 2007), but are distinct from large tracts of unburnt vegetation adjacent to the fire boundary. Conceptually, refuges partially overlap with the idea of 'biological legacies' (Franklin *et al.* 2000). However, the latter concept is broader and refers to all biological or biologically derived features that persist following disturbance (including organisms themselves) and the range of functions these may fulfil. Whilst some biological legacies can act as refuges (e.g. hollow trees, undisturbed patches of vegetation), others have extremely limited capacity to fulfil this role (e.g. plant propagules, faeces). In addition, there are features that function as refuges that are not biological in origin (e.g. rock outcrops).

In many fire-prone environments, synergies with anthropogenic threats, such as habitat fragmentation and invasive species, suggest that present-day impacts of fire potentially are greater than those experienced by species during their evolutionary history (Brook, Sodhi & Bradshaw2008). In these circumstances, refuges may have an even greater role in sustaining species and communities. Further, with global climate change, fire-prone regions are predicted to differentially experience changes in the length of fire seasons and the frequency and/or intensity of wildfires (Flannigan *et al.* 2009). This may increase the importance of refuges for the persistence of fire-sensitive fauna, whilst potentially also decreasing the likelihood of refuges existing (McKenzie *et al.* 2004). The limited understanding of the role of refuges and the factors that determine their value for the persistence of biota in fire-prone landscapes means that land managers have little guidance for incorporating the maintenance or creation of refuges into fire planning.

We outline a conceptual model of the functions of refuges in relation to fire, describe the origins of refuges, review current understanding of the factors that influence the value of refuges for fauna and identify knowledge gaps. We acknowledge that some species are dependent on fire, being either pyrophilic or associated with early postfire successional stages (e.g. Hutto 2008), but focus here on species that are likely to do less well in a world experiencing more frequent and severe fires.

Refuges and their role in survival and postfire recovery of fauna

Refuges have three primary roles in relation to fire: (i) they enable survival of organisms during and immediately after a fire event; (ii) they facilitate *in situ* persistence of organisms and populations within the fire boundary; and (iii) they assist the re-establishment of populations within the burnt area as it recovers. The length of time that a specific habitat component may fulfil a refuge role for an organism will vary, and through time, organisms and populations may use different habitat components for different roles.

SURVIVAL DURING A FIRE

The likelihood of immediate survival of an individual during a fire will be influenced by the severity of the fire, the individual's location in relation to potential refuges in the landscape and the physical or behavioural mechanisms the organism may use to avoid direct flames and radiant heat (Friend 1993; Whelan 1995).

Numerous studies have linked postfire population sizes with fire severity (e.g. Smucker, Hutto & Steele 2005). Individual survival may be relatively high after low intensity or patchy fires in which vegetative components remain unburnt or only partially burnt (Ford *et al.* 1999; Brennan, Moir & Wittkuhn 2011). In contrast, severe fires can result in large declines in population sizes (Newsome, McIlroy & Catling 1975; Banks *et al.* 2011; Couturier *et al.* 2011).

Species that live permanently within less flammable habitats (e.g. rock outcrops, rain forest gullies) may rarely have direct contact with fire (Whelan 1995). For other species, individuals may either seek out or fortuitously be present within a refuge when the fire passes (Grafe, Döbler & Linsenmair 2002; Garvey *et al.* 2010). Individual or social behaviour can also influence access to refuges and affect survival rates (Whelan *et al.* 2002). For example, swamp wallabies *Wallabia bicolor* moved to moist creekline vegetation during a fire, and then, individuals doubled back through the fire front to safety in burned areas (Garvey *et al.* 2010). Savanna chimpanzees *Pan troglodytes verus* exhibit a complex suite of behaviours in avoiding fire, including individuals apparently warning other group members of approaching fire and monitoring the progress of fires at close range (Pruetz & LaDuke 2010).

PERSISTENCE OF INDIVIDUALS AND POPULATIONS POSTFIRE

Whilst all animals must avoid the immediate passage of fire, by using either a refuge or fleeing, refuges can also facilitate the postfire persistence of individuals and populations within the burned landscape. The importance of refuges for the species' persistence depends on the degree to which they provide resources that, otherwise, are unavailable in the burnt matrix. Species exhibit a continuum of levels of reliance on refuges for postfire persistence (e.g. Legge *et al.* 2008), and at least five patterns of refuge use can be recognized.

First, individuals may use a refuge temporarily to survive the fire front, but then live within the burned area with no further dependence on the refuge (e.g. Garvey *et al.* 2010). Second, individuals may persist within the burned area, albeit at a reduced density, assisted by the presence of postfire legacies (e.g. partly burned logs, stumps) that provide physical refuge or shelter (Banks *et al.* 2011). Third, individuals of some species may survive postfire by using both unburnt refuge habitat and adjacent burned areas (Fraser *et al.* 2003). Such species are likely to be favoured by fine-grained fire mosaics. Fourth, persistence of a species may depend primarily on unburned patches of vegetation to meet all their resource requirements in the short term (up to several years) (Watson *et al.* 2012a), before they gradually recolonize the surrounding environment. Lastly, species that are late-successional specialists may depend on unburned refuges for many years. For example, the Mallee Emu-wren *Stipiturus mallee* is essentially absent from burned vegetation until at least 17 years postfire (Brown, Clarke & Clarke 2009). In the absence of suitable refuges, such specialists will be at high risk of local extinction (Silveira *et al.* 1999; Peres, Barlow & Haugaasen 2003).

RE-ESTABLISHMENT OF POPULATIONS

In the longer term, refuges may contribute to re-establishment of populations in extensively burned landscapes in two ways: as a source for population expansion from within the fire boundary and by facilitating the colonization of individuals from outside the fire boundary (Banks *et al.* 2011; Watson *et al.* 2012a).

If a species survives and persists within refuges, this offers the potential for population expansion into the surrounding landscape from multiple dispersed nuclei when conditions in the burnt environment become suitable (Watson *et al.* 2012a). Little is known, however, of the spatial dynamics of species in such situations, despite the potential importance in recolonization processes (Banks *et al.* 2011). Depending on the spatial isolation of refuges relative to the mobility of the organism, spatial population structure within the burned landscape may vary through time along a gradient from a series of disjunct isolated populations, to a metapopulation and to a patchy population linked by frequent movements (Templeton, Brazeal & Neuwald 2011; Driscoll, Whitehead & Lazzari 2012).

Alternatively, refuges may facilitate colonization by individuals from outside the fire boundary, by providing resources in the short term (food, shelter) or longer term (resident habitat). The distance from the fire boundary and the spatial arrangement of refuges within the burned area will influence the rate and capacity for colonization by different species (Turner *et al.* 1998). Refuges close to the boundary are more likely to be occupied (Watson *et al.* 2012a).

Origins of refuges

Refuges can be created by natural processes, or by human manipulation of the environment, often with the intent of conserving organisms and communities. In both cases, the processes giving rise to refuges may be deterministic or stochastic.

NATURAL REFUGES

Patches of unburnt vegetation and features such as logs and rock outcrops that provide refuge occur naturally in burned landscapes (Burton *et al.* 2008). Few studies have quantified the proportion of vegetation remaining unburnt during wildfires. Reported values range from as little as approximately 1–22%, of the fire-affected landscape, with this value largely depending on weather conditions during the fire and landscape characteristics (Román-Cuesta, Gracia & Retana 2009; Madoui *et al.* 2010; S.W.J. Leonard, A.F. Clarke & M.F. Bennett, in review).

Due to the influence of topographic position and environmental features, unburnt patches often occur in a non-random (deterministic) manner (Mackey *et al.* 2002; Bradstock *et al.* 2005). Typically, the vegetation differs in composition or moisture content from that in the surrounding fire-prone landscape, such as moist gullies within temperate eucalypt forests (Penman *et al.* 2007), rain forest patches within savanna woodlands (Bowman 2000) or deciduous forest within mixedwood boreal forests (Burton *et al.* 2008). In some instances, negative feedback between vegetation succession and flammability reduces the probability of fire over time (e.g. succession from eucalypt forest to rain forest, Jackson 1968). Sites that exhibit reduced flammability due to topography, microclimate or vegetation type may remain unburnt over several fire cycles in the surrounding landscape and therefore escape fire for extended periods (Camp *et al.* 1997). In extreme fire weather conditions, however, even these sites can burn (Gill & Allan 2008). In addition, deterministic refuges may be compromised or lost if they are subject to anthropogenic disturbances such as logging or land clearing (Lindenmayer *et al.* 2011).

Natural refuges also arise due to stochastic processes (Mackey *et al.* 2002). The interaction of weather and fire is complex and can be unpredictable, particularly at the local scale. Sudden variation in wind speed or direction results in localized changes in fire intensity or direction of travel, which in turn has the potential to result in patches remaining unburnt. Such unburnt patches can be considered 'transient' refuges, as they 'escape' one fire event, but not necessarily the next (Bradstock *et al.* 2005).

Animals may modify fuel characteristics within a site, such that the likelihood of burning is reduced. Intense herbivory may reduce fuel loads to the extent that fire is excluded (Leonard, Kirkpatrick & Marsden-Smedley 2010). Burrowing animals can create bare or sparsely vegetated areas around warrens that inhibit fire spread (Kotliar *et al.* 1999). Other soil-disturbing activities such as wallowing (Knapp *et al.* 1999) may have similar effects. Animals may also reduce fuel loads and hence flammability through removing leaf litter (Mikami *et al.* 2010). The duration of fire suppression from these actions varies from weeks to months (e.g. migratory herbivores, McNaughton 1992) to decades (e.g. *Cynomys* spp. colonies, Kotliar *et al.* 1999).

REFUGES OF ANTHROPOGENIC ORIGIN

Land management practices can reduce fuel loads so that areas adjacent to a treated area function as refuges or to create potential refuges within a large treated area.

Prescribed burning may be used in a deterministic fashion (i.e. in a particular place and time) to maintain designated refuges by manipulating the location, size and frequency of burns such that they prevent future wildfire from spreading into adjacent designated areas (Burrows 2008). Other means of reducing fuel loads, such as mechanical removal of fuel (Waldrop, Phillips & Simon 2010) or manipulation of grazing or browsing animals (Valderrabano & Torrano 2000), may also be used to protect areas from fire. However, fuel reduction by such means needs to be carefully considered as there are examples of both mechanical fuel removal (e.g. salvage logging, Donato *et al.* 2006) and herbivory (Leonard, Kirkpatrick & Marsden-Smedley 2010) that increased vegetation flammability.

Prescribed burning can also be used to create potential refuges within a large treated area. Conservation managers often adopt some form of patch mosaic burning with the aim of introducing or maintaining landscape heterogeneity by creating patches that vary in fire history and severity of the most recent fire, including patches that remain unburnt (Parr & Andersen 2006). The exact location and size of unburnt patches is usually not predetermined, but the general pattern of the mosaic (e.g. overall burn cover, patch grain) may be managed by selecting the timing and pattern of ignition (Yibarbuk *et al.* 2001). For example, to maintain populations of relatively sedentary, refuge-dependent fauna in northern Australian savanna, a fine-grained fire mosaic is required in which fire patch size is less than the home range of the species concerned (in some cases <1 ha; Fraser *et al.* 2003; Yates, Edwards & Russell-Smith 2008). The resultant mosaic may limit the spread and intensity of subsequent wildfire, such that a higher proportion of the landscape remains unburnt and natural refuge patches are protected from fire incursion.

Alternatively, patches recently burnt by prescribed fire may escape burning during a subsequent wildfire and thus act as a refuge. However, their ability to function as a long-term refuge may be limited by their simplified (fuel reduced) structure (Catling 1991). The fate of prescribed burns during subsequent wildfire depends on numerous factors, including severity of the prescribed burn, time since burn, rates of fuel re-accumulation, weather (both between and during fires) and intensity of the wildfire (Cary *et al.* 2009).

The likelihood of areas burning, or not burning, can also be an unintentional effect of human activities. Vegetation fragmentation, for instance, can inhibit fire spread and result in unburnt patches (Duncan & Schmalzer 2004). Other anthropogenic changes, such as invasion of exotic plant species, can reduce or increase vegetation flammability (Brooks *et al.* 2004). A widely observed example of the latter effect is a positive feedback between exotic grass invasion and fire intensity (the 'grass–fire cycle'; D'Antonio & Vitousek 1992), which may result in an increased extent and decreased patchiness of fires (Miller *et al.* 2010).

What attributes of refuges contribute to their value?

The attributes of faunal refuges can be considered in relation to temporal requirements of fauna associated with a fire event (see Fig. 1).

SHORT-TERM SURVIVAL

The immediate survival of organisms during fire will be greatest in patches or components that provide shelter and physical protection from flames and radiant heat (Fig. 1). Several types of refuges enhance the immediate survival of organisms. These include habitat components

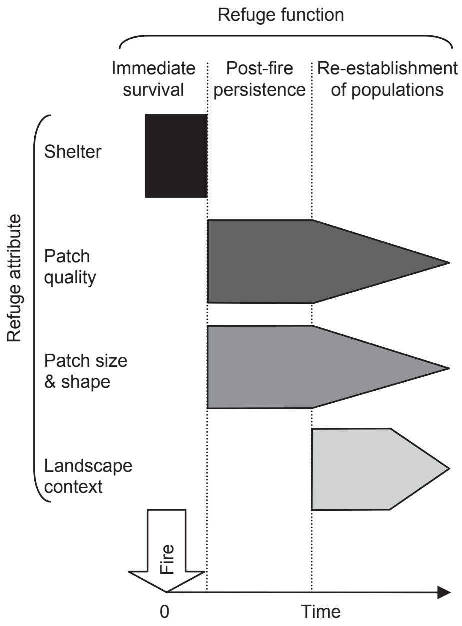

Fig. 1. A conceptual diagram of refuge function through time in relation to fire. Bar width indicates the relative importance of each attribute to function. At the onset of fire, refuges provide immediate shelter. Following fire, they may enhance the persistence of individuals and populations, and later the re-establishment of populations in the burnt landscape.

that are not flammable (e.g. burrows, termite mounds, Yarnell *et al*. 2008), components that are less flammable (e.g. topographic locations such as gullies, or specific vegetation types, Penman *et al*. 2007), through to vegetation components or habitat features that are intrinsically flammable, but due to fire behaviour do not burn or burn at lower intensity (e.g. hollows in large trees, *Xanthorrhoea preissii*, Brennan, Moir & Wittkuhn 2011). Each of these functions at a range of scales: for example, intrinsically flammable refuge habitats range from microhabitats associated with logs (Andrew, Rodgerson & York 2000) and unburned litter (Kiss & Magnin 2006) to larger patches of unburned vegetation (Swengel & Swengel 2007; Watson *et al*. 2012a). Biotic interactions also influence immediate survival, including competition for refuges just prior to and during the fire event, and predation during or shortly after the event (Whelan *et al*. 2002).

LONGER TERM PERSISTENCE AND RECOLONIZATION

In the longer term, refuge attributes that allow species to persist or recolonize are complex and species specific. There are few empirical studies on the relative value of different attributes of refuges. However, the body of literature on the occurrence of species in habitat patches in fragmented landscapes (Mazerolle & Villard 1999; Lindenmayer & Fischer 2006; Thornton, Branch & Sunquist 2011) suggests that three kinds of attributes will influence the longer term value of refuges: within-patch structural and biotic attributes, size and shape of the patch and landscape context of the patch (Fig. 1). The temporal context of the fire, with respect to other disturbances, biotic interactions and climatic events (e.g. drought or rain), may further influence refuge quality.

Patch quality

For an individual to persist in a refuge, suitable resources need to be available (Fig. 1). Within-patch attributes that influence longer term survival include vegetation composition and habitat structural features (e.g. Pereoglou *et al*. 2011). Attributes of patches are likely to be most important in the short- to medium-term postfire, when the contrast between patches and the surrounding environment may be stark. However, as the burned environment recovers, resources become available more widely (Lindenmayer *et al*. 2009) and the distinctiveness of within-patch attributes declines (Fig 1). Patch characteristics partly depend on the mechanism through which a refuge is created. Environmental conditions that contribute to the creation of natural deterministic refuges typically lead to different habitat qualities than those found within refuges created by chance. Natural deterministic refuges such as riparian zones and gallery forests (Palmer & Bennett 2006) or rock outcrops (Clarke 2002) have intrinsically different vegetation and harbour different assemblages than those in the broader, more flammable landscape. Deterministic refuges, including those of both natural and anthropogenic origin, are likely to have older, more mature vegetation than those arising stochastically, due to the lower probability of burning in the former (DeLong & Kessler 2000; Gandhi *et al*. 2001).

Stochastic refuges, on the other hand, may reflect the broader vegetation composition and structure of the landscape prior to disturbance. The fire history, or fire regime, influences these habitat attributes. Long fire intervals result in older vegetation of greater structural complexity within patches created stochastically. Patches burnt recently, or at high frequency, are likely to have a simplified vegetation structure and provide less suitable refuge for species requiring resources associated with long-undisturbed vegetation (Catling 1991). However, they may provide other services to the fauna, such as protection during fire, foraging areas and habitat for early-seral species (Brotons, Pons & Herrando 2005).

Patch size and shape

The size of a refuge patch influences its detectability and availability to different organisms and the number of individuals it can support, whilst patch shape determines the availability of core habitat uncompromised by edge effects (Forman 1995). In general, the probability of species occurring within a patch increases with increasing patch area and decreasing isolation (Lindenmayer & Fischer 2006). However, the relationship between patch metrics and occurrence of species in large fire mosaics is more complex than, for example, forest fragments in agricultural landscapes. First, the postfire environment is a complex array of different fire severities, compounded by environmental gradients (e.g. topography, vegetation) and spatial variation in the number and type of biological legacies after fire (Burton *et al.* 2008). Consequently, patch boundaries are often indistinct and represent gradients in quality rather than marked contrasts. Second, what constitutes a refuge patch differs amongst species. In some instances, such as unburnt vegetation surrounded by severely burnt vegetation, patches are visibly distinct. In other situations, such as the persistence of small mammals (Banks *et al.* 2011) or ants (Andrew, Rodgerson & York 2000) amongst logs and rocks in burnt vegetation, the difference between refuge and matrix may be subtle. Third, the postfire mosaic is temporally dynamic, changing in quality and contrast as vegetation recovery proceeds (e.g. Ashton 1981). To the degree that patches become less distinct from their surroundings over time, it is likely that the importance of patch size and shape will also diminish (Fig. 1).

Landscape context

The spatial arrangement of refuge patches and their context in the broader fire mosaic is important for re-establishing and maintaining populations over time (Watson *et al.* 2012a) (Fig. 1). For species that depend on refuge patches, the ability of individuals to either disperse through the burned landscape or use refuge patches as 'stepping stones' is an important determinant of (re)colonization of unoccupied habitat (Brotons, Pons & Herrando 2005; Pereoglou *et al.* 2013). A greater potential for individuals to (re)establish local populations in unoccupied habitat increases the chances of species surviving in patchy habitats (Templeton, Brazeal & Neuwald 2011). The dispersal ability of a species is determined by the mobility of individuals and the extent to which they perceive the burned landscape as hostile or benign.

The optimal spatial arrangement of refuge patches within the postfire environment will vary amongst species (Bradstock *et al.* 2005; Clarke 2008), and the value of different configurations may also differ between ecosystems. For example, in fire-prone savanna woodlands of northern Australia, a fine-grained mosaic of burned and unburned vegetation is considered desirable for many species, such as the partridge pigeon *Geophaps smithii* (Fraser *et al.* 2003). A trend towards coarse-grained fire mosaics in this system has been linked to declines of small mammal species (Andersen, Woinarski & Parr 2012). In contrast, in other ecosystems, a fine-scale patch arrangement may be detrimental to taxa if perceived as fragmentation (Taylor *et al.* 2012).

Biotic interactions

The value of a refuge is also influenced by interactions with other species. Although few examples are available from fire ecology, changes in interactions including predation, competition, parasitism and mutualisms have been documented after landscape change and isolation of habitats in other situations (Lindenmayer & Fischer 2006; Ritchie *et al.* 2009). For example, loss of predators in isolated fragments can lead to cascading effects on ecosystems, with resultant outbreaks of herbivores significantly altering habitat structure (Ritchie & Johnson 2009). Many generalist predators are not restricted to unburned refuges and may be favoured by fire (Dees, Clark & Manen 2001). In the immediate postfire environment, predator abundance can increase due to greater availability of food from burnt carcasses and increased hunting efficiency due to reduced vegetative cover for prey (Conner, Castleberry & Derrick 2011).

Knowledge gaps and further steps in understanding refuges

The commonly assumed importance of refuges for survival, persistence and recovery of fauna from fire contrasts with the paucity of published evidence. Studies relating to the value of faunal refuges, often undertaken opportunistically after wildfire, have frequently been limited by issues such as inadequate documentation of fire severity, history and spatial properties; monitoring on limited spatial and temporal scales; inadequate replication; inability to separate mortality from emigration; and interactions with other disturbances (e.g. Newsome, McIlroy & Catling 1975; Murphy *et al.* 2010; Zozaya, Brotons & Vallecillo 2011). The limited understanding of fire refuges contrasts with that for refuges in freshwater systems where knowledge is more advanced and functions and attributes have been outlined (Sedell *et al.* 1990). To give direction to future research, we highlight knowledge gaps in three broad areas.

POSTFIRE PATTERNS AND DYNAMICS OF POTENTIAL REFUGE HABITATS

An important step is to develop a stronger, predictive understanding of the relationship between fire characteristics (e.g. severity, size, seasonality) and the spatial pattern of potential refuge areas that occurs postfire. Systematic mapping of areas remaining unburnt in relation to vegetation type and topography (e.g. Madoui *et al.* 2010) provides a valuable opportunity to determine the spatial patterns of potential refuges, including natural deterministic refuges (moist drainage lines, less flammable vegetation), natural stochastic refuges (e.g. patches that escape burning) and anthropogenic refuges arising from prior prescribed burns. The occurrence and dynamics of other types of refuges, such as burrows, rock outcrops and unburnt habitat components (e.g. logs, tree hollows, litter patches), are less readily mapped remotely, but can be assessed by systematic survey of the postfire environment. Of particular value are quantitative studies that examine spatial attributes of potential refuges – including number, size, location and configuration – in relation to aspects of fire regime and land management (e.g. Collins *et al.* 2012). Such studies are required in relation to both wildfires and prescribed burns in different ecosystems.

FAUNAL USE OF REFUGES

A comprehensive understanding of how refuges mitigate the effects of fire requires more empirical data on refuge use by a wide range of taxa from different types of fire-prone ecosystems. This includes greater insight into what constitutes a refuge for particular taxa, specific attributes of the refuge and when it is used (e.g. during fire, immediate postfire, longer term). A key challenge is to identify potential relationships between life-history attributes of species and their need for, and use of, different types of refuges. Opportunistic studies after wildfire will continue to be an important source of information, as will planned studies of responses of individuals and populations to prescribed burns of different severity, size and season (e.g. Fraser *et al.* 2003). Longitudinal studies of responses of fire-sensitive species that extend beyond a few years are scarce (Driscoll *et al.* 2010). Consequently, there is little knowledge of the time period over which species may depend on refuges or how refuge use changes over time. Such insights are particularly important for species known to favour late-successional vegetation or that rely on habitat components that take many years to recover (Haslem *et al.* 2011; Watson *et al.* 2012b).

A major knowledge gap relates to the spatial patterns and dynamics of populations within postfire mosaics. Such knowledge would assist in conservation planning for fire-sensitive species by determining whether there is a need for management intervention to protect or create refuge habitats, and if so, their spatial arrangement. Empirical data on species' dependence on refuges, refuge spatial isolation and patterns of movement by individuals between them will give important insight into the spatial structure (or continuity) of the population within the fire boundary.

ANTHROPOGENIC CREATION AND MANAGEMENT OF REFUGES

As natural fire regimes are increasingly altered by land-use change, wildfire suppression, anthropogenic burning and effects of climate change (Flannigan *et al.* 2009), active management of refuges to safeguard sensitive species from displacement or local extinction will become more important. Knowledge of the location of natural refuges should be used to highlight areas for protection, either from natural or from anthropogenic disturbances (Mackey *et al.* 2002). Management actions that improve connectivity between such refuges may also be beneficial (e.g. Brown, Clarke & Clarke 2009). However, planning in this regard will need to consider potential risks such as increased wildfire propagation and spread of pests and disease (Camp *et al.* 1997). Planned burns can be used to protect or create refuge habitats, either in specific locations or as part of a landscape mosaic (Parr & Andersen 2006; Andersen, Woinarski & Parr 2012), but this requires a sound understanding of what constitutes a suitable landscape pattern, as well as technical skills to deliver the required burn pattern under a range of fire conditions.

There is a great need for further evaluation of the outcomes of fire management practices designed to mitigate the effects of fire on biodiversity, including their effectiveness in creating or maintaining refuges. It is also essential to evaluate the effects of fire management for purposes such as hazard reduction and other land management practices that may result in the loss or degradation of refuges. Much progress could be made by the integration of experimental management with systematic monitoring and research (Driscoll *et al.* 2010). This includes experimentally testing different management options for creating or protecting refuge habitats, together with long-term monitoring of faunal abundance and habitat use at the landscape scale.

Faunal fire refuges are likely to become increasingly important under expected changes in the occurrence, intensity and extent of wildfires (McKenzie *et al.* 2004). Managing for the refuge needs of fauna will help mitigate the detrimental impacts of fire and facilitate biodiversity conservation in fire-prone landscapes.

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References

Andersen, A.N., Woinarski, J.C.Z. & Parr, C.L. (2012) Savanna burning for biodiversity: fire management for faunal conservation in Australian tropical savannas. *Austral Ecology*, **37**, 658–667.

Andrew, N., Rodgerson, L. & York, A. (2000) Frequent fuel-reduction burning: the role of logs and associated leaf litter in the conservation of ant biodiversity. *Austral Ecology*, **25**, 99–107.

Ashton, D.H. (1981) Fire in tall open-forests (wet sclerophyll forests). *Fire and the Australian Biota* (eds A.M. Gill, R.H. Groves & I.R. Noble), pp. 339–366. Australian Academy of Science, Canberra.

Banks, S.C., Dujardin, M., McBurney, L., Blair, D., Barker, M. & Lindenmayer, D.B. (2011) Starting points for small mammal population recovery after wildfire: recolonisation or residual populations? *Oikos*, **120**, 26–37.

Bond, W.J., Woodward, F.I. & Midgley, G.F. (2005) The global distribution of ecosystems in a world without fire. *New Phytologist*, **165**, 525–538.

Bowman, D.M.J.S. (2000) *Australian Rainforests: Islands of Green in an Ocean of Fire*. Cambridge University Press, Cambridge.

Bradstock, R.A., Bedward, M., Gill, A.M. & Cohn, J.S. (2005) Which mosaic? A landscape ecological approach for evaluating interactions between fire regimes, habitat and animals. *Wildlife Research*, **32**, 409–423.

Brennan, K.E.C., Moir, M.L. & Wittkuhn, R. (2011) Fire refugia: the mechanism governing animal survivorship within a highly flammable plant. *Austral Ecology*, **36**, 131–141.

Brook, B.W., Sodhi, N.S. & Bradshaw, C.J.A. (2008) Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, **23**, 453–460.

Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M. & Pyke, D. (2004) Effects of invasive alien plants on fire regimes. *BioScience*, **54**, 677–688.

Brotons, L., Pons, P. & Herrando, S. (2005) Colonization of dynamic Mediterranean landscapes: where do birds come from after fire? *Journal of Biogeography*, **32**, 789–798.

Brown, S., Clarke, M.F. & Clarke, R. (2009) Fire is a key element in the landscape-scale habitat requirements and global population status of a threatened bird: the Mallee Emu-wren (*Stipiturus mallee*). *Biological Conservation*, **142**, 432–445.

Burrows, N.D. (2008) Linking fire ecology and fire management in south-west Australian forest landscapes. *Forest Ecology and Management*, **255**, 2394–2406.

Burton, P.J., Parisien, M.A., Hicke, J.A., Hall, R.J. & Freeburn, J.T. (2008) Large fires as agents of ecological diversity in the North American boreal forest. *International Journal of Wildland Fire*, **17**, 754–767.

Camp, A., Oliver, C., Hessburg, P. & Everett, R. (1997) Predicting late-successional fire refugia pre-dating European settlement in the Wenatchee Mountains. *Forest Ecology & Management*, **95**, 63–77.

Cary, G.J., Flannigan, M.D., Keane, R.E., Bradstock, R.A., Davies, I.D., Lenihan, J.M., Li, C., Logan, K.A. & Parsons, R.A. (2009) Relative importance of fuel management, ignition management and weather for area burned: evidence from five landscape-fire-succession models. *International Journal of Wildland Fire*, **18**, 147–156.

Catling, P.C. (1991) Ecological effects of prescribed burning practices on the mammals of southeastern Australia. *Conservation of Australia's Forest Fauna* (ed. D. Lunney), pp. 353–363. Royal Zoological Society of New South Wales, Mosman.

Clarke, P.J. (2002) Habitat islands in fire-prone vegetation: do landscape features influence community composition? *Journal of Biogeography*, **29**, 677–684.

Clarke, M.F. (2008) Catering for the needs of fauna in fire management: science or just wishful thinking? *Wildlife Research*, **35**, 385–394.

Collins, L., Bradstock, R.A., Tasker, E.M. & Whelan, R.J. (2012) Impact of fire regimes, logging and topography on hollows in fallen logs in eucalypt forest of south eastern Australia. *Biological Conservation*, **149**, 23–31.

Conner, L.M., Castleberry, S.B. & Derrick, A.M. (2011) Effects of meso-predators and prescribed fire on hispid cotton rat survival and cause-specific mortality. *The Journal of Wildlife Management*, **75**, 938–944.

Couturier, T., Cheylan, M., Guérette, E. & Besnard, A. (2011) Impacts of a wildfire on the mortality rate and small-scale movements of a Hermann's tortoise *Testudo hermanni hermanni* population in southeastern France. *Amphibia Reptilia*, **32**, 541–545.

D'Antonio, C.M. & Vitousek, P.M. (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, **23**, 63–87.

Dees, C.S., Clark, J.D. & Manen, F.T.V. (2001) Florida Panther habitat use in response to prescribed fire. *The Journal of Wildlife Management*, **65**, 141–147.

DeLong, S.C. & Kessler, W.B. (2000) Ecological characteristics of mature forest remnants left by wildfire. *Forest Ecology and Management*, **131**, 93–106.

Donato, D.C., Fontaine, J.B., Campbell, J.L., Robinson, W.D., Kauffman, J.B. & Law, B.E. (2006) Post-wildfire logging hinders regeneration and increases fire risk. *Science*, **311**, 352.

Driscoll, D., Whitehead, C. & Lazzari, J. (2012) Spatial dynamics of the knob-tailed gecko *Nephrurus stellatus* in a fragmented agricultural landscape. *Landscape Ecology*, **27**, 829–841.

Driscoll, D.A., Lindenmayer, D.B., Bennett, A.F., Bode, M., Bradstock, R., Carey, G. *et al.* (2010) Fire management for biodiversity conservation: key research questions and our capacity to answer them. *Biological Conservation*, **143**, 1928–1939.

Duncan, B. & Schmalzer, P. (2004) Anthropogenic influences on potential fire spread in a pyrogenic ecosystem of Florida, USA. *Landscape Ecology*, **19**, 153–165.

Flannigan, M.D., Krawchuk, M.A., de Groot, W.J., Wotton, B.M. & Gowman, L.M. (2009) Implications of changing climate for global wildland fire. *International Journal of Wildland Fire*, **18**, 483–507.

Ford, W.M., Menzel, M.A., McGill, D.W., Laerm, J. & McCay, T.S. (1999) Effects of a community restoration fire on small mammals and herpetofauna in the southern Appalachians. *Forest Ecology and Management*, **114**, 233–243.

Forman, R.T.T. (1995) *Land Mosaics: The Ecology of Landscapes and Regions*. Cambridge University Press, Cambridge.

Franklin, J.F., Lindenmayer, D., MacMahon, J.A., McKee, A., Magnuson, J., Perry, D.A., Waide, R. & Foster, D. (2000) Threads of continuity. *Conservation Biology in Practice*, **1**, 8–17.

Fraser, F., Lawson, V., Morrison, S., Christophersen, P., McGreggor, S. & Rawlinson, M. (2003) Fire management experiment for the declining partridge pigeon, Kakadu National Park. *Ecological Management and Restoration*, **4**, 94–102.

Friend, G.R. (1993) Impact of fire on small vertebrates in mallee woodlands and heathlands of temperate Australia: a review. *Biological Conservation*, **65**, 99–114.

Gandhi, K.J.K., Spence, J.R., Langor, D.W. & Morgantini, L.E. (2001) Fire residuals as habitat reserves for epigaeic beetles (Coleoptera: Carabidae and Staphylinidae). *Biological Conservation*, **102**, 131–141.

Garvey, N., Ben-Ami, D., Ramp, D. & Croft, D.B. (2010) Survival behaviour of swamp wallabies during prescribed burning and wildfire. *Wildlife Research*, **37**, 1–12.

Gill, A.M. (1975) Fire and the Australian flora: a review. *Australian Forestry*, **38**, 4–25.

Gill, A.M. & Allan, G. (2008) Large fires, fire effects and the fire-regime concept. *International Journal of Wildland Fire*, **17**, 688–695.

Grafe, T.U., Döbler, S. & Linsenmair, K.E. (2002) Frogs flee from the sound of fire. *Proceedings of the Royal Society B*, **269**, 999–1003.

Haslem, A., Kelly, L.T., Nimmo, D.G., Watson, S.J., Kenny, S.A., Taylor, R.S. *et al.* (2011) Habitat or fuel? Implications of long-term post-fire dynamics for the development of key resources for fauna and fire. *Journal of Applied Ecology*, **48**, 247–256.

Hutto, R.L. (2008) The ecological importance of severe wildfires: some like it hot. *Ecological Applications*, **18**, 1827–1834.

Jackson, W.D. (1968) Fire, air, water and earth - an elemental ecology of Tasmania. *Proceedings of the Ecological Society of Australia*, **3**, 9–16.

Kiss, L. & Magnin, F. (2006) High resilience of Mediterranean land snail communities to wildfires. *Biodiversity and Conservation*, **15**, 2925–2944.

Knapp, A.K., Blair, J.M., Briggs, J.M., Collins, S.L., Hartnett, D.C., Johnson, L.C. & Towne, E.G. (1999) The keystone role of bison in North American tallgrass prairie. *BioScience*, **49**, 39–50.

Kotliar, N.B., Baker, B.W., Whicker, A.D. & Plumb, G. (1999) A critical review of assumptions about the prairie dog as a keystone species. *Environmental Management*, **24**, 177–192.

Legge, S., Murphy, S., Heathcote, J., Flaxman, E., Augusteyn, J. & Crossman, M. (2008) The short-term effects of an extensive and high-intensity fire on vertebrates in the tropical savannas of the central Kimberley, northern Australia. *Wildlife Research*, **35**, 33–43.

Leonard, S., Kirkpatrick, J. & Marsden-Smedley, J. (2010) Variation in the effects of vertebrate grazing on fire potential between grassland structural types. *Journal of Applied Ecology*, **47**, 876–883.

Lindenmayer, D.B. & Fischer, J. (2006) *Habitat Fragmentation and Landscape Change: An Ecological and Conservation Synthesis*. Island Press, Washington, DC.

Lindenmayer, D.B., MacGregor, C., Wood, J.T., Cunningham, R.B., Crane, M., Michael, D. *et al.* (2009) What factors influence rapid post-fire site re-occupancy? A case study of the endangered Eastern Bristlebird in eastern Australia. *International Journal of Wildland Fire*, **18**, 84–95.

Lindenmayer, D.B., Hobbs, R.J., Likens, G.E., Krebs, C.J. & Banks, S.C. (2011) Newly discovered landscape traps produce regime shifts in wet forests. *Proceedings of the National Academy of Sciences*, **108**, 15887–15891.

Mackey, B., Lindenmayer, D.B., Gill, A.M., McCarthy, M.A. & Lindesay, J. (2002) *Wildfire, Fire & Future Climate: A Forest Ecosystem Analysis*. CSIRO, Collingwood.

Madoui, A., Leduc, A., Gauthier, S. & Bergeron, Y. (2010) Spatial pattern analyses of post-fire residual stands in the black spruce boreal forest of western Quebec. *International Journal of Wildland Fire*, **19**, 1110–1126.

Mazerolle, M.J. & Villard, M.A. (1999) Patch characteristics and landscape context as predictors of species presence and abundance: a review. *Ecoscience*, **6**, 117–124.

McKenzie, D., Gedalof, Z.E., Peterson, D.L. & Mote, P. (2004) Climatic change, wildfire, and conservation. *Conservation Biology*, **18**, 890–902.

McNaughton, S.J. (1992) The propagation of disturbance in savannas through food webs. *Journal of Vegetation Science*, **3**, 301–314.

Mikami, O.K., Katsuno, Y., Yamashita, D.M., Noske, R. & Eguchi, K. (2010) Bowers of the Great Bowerbird (*Chlamydera nuchalis*) remained unburned after fire: is this an adaptation to fire? *Journal of Ethology*, **28**, 15–20.

Miller, G., Friedel, M., Adam, P. & Chewings, V. (2010) Ecological impacts of buffel grass (*Cenchrus ciliaris* L.) invasion in central Australia – does field evidence support a fire-invasion feedback? *The Rangeland Journal*, **32**, 353–365.

Murphy, S.A., Legge, S.M., Heathcote, J. & Mulder, E. (2010) The effects of early and late-season fires on mortality, dispersal, physiology and breeding of red-backed fairy-wrens (*Malurus melanocephalus*). *Wildlife Research*, **37**, 145–155.

Newsome, A.E., McIlroy, J. & Catling, P.C. (1975) The effects of an extensive wildfire on populations of twenty ground vertebrates in south-east Australia. *Proceedings of the Ecological Society of Australia*, **9**, 107–123.

Palmer, G.C. & Bennett, A.F. (2006) Riparian zones provide for distinct bird assemblages in forest mosaics of south-east Australia. *Biological Conservation*, **130**, 447–457.

Parr, C.L. & Andersen, A.N. (2006) Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. *Conservation Biology*, **20**, 1610–1619.

Penman, T.D., Kavanagh, R.P., Binns, D.L. & Melick, D.R. (2007) Patchiness of prescribed burns in dry sclerophyll eucalypt forests in south-eastern Australia. *Forest Ecology and Management*, **252**, 24–32.

Pereoglou, F., Macgregor, C., Banks, S.C., Ford, F., Wood, J. & Lindenmayer, D.B. (2011) Refuge site selection by the eastern chestnut mouse in recently burnt heath. *Wildlife Research*, **38**, 290–298.

Pereoglou, F., Lindenmayer, D.B., MacGregor, C., Ford, F., Wood, J. & Banks, S.C. (2013) Landscape genetics of an early successional specialist in a disturbance-prone environment. *Molecular Ecology*, **22**, 1267–1281.

Perera, A.H., Buse, L.J. & Routledge, R.G. (2007). A review of published knowledge on post-fire residuals relevant to Ontario's policy directions for emulating natural disturbance. Forest Research Information Paper No. 168. Ontario Ministry of Natural Resources, Sault Ste. Marie.

Peres, C.A., Barlow, J. & Haugaasen, T. (2003) Vertebrate responses to surface wildfires in a central Amazonian forest. *Oryx*, **37**, 97–109.

Pruetz, J.D. & LaDuke, T.C. (2010) Reaction to fire by savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal: conceptualization of "fire behavior" and the case for a chimpanzee model. *American Journal of Physical Anthropology*, **141**, 646–650.

Ritchie, E.G. & Johnson, C.N. (2009) Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, **12**, 982–998.

Ritchie, E.G., Martin, J.K., Johnson, C.N. & Fox, B.J. (2009) Separating the influences of environment and species interactions on patterns of distribution and abundance: competition between large herbivores. *Journal of Animal Ecology*, **78**, 724–731.

Román-Cuesta, R.M., Gracia, M. & Retana, J. (2009) Factors influencing the formation of unburned forest islands within the perimeter of a large forest fire. *Forest Ecology and Management*, **258**, 71–80.

Sedell, J.R., Reeves, G.H., Hauer, F.R., Stanford, J.A. & Hawkins, C.P. (1990) Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. *Environmental Management*, **14**, 711–724.

Silveira, L., De Almeida Jácomo, A.T., Diniz Filho, J.A.F. & Rodrigues, F.H.G. (1999) Impact of wildfires on the megafauna of Emas National Park, central Brazil. *Oryx*, **33**, 108–114.

Smucker, K.M., Hutto, R.L. & Steele, B.M. (2005) Changes in bird abundance after wildfire: importance of fire severity and time since fire. *Ecological Applications*, **15**, 1535–1549.

Sousa, W.P. (1984) The role of disturbance in natural communities. *Annual Review of Ecology and Systematics*, **15**, 353–391.

Swengel, A.B. & Swengel, S.R. (2007) Benefit of permanent non-fire refugia for Lepidoptera conservation in fire-managed sites. *Journal of Insect Conservation*, **11**, 263–279.

Taylor, R.S., Watson, S.J., Nimmo, D.G., Kelly, L.T., Bennett, A.F. & Clarke, M.F. (2012) Landscape-scale effects of fire on bird assemblages: does pyrodiversity beget biodiversity? *Diversity and Distributions*, **18**, 519–529.

Templeton, A.R., Brazeal, H. & Neuwald, J.L. (2011) The transition from isolated patches to a metapopulation in the eastern collared lizard in response to prescribed fires. *Ecology*, **92**, 1736–1747.

Thornton, D.H., Branch, L.C. & Sunquist, M.E. (2011) The influence of landscape, patch, and within-patch factors on species presence and abundance: a review of focal patch studies. *Landscape Ecology*, **26**, 7–18.

Turner, M.G., Baker, W.L., Peterson, C.J. & Peet, R.K. (1998) Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems*, **1**, 511–523.

Valderrabano, J. & Torrano, L. (2000) The potential for using goats to control *Genista scorpius* shrubs in European black pine stands. *Forest Ecology and Management*, **126**, 377–383.

Waldrop, T., Phillips, R.A. & Simon, D.A. (2010) Fuels and predicted fire behavior in the southern Appalachian Mountains after fire and fire surrogate treatments. *Forest Science*, **56**, 32–45.

Watson, S.J., Taylor, R.S., Nimmo, D.G., Kelly, L.T., Clarke, M.F. & Bennett, A.F. (2012a) The influence of unburnt patches and distance from refuges on post-fire bird communities. *Animal Conservation*, **15**, 499–507.

Watson, S.J., Taylor, R.S., Nimmo, D.G., Kelly, L.T., Haslem, A., Clarke, M.F. & Bennett, A.F. (2012b) Effects of time since fire on birds: how informative are generalized fire response curves for conservation management? *Ecological Applications*, **22**, 685–696.

Whelan, R.J. (1995) *The Ecology of Fire*. Cambridge University Press, Cambridge.

Whelan, R.J., Rodgerson, L., Dickman, C.R. & Sutherland, E.F. (2002) Critical life cycles of plants and animals: developing a process-based understanding of population changes in fire-prone landscapes. *Flammable Australia: The Fire Regimes and Biodiversity of a Continent* (eds R.A. Bradstock, J. Williams & A.M. Gill), pp. 94–124. Cambridge University Press, Cambridge.

Yarnell, R.W., Metcalfe, D.J., Dunstone, N., Burnside, N. & Scott, D.M. (2008) The impact of fire on habitat use by the short-snouted elephant shrew (*Elephantulus brachyrhynchus*) in North West Province, South Africa. *African Zoology*, **43**, 45–52.

Yates, C.P., Edwards, A.C. & Russell-Smith, J. (2008) Big fires and their ecological impacts in Australian savannas: size and frequency matters. *International Journal of Wildland Fire*, **17**, 768–781.

Yibarbuk, D., Whitehead, P.J., Russell-Smith, J., Jackson, D., Godjuwa, C., Fisher, A., Cooke, P., Choquenot, D. & Bowman, D.M.J.S. (2001) Fire ecology and Aboriginal land management in central Arnhem Land, northern Australia: a tradition of ecosystem management. *Journal of Biogeography*, **28**, 325–343.

Zozaya, E.L., Brotons, L. & Vallecillo, S. (2011) Bird community responses to vegetation heterogeneity following non-direct regeneration of Mediterranean forests after fire. *Ardea*, **99**, 73–84.

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