Diversity

Putting pyrodiversity to work for animal conservation

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Introduction

An influential concept in ecology commonly guides conservation decision makers: 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 (2006) argued that how different patterns of burning influence biodiversity was largely unknown. Subsequently, research on pyrodiversity surged. 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 the assumption that pyrodiversity promotes biodiversity can negatively impact animal populations.

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

Definition of *Pyrodiversity*

Fire regimes vary in the intervals between fires, seasons when fires occur, spatial arrangement of fires, and in their type, severity, and intensity. This variation is termed *pyrodiversity* (Martin & Sapsis 1992). Recent work emphasizes how feedback among fires, biodiversity, and ecosystems influences 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 (Parr & Andersen 2006). The expectation behind the pyrodiversity hypothesis is that biodiversity increases as spatiotemporal variation in fire increases (Martin & Sapsis 1992). This hypothesis has also been expressed using the terms ***fire mosaic***, ***patch mosaic burn***, ***successional mosaic***, ***shifting mosaic***, and ***vegetation mosaic*** (Supporting Information).

Increasing pyrodiversity does not necessarily increase biodiversity. For example, research in semiarid woodlands challenged the unqualified application of the idea that pyrodiversity promotes biodiversity because some fire age classes provide disproportionately important habitat for vertebrates (Kelly et al. 2012; Taylor 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) is resilient to changing levels of pyrodiversity, which strengthens the thesis of Parr and Andersen (2006) that not all patterns of fires are ecologically meaningful.

Other studies show that biodiversity increases as pyrodiversity increases. For example, pollinator diversity increases with pyrodiversity in mixed-conifer forests in North America (Ponisio et al. 2016). The number of fire age classes increases bird diversity in temperate Australian forests (Sitters et al. 2014). Spatiotemporal variation in fire and grazing regimes benefits populations of birds, insects, and mammals in grasslands in North America (Fuhlendorf et al. 2009). And, ant diversity in tropical savanna in South America increases as variation in the frequency and season of fires increases (Maravalhas & Vasconcelos 2014). These studies show that the relationship between pyrodiversity and biodiversity depends

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on context, including the taxa, ecosystem type, and scale of study. (More examples are given in Supporting Information.) How biodiversity is measured is also important (Giljohann et al. 2015).

A Pragmatic Approach for Achieving Desirable Levels of Pyrodiversity

Despite the inadequacy of the pyrodiversity hypothesis, scientists and decision makers can achieve desirable outcomes for animal conservation in fire-prone ecosystems by recognizing the importance of context; differentiating among hypotheses; focusing on functional heterogeneity; and applying decision frameworks that consider uncertainty.

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 from a desirable level in another. Martin and Sapsis (1992) argue that "it makes no sense" to apply the same fire management policy to different vegetation types, regardless of the role of fires in them. Scientists should not gloss over this when communicating with each other, decision makers, and the public.

Differentiation among Hypotheses

The pyrodiversity hypothesis encompasses many hypotheses. It is based on several mechanisms related to how variation in fire regimes enhances the persistence of individual species and the coexistence of multiple species. Variation in fire regimes includes compositional heterogeneity (number, amount, and type of fire elements); configurational heterogeneity (spatial arrangements of fire elements); temporal variation relating to fire interval, duration, and season; and interactions between fire and other processes (e.g., climate, disease, fragmentation, grazing, and predation). These measures and their interactions in time and space have been used to test subhypotheses relating to pyrodiversity (Fig. 1 & Supporting Information). An overarching pyrodiversity hypothesis has usefully galvanized 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 animal conservation.

One way to further pyrodiversity research is to clarify the subhypotheses or alternative hypotheses being tested. Recent pyrodiversity studies have tested mechanisms related to habitat amount, complementation, fragmentation, heterogeneity, and refuges and to variation in fire season (Supporting Information). Such mechanisms and hypotheses must be organized more clearly to guide management. More useful outputs for animal conservation could be developed by asking specific questions such as how does spatiotemporal variation in the fire regime influence biota rather than by asking does pyrodiversity promote biodiversity?

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" (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 and the habitats and landscape elements they depend on (i.e., "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) propose a conceptual model that explores functional heterogeneity based on 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 can be used to identify fire-sensitive species and inform ecosystem management (Kelly et al. 2015). In each case, differentiating between subhypotheses of the general model helps define desirable levels of functional landscape heterogeneity for biodiversity. A continuing challenge is to ensure that functional heterogeneity represents both vertebrates and invertebrates.

Decision Frameworks that Consider Uncertainty

How can desirable levels of pyrodiversity be achieved over time and while considering uncertainty such as unplanned fire? In one approach, managers use decision tools that 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 maximize biodiversity in semiarid woodlands,

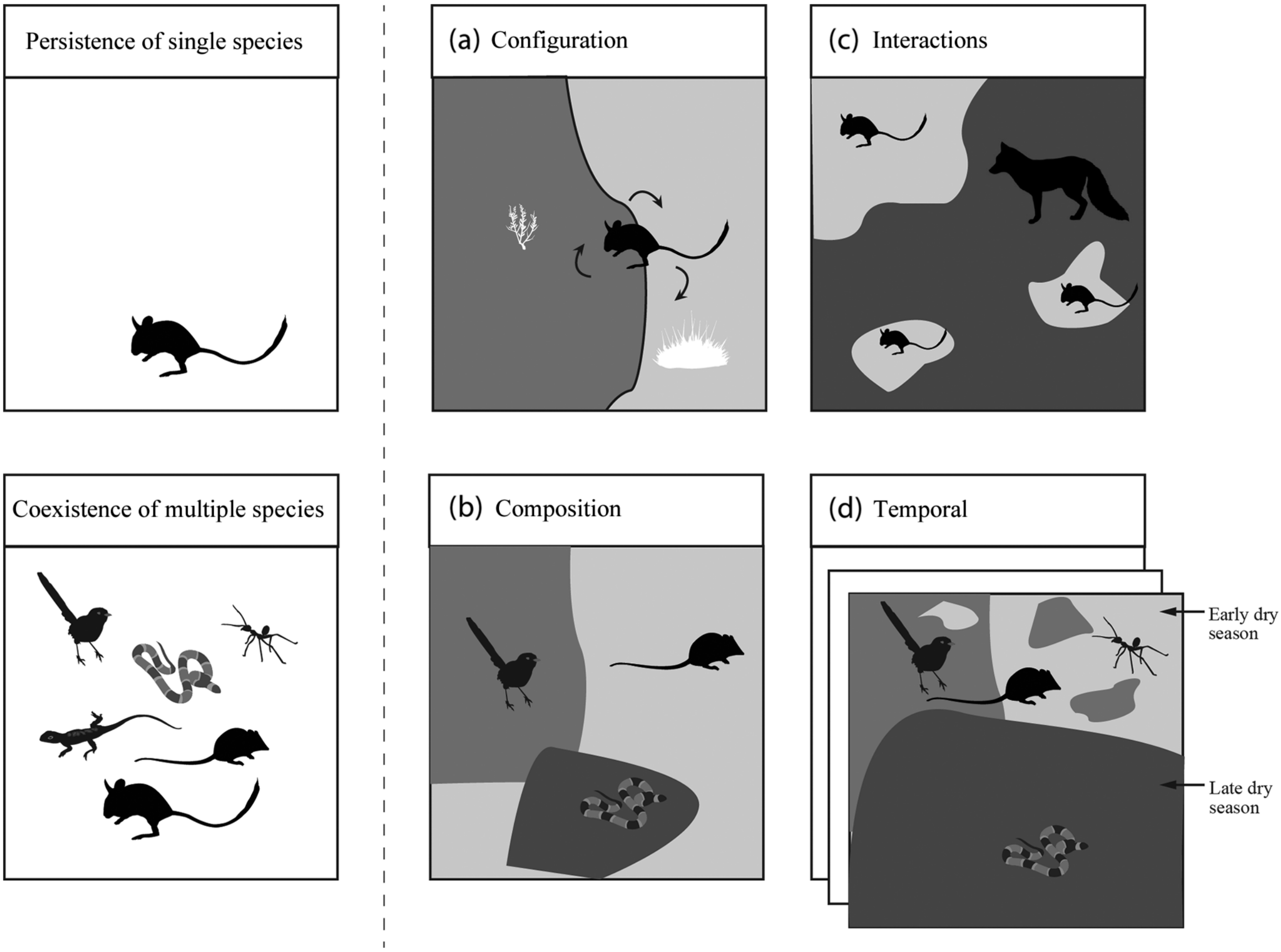

Figure 1. Four subhypotheses of the pyrodiversity hypothesis that should continue to be tested in different contexts to enhance animal conservation in fire-prone ecosystems: (a) habitat-complementation hypothesis in which multiple fire elements within the landscape supplement the requirements of individual species (configurational heterogeneity); (b) habitat-heterogeneity hypothesis in which increased variation in fire elements enhances the coexistence of multiple species (compositional heterogeneity); (c) habitat-refuge hypothesis in which the quality and spatial configurations of fire elements influence immediate survival and recolonization of multiple species after a fire (interactions between fire and predation); and (d) fire-season hypothesis in which prescribed burning in cooler months reduces wildfire size and enhances the survival of multiple animals (temporal variation).

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 composed of early-, mid-, and late-successional vegetation (i.e., depended on context) (Giljohann et al. 2015).

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 underestimates the extent of unplanned burning and has negative consequences for animal conservation. Decision tools and scenario planning allow unplanned fires to be better understood and incorporated in fire-management plans (Regos et al. 2016). These approaches will be most effective when developed in conjunction 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 studies have helped define desirable levels of pyrodiversity worldwide (Supporting Information). Over the last decade, 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, understanding of animal responses to fire should be used to determine management objectives and actions. We believe that our pragmatic recommendations—emphasizing the importance of context, mechanisms, functional heterogeneity, and uncertainty—will aid in interpretation of pyrodiversity studies and improve conservation efforts globally.

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Supporting Information

Alternative terms to describe spatiotemporal variation in fire regimes (Appendix S1) and a sample 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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