Putting pyrodiversity to work for animal conservation

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Introduction

An influential concept in ecology commonly guides conservation decision makers: that environmental heterogeneity drives biodiversity (Stein et al. 2014). In the context of fire management for animal conservation, this concept has encouraged heterogeneity in fire regimes under the assumption that 'pyrodiversity promotes biodiversity" (Martin & Sapsis 1992).

Parr and Andersen's (2006) important critique of the pyrodiversity hypothesis argued that it was largely unknown how different patterns of burning influenced biodiversity. Subsequently, research on pyrodiversity surged. We recognise that animal conservation in fire-prone ecosystems requires environmental heterogeneity. However, research over the last decade shows that increasing pyrodiversity does not universally promote biodiversity. The misapplication of this assumption, that pyrodiversity promotes biodiversity, can negatively impact animal populations.

We reason that applying appropriate levels of pyrodiversity for animal conservation requires (1) recognising that context is important – there is no one-size-fits-all approach, (2) understanding the different mechanisms underpinning the overarching pyrodiversity hypothesis, (3) focusing on 'functional landscape heterogeneity' where management of fires is based on species' demonstrated habitat requirements, and (4) using robust decision analyses that link measurable conservation objectives with strategies to achieve them.

What is pyrodiversity?

Fire regimes vary in the intervals between fires, the seasons when fires occur, the spatial arrangement of fires and their type, severity and intensity. Variation in fire regimes has been termed *pyrodiversity* (Martin & Sapsis 1992). Recent work emphasises how feedbacks between fires, biodiversity and ecosystems influence this variation (Bowman et al. 2016). Because animal species may depend on resources that vary spatially and temporally in response to fires, it is argued that heterogeneous fire regimes provide a range of resources that enable the persistence of a diverse community (reviewed by Parr & Andersen 2006). The expectation of the *pyrodiversity hypothesis* is that biodiversity will increase as spatiotemporal variation in fire increases (Martin & Sapsis 1992). This hypothesis has also been described using the terms 'fire mosaic', 'patch mosaic burn', 'successional mosaic', 'shifting mosaic' and 'vegetation mosaic' (Supporting Information).

What's wrong with the general 'pyrodiversity hypothesis'?

Several studies demonstrate that increasing pyrodiversity does not necessarily increase biodiversity. For example, research in semi-arid woodlands challenged the unqualified application of 'pyrodiversity promotes biodiversity' because some fire age-classes provide disproportionately important habitat for vertebrates (Taylor et al. 2011; Kelly et al. 2012; Nimmo et al. 2013). Work in tropical savannas shows that the diversity of termites in South Africa (Davies et al. 2012) and ants in Australia (Andersen et al. 2014) are resilient to changing levels of pyrodiversity – strengthening the thesis of Parr and Andersen (2006) that not all patterns of fires are ecologically meaningful.

Other studies show biodiversity can increase with pyrodiversity. For example, pollinator diversity increased with pyrodiversity in mixed-conifer forest in North America (Ponisio et al. 2016). The number of fire age-classes increased bird diversity in temperate Australian forests (Sitters et al. 2014). Spatiotemporal variation in fire and grazing regimes enhanced populations of birds, insects and mammals in grasslands in North America (Fuhlendorf et al. 2009). Finally, ant diversity in tropical savanna in South America was promoted by diversity in the frequency and season of fires (Maravalhas & Vasconcelos 2014).

This snapshot of studies shows that the relationship between pyrodiversity and biodiversity depends on context, being influenced by taxa, ecosystem, scale and location (more examples in Supporting Information). How biodiversity is measured is also important (Giljohann et al. 2015). Given the inadequacy of the general pyrodiversity model, how can scientists and decision makers achieve desirable outcomes for animal conservation?

A pragmatic approach for achieving desirable levels of pyrodiversity

Recognise the importance of context

Natural ecosystems are not uniform. They contain different species, have different fire regimes and fuels, and present different fire risks to people and biodiversity (DellaSala & Hanson 2015). General statements that pyrodiversity promotes biodiversity ignore this critical detail. A desirable level of pyrodiversity in one context is quite different to a desirable level in another. Martin and Sapsis (1992) noted carefully that ‘It makes no sense to have the same policy for all [vegetation] types, regardless of the role of fires in them’. Scientists should not gloss over this important detail when communicating with each other, decision makers and the public.

Differentiate between different hypotheses

The pyrodiversity hypothesis is not just one hypothesis – it is many. It is based on several mechanisms concerning how variation in fire regimes enhances the persistence of individual species and the coexistence of multiple species. This includes variation in fires related to compositional heterogeneity, configurational heterogeneity, temporal change, and interactions between fires and other processes (Figure 1; Supporting Information). An overarching pyrodiversity hypothesis has usefully galvanised fire research but it has also led to difficulties when comparing studies done in different places and at different scales. Multiple underlying mechanisms make it difficult to communicate particular effects under the general pyrodiversity hypothesis. This in turn makes it difficult to implement effective management for animal conservation.

One way to progress pyrodiversity research is to better clarify the sub-hypotheses or alternative hypotheses that are tested. Recent pyrodiversity studies have tested mechanisms related to *habitat amount*, *habitat complementation*, *habitat fragmentation*, *habitat heterogeneity*, *habitat refuges* and variation in *fire season* (Supporting Information). Such mechanisms and hypotheses must be organised more clearly to guide management. More useful outputs for animal conservation will now be developed by asking specific questions such as “How does spatiotemporal variation in the fire regime influence biota?” than by asking “Does pyrodiversity promote biodiversity?”.

Focus on functional heterogeneity

Measures of fires without reference to particular animal species traditionally underpin fire management (Clarke 2008). Most fire management plans are based on measures that represent ‘structural landscape heterogeneity’ (*sensu* Fahrig et al. 2011) where landscape elements are identified by physical characteristics without reference to particular taxa (e.g.

satellite images). But changes in structural heterogeneity, such as the number of fire age classes, do not necessarily represent changes in animal diversity. Consequently, fire management for biodiversity conservation should be based on the demonstrated requirements of animals *and* the plants, habitats and landscape elements they depend on: 'functional landscape heterogeneity' (Fahrig et al. 2011). Functional heterogeneity could be defined by classifying and mapping fire elements based on the known requirements of multiple species and their life histories, such as feeding and nesting sites. For example, Bradstock et al. (2005) proposed a conceptual model that explores functional heterogeneity using combinations of permanent and seral (changing) habitat. Models of how fires influence species' distributions can also define desirable levels of functional heterogeneity, and these empirical outputs used to identify fire-sensitive species and to inform ecosystem management (Kelly et al. 2015). In each case, differentiating between sub-hypotheses of the general model helps to define desirable levels of functional landscape heterogeneity for biodiversity. A continuing challenge is to ensure functional heterogeneity represents both vertebrates and invertebrates.

Implement decision frameworks that consider uncertainty

How can desirable levels of pyrodiversity be achieved over time and while considering uncertainty such as unplanned fire? One approach uses decision tools that encourage conservation managers to explicitly state objectives and alternative management options while accounting for uncertainty (Driscoll et al. 2010; McCarthy 2014). For example, recent work demonstrates that if fire managers aim to maximise biodiversity in semi-arid woodlands then they need to make different decisions depending on the state of the landscape. The best prescribed burning strategy for maximizing the relative abundance of

22 species of birds, mammals and reptiles depended on how much of the landscape was comprised of early, middle and late successional vegetation (i.e. context) (Giljohann et al. 2015).

Importantly, fire planning must consider the combined effects of prescribed and unplanned fires. Most fire management plans implicitly assume that unplanned fires will not occur. This myopia to the likelihood of unplanned fires will underestimate the extent of burning, with negative consequences for animal conservation. Decision tools and scenario planning enable the role of unplanned fires to be better understood (Regos et al. 2016). These approaches will be most effective when developed with local stakeholders and traditional land owners.

Challenges for animal conservation

The relationship between pyrodiversity and biodiversity is much better understood following research over the last decade. These advances have helped to define desirable levels of pyrodiversity worldwide (Supporting Information). In that time, fire-prone ecosystems have also experienced significant changes, including more extreme fire weather, growing use of prescribed burning and serious declines in some animal assemblages (Moritz et al. 2014). Now, more than ever, our understanding of animal responses to fire should be used to determine management objectives and actions. We think that these four pragmatic recommendations – emphasising the importance of context, mechanisms, functional heterogeneity and uncertainty - will aid interpretation of pyrodiversity studies and improve conservation efforts globally.

Supporting Information

Alternative terms to describe spatiotemporal variation in fire regimes (Appendix S1) and A ‘snapshot’ of recent pyrodiversity studies (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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Figure legend

Figure 1. The overarching pyrodiversity hypothesis is underpinned by multiple mechanisms and hypotheses. Mechanisms can be classified according to their influence on the persistence of single species and the coexistence of multiple species. Pyrodiversity can be measured in several ways relating to compositional heterogeneity (the number, amount and type of fire elements), configurational heterogeneity (the spatial arrangement of fire elements), various temporal mechanisms relating to fire interval, duration and season, and interactions with other processes (including climate, disease, fragmentation, grazing and predation). These measures, and their interactions in time and space, have been used to test a range of sub-hypotheses relating to pyrodiversity. Here we highlight four sub-hypotheses that will be important to continue to test, in different contexts, to enhance animal conservation in fire-prone ecosystems: the *habitat complementation hypothesis* – that multiple fire elements within the landscape supplement the requirements of individual species (configurational heterogeneity); *the habitat heterogeneity hypothesis* - that increased variation in fire elements will enhance the coexistence of multiple species (compositional heterogeneity); the *habitat refuge hypothesis* – that the quality and spatial configuration of fire elements influence immediate survival and recolonization after a fire (interactions between fire and predation); and the *fire season hypothesis* - that prescribed burning in cooler months will reduce wildfire size and enhance the survival of animals (temporal variation).

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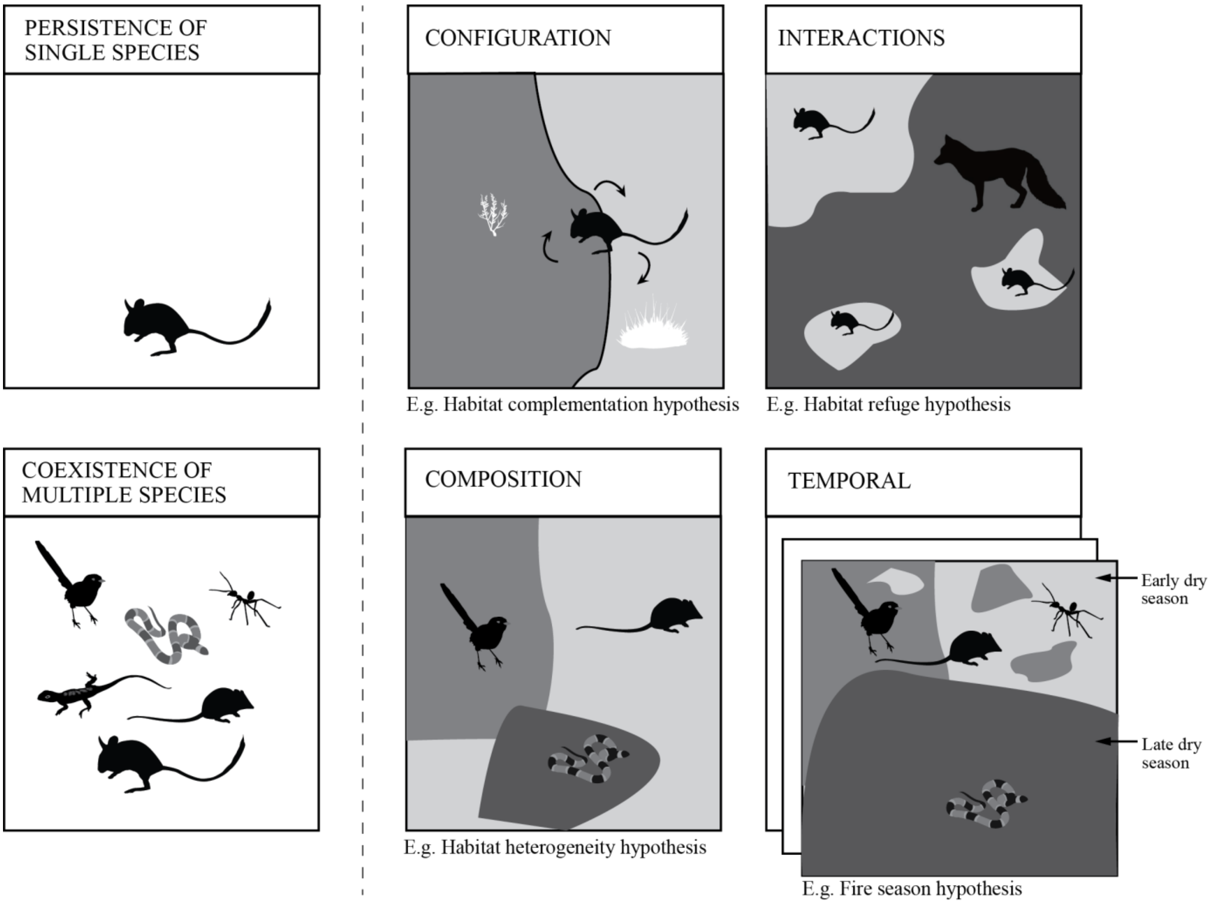

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