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Fire frequency matters more than fire size: Testing the pyrodiversity–biodiversity paradigm for at-risk small mammals in an Australian tropical savanna

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ABSTRACT

Patch-mosaic burning is a widely accepted practical approach to managing biodiversity, whereby spatial and temporal diversity of fire is manipulated to benefit biotic diversity. We use simulation experiments based on stochastic population viability analysis to evaluate the implications of contrasting patch-mosaic burning scenarios for the population dynamics and risk of decline of four species of small mammals in northern Australia. Our results, based on models developed from detailed mark-recapture data, suggest that fire frequency has more influence on small-mammal persistence than fire extent. Risk of extinction increased for all four species when fire frequency exceeded once every five years. Under current ambient fire regimes most Australia tropical savannas burn more frequently and therefore seem to have unfavourable consequences for this faunal group and risk precipitating severe future declines.

1. Introduction

Fire is used extensively to manage the composition, structure and dynamics of plant and animal communities, especially in fire-prone environments like the dry sclerophyllous forests and savannas of Australia and southern Africa (Bowman et al., 2009; Bradstock et al., 2002). When management aims target the conservation of biodiversity, it is widely assumed that heterogeneous fire regimes best maintain the diversity and resilience of these communities. This approach is based on the patch-mosaic hypothesis, which predicts that greater biodiversity will result from increased fire diversity – that is, “pyrodiversity begets biodiversity” (Parr and Andersen, 2006). Large, intense fires may homogenise the vegetation structure in an area whereas small, moderate fires are seen as creating a more heterogeneous vegetation structure (e.g. Price et al., 2005). A mosaic of patches in a landscape burnt at different times is assumed to be important because different taxa exhibit different responses to fires and fire-induced heterogeneity will enable the persistence of a full range of biota (Bradstock et al., 2005; Parr and Andersen, 2006).

There is, however, limited empirical data to support the real-world applicability of the patch-mosaic burning hypothesis (Parr and Andersen, 2006). Recent faunal studies testing the relationship between species richness and fire histories have uncovered scant evidence to support the hypothesis due to taxon-dependent variation in distribution and abundance which are more likely to be influenced by rainfall and other local conditions (Davies et al., 2012; Driscoll and Henderson, 2008; Farnsworth et al., 2014; Lindenmayer et al., 2008; Pastro et al., 2011, 2014). A key potential weakness of the patch-mosaic-burning paradigm is that it assumes species are dependent on a finely fire-variegated state of habitat whereas the optimal scale of any fire-mosaic is likely to be species specific and vary with home range size (Bradstock et al., 2005). Furthermore, the hypothesis has largely been built on the assumption that meeting needs of plant communities will automatically meet the needs of animal species (Clarke, 2008). Given the possible inadequacies of the current dominant fire-management paradigm, there is a need for further information to determine appropriate fire regimes to support management of at-risk fauna.

Simulation models are a useful tool in fire-related research and management, especially when grounded on robust field data.

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Driscoll et al. (2010) identify three major areas where simulation models contribute to extending empirical research on fire impacts and management: (1) as a systematic way of identifying disturbance and life-history processes that will most influence extinction probability (or community composition); (2) as a way of translating empirical research into a currency (model parameters and a logical framework) that can be applied in a formal decision-making process, and (3) as a means to extend empirical data by modelling at large temporal and/or spatial scales, which is essential for exploring consequences for biodiversity of contrasting management options. Although the majority of fire-related population viability models have been based on plants (e.g. Bradstock et al., 1998; Satterthwaite et al., 2002), simulation models have also been successfully applied to vertebrate species (Brook and Griffiths, 2004).

The tropical savannas of northern Australia are one of the most fire-prone landscapes on Earth (Giglio et al., 2013). Fire frequency and resultant structural vegetation changes have been implicated in the decline of small mammal fauna in this region (Woinarski et al., 2010, 2001). Fire events can decrease the survival (via direct killing and impacts on food and shelter) and suppress recruitment of small mammal species (Griffiths and Brook, 2014; Pardon et al., 2003), but the fire regime best suited to the life history of a given species has yet to be determined (or indeed whether any regime is beneficial for multiple species). For example, managers of conservation reserves in the tropical savannas of the Northern Territory have concentrated their efforts at imposing more benign and variable fire regimes (Edwards et al., 2001). Yet, because of the limited empirical basis for the patch-mosaic hypothesis described above, land managers still lack clear guidance on how to optimise fire management strategies for faunal groups potentially at risk from inappropriate fire regimes.

In this study we aim to build on extensive monitoring data and a landscape-scale field manipulation of fire regimes, by using simulation experiments to examine the effect of fire frequency and extent on the decadal-scale population viability of four small mammal species in a tropical savanna. We hypothesise that more frequent fires would increase the threat to population persistence by reducing survival and recruitment and thereby population growth. We expect larger fires would increase the risk to small mammal populations by causing widespread reduction in population size over geographically large areas. At this stage we can make no predictions about the relative importance of scale and frequency.

2. Materials and methods

2.1. Ecological system

The wet-dry tropical savannas of northern Australia contain a diverse small mammal fauna and are subject to seasonal fire regimes. Variation in fire regimes is related to available moisture, dominance of either woody or herbaceous plant cover or weather conditions (Bradstock, 2010). Fires in the tropics of northern Australia are characterised by low-intensity fires (average intensity 2.1 MW^{-1}) when available moisture is high and high-intensity fires (average intensity 7.7 MW^{-1}) when available moisture is low (Williams et al., 1998, 2003). Fire frequency is relatively high, with up to two-thirds of the landscape burned annually in some conservation reserves (Edwards et al., 2001; Gill et al., 2000). Data for four small mammal species from Kapalga, Kakadu National Park, were available to determine the effects of fire: northern brown bandicoot (*Isoodon macrourus*), brushtail possum (*Trichosurus vulpecula*), northern quoll (*Dasyurus hallucatus*) and grassland melomys (*Melomys burtoni*) (Griffiths and Brook, 2014). All four species are wide-ranging, being distributed across northern Australia, and represent distinctly different life histories: two are arboreal (northern quoll and brushtail possum) and two are terrestrial (northern brown bandicoot and grassland melomys), one species has synchronous reproduction, annual male die-off and is a specialist carnivore (northern quoll), while the other three species are able to reproduce continuously and are primarily herbivorous (Strahan, 1995).

2.2. Model structure and output

We used stage-structured matrix models to explore the impact of fire management on these species, based on capture-mark-recapture studies from a fire experiment at ‘Kapalga’, a management zone within the wooded tropical savannas of Kakadu National Park in northern Australia (latitude 12°30′S, longitude 132°20′E). All models were developed and run in RAMAS Metapop software program v5 (Akcakaya, 2002; www.ramas.com). Stage-structured matrices are often used when it is difficult to determine accurately the age of individuals or when developmental stage is better than age as a predictor of demographic fate (Caswell, 2001); both were the case with the small mammal fauna at Kapalga. The pre-breeding census model included two stages (juvenile and adult) and four elements or probabilities representing survival, fecundity (recruitment) and transition probabilities. We classed juveniles as individuals that had entered the trappable population (i.e., post-weaning) but had not reproduced, and adults as reproductively active individuals. The transition probabilities of stage-based models incorporate the probability of making a transition from one stage to the next between time i and $i + \mathrm{t}$, conditional on surviving (Nichols et al., 1992). The probability of surviving and remaining in the same stage (P), the probability of surviving and becoming a reproductive adult (G) and probability of recruitment (F) are combined to estimate projected population growth. The model simulated demographic and environmental stochasticity (Lande, 1993), no explicit sex structure (for northern quolls only females were modelled due to annual male die-off), two types of disturbance (low- and high-intensity fires), ceiling-type density dependence, and a metapopulation-like spatial structure with 22 patches (based on Kapalga fire experiment compartments, labelled A through X (Andersen et al., 1998), connected through relatively high dispersal rates (given that these represent an experimental compartmentalisation of an effectively continuous landscape, with no physical barriers and extensive borders between neighbouring patches). The Kapalga peninsula is surrounded by floodplain which was considered to be inhospitable habitat (‘matrix’) for the four small mammal species, but it is open along the southern boundary (other than the sealed road of the Arnhem Highway) and thus migration might have been underestimated (Fig. 1).

2.3. Demographic parameters

All matrix probabilities were estimated using a capture-mark-recapture dataset collected for the four small mammal species at Kapalga Research Station during a landscape-scale fire experiment over six years from 1989 to 1995. Survival and stage-transition rates were estimated using multi-state models (Nichols et al., 1992) in Program MARK ver. 6.2 (White and Burnham, 1999). The multi-state model estimates three parameters: (a) probability that an animal alive in state r at time i remains in state r in time $i + 1$; (b) probability that an animal alive in state r at time i is captured at that time; and (c) probability that an animal alive in state r at time i is alive and in state s in time $i + 1$.

Body mass was used to classify individuals into one of two states (juvenile and adult) based on previously determined age-size allometric relationships (Griffiths and Brook, 2005). When data for transition of juveniles to adults was sparse and the model was unable to estimate the parameters (e.g. less than 10% of