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Are forest gullies refuges for birds when burnt? The value of topographical heterogeneity to avian diversity in a fire-prone landscape

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ABSTRACT

In forest ecosystems, uniformity in fire spread may be moderated by topography such that sheltered areas (e.g. gullies) escape fire. However, gullies are not immune to fire and, under extreme fire weather conditions, can burn. This may compromise their habitat value, and diminish differences in faunal communities across topographical gradients. We investigated the extent to which differences in avian communities persist when subjected to uniform fire severity and fire history across the gully and slope components of a forest site. We predicted that there would be less difference with increasing fire severity or long absence of fire. Birds were surveyed at 91 paired gully/slope sites in foothill eucalypt forests, two to three years after a large, severe wildfire in south-eastern Australia. Sites were stratified in relation to four levels of fire severity (unburnt through to crown burnt) and two levels of fire history prior to the wildfire (burnt <3 years, or >20 years). Under similar conditions of fire severity and fire history, gullies maintained greater species richness and abundance than did slopes; averaging 13% greater species richness and 32% greater abundance, along with a distinct bird assemblage. However, contrary to predictions, topographical differences for most avian responses did not diminish with increasing fire severity or in the long absence of fire prior to the wildfire. This study highlights the value of forest gullies in maintaining or facilitating the recovery of distinct avian communities after wildfire, even when the gullies themselves have been burnt.

1. Introduction

The distribution of plant and animal species in fire-prone landscapes is inextricably linked to variation in the spatial and temporal patterning of fires, or pyrodiversity (e.g. Burrows and Wardell-Johnson, 2004). Spatial heterogeneity within fires is evident at all scales and within all types of fires (Agee, 1993; Turner et al., 2003; Schoennagel et al., 2008). However, despite this inherent variability, there remains concern that mega-fires compromise spatial heterogeneity by burning large areas more intensely, leading to greater uniformity of forest age-classes across landscapes (Adams and Attiwill, 2011; Williams, 2013). With increasing fire intensity, habitat is more severely altered and there is increased likelihood of faunal mortality or displacement (Newsome et al., 1975; Silveira et al., 1999; Sanz-Aguilar et al., 2011). Unburnt areas within mega-fires can serve as faunal refuges, that support higher frequencies of fire-sensitive species than areas burnt within the fire boundary (Robinson et al., 2014), yet comprise only a small proportion of the total fire area (<1–22%; Román-Cuesta et al., 2009; Madoui et al., 2010; Leonard et al., 2014). In topographically diverse landscapes, unburnt areas often are associated with sheltered, mesic locations (e.g. gullies) (Eberhart and Woodard, 1987; Leonard et al., 2014). As such, gullies are considered to be natural and deterministic faunal refuges in fire-prone landscapes (Gandhi et al., 2001; Mackey et al., 2002; Robinson et al., 2013). Gullies, however, are not immune from fire and, during severe wildfire conditions, can sometimes burn even more intensely than adjacent slopes (Segura and Snook, 1992; Pettit and Naiman, 2007). In such instances, this may compromise the habitat value of gullies and potentially reduce landscape heterogeneity.

Due to moisture and soil nutrient gradients, vegetation in forest gullies typically has greater structural complexity than that on upland slopes and ridges (Dwire and Kauffman, 2003; Huston, 2003). Accordingly, forest gullies can harbour richer and more abundant faunal assemblages (Mac Nally et al., 2000; Palmer and Bennett, 2006) that are distinct in composition compared with upland slopes and ridges (Sabo et al., 2005). In dry forests, topographical differences in habitat and

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faunal communities can be quite marked due to large differences in moisture (Mac Nally et al., 2000); in contrast with wet forests where moisture is not limiting and faunal differences are less pronounced (McGarigal and McComb, 1992; Lindenmayer et al., 2009). This moisture gradient, along with topographical position, reduces the probability of gullies burning (Pettit and Naiman, 2007; Leonard et al., 2014). Fire that burns the surrounding landscape, leaving gullies unburnt, accentuates habitat differences already present due to topography (Keeton and Franklin, 2004).

Over a long period, forest gullies that repeatedly escape fire may be defined by distinct habitat features and harbour fauna not found in the broader landscape (Camp et al., 1997; Gandhi et al., 2001). Even when burnt at low severities, gullies may retain important biological legacies (e.g. logs, hollows) that distinguish them from slopes burnt at similar low severity (Collins, 2012; Bassett et al., 2015). However, intense, high severity fire that burns across both gully and slope may diminish topographically driven differences in vegetation structure and habitat components due to the overriding effect of flammable habitat components being combusted. If severe fire results in homogenisation of vegetation structure, post-fire faunal assemblages are predicted to be more similar between gullies and slopes burnt with greater level of fire severity.

In topographically diverse landscapes, potential uniformity in vegetation structure imposed by fire is likely to be temporary (Huston, 2003). Gullies are expected to recover vegetation structure more quickly after a fire than forest slopes due to greater availability of moisture and nutrients (Romme and Knight, 1981; Segura and Snook, 1992; Huston, 2003). If not occupied during the fire, gullies may be the first sites to be colonised by fauna post-fire (Banks et al., 2011; Chia et al., 2015). It could be expected that beta diversity in the landscape is greatest at intermediate levels of time-since-fire due to maximising the structural differences in vegetation between gullies and slopes (Connell, 1978; Huston, 1979). Over a longer time period, slopes likewise develop more structurally complex vegetation such that in the long absence of fire, differences between gullies and slopes may again diminish but not completely converge (Skinner, 1995; Donnegan and Rebertus, 1999). Accordingly, faunal assemblages are expected to become more similar across topographical locations with increasing time-since-fire due to a growing similarity in available resources. At this stage, species requiring long unburnt or structurally complex habitat may be found more broadly in the landscape (Camp et al., 1997), whereas early successional species become scarce (Hutto, 2008).

Species distributions in fire-prone landscapes are driven by more than fire. Irrespective of the fire regime, avian communities in forest gullies are expected to remain distinct from those on forested slopes, due to inherent topographical variation in habitat attributes. However, with increasing fire severity, or long periods without fire, it is expected that topographical habitat differences will diminish leading to less distinct differences in associated post-fire bird communities. Here, we examined differences in avian communities between paired gully and slope sub-sites, subject to similar fire severity and fire history, 2–3 years after a large, intense wildfire. We predicted that under equivalent conditions of fire severity and underlying fire history: 1) gullies would harbour greater richness and abundance of birds, and a distinct avian composition, to that of slopes; but that the magnitude of this difference will diminish with 2) increasing severity or with 3) long absences of fire.

2. Methods

2.1. Study area

On the 7th February 2009 (‘Black Saturday’), two wildfires began burning in the central highlands of Victoria, Australia (37.5° S, 145.5° E). These fires later joined to become the Kilmore East-Murrindindi Fire complex; a large high-intensity wildfire that burnt 228,000 ha of eucalypt forests with severity ranging from extreme crown burn through to low severity understorey burns and unburnt patches (for more details of this fire, including severity and intensity, see Teague et al., 2010; Cruz et al., 2012; Price and Bradstock, 2012; Leonard et al., 2014). Approximately half of the fire complex occurred in foothill eucalypt forest intermixed with gullies of damp eucalypt forest (DSE, 2005), the focus of this study.

Topography within the study region is hilly to mountainous (200–1500 m elevation), with numerous, often steep, gullies. Gullies, or drainage lines, occupy the lower topographic position in the landscape and generally do not have perennial flow or free standing water. Eucalypts form the forest canopy in both gullies and slopes; messmate (*Eucalyptus obliqua*) commonly dominates in both situations, along with peppermints (*E. radiata* and *E. dives*) on slopes, and blue gum (*E. globulus*) in gullies. On slopes, the understorey is characterised by sclerophyllous shrubs (e.g. Fabaceae spp., Epacridaceae spp.) 0.5–1.5 m tall, with cover varying from very sparse to about 50% and bracken fern (*Pteridium esculentum*), which often forms a near continuous layer approximately 1 m in height. Gullies have less floristic diversity than the drier slope vegetation but tend towards greater structural complexity (Cheal, 2010). Trees are larger and the shrub layer taller (2–4 m) and denser (>50% cover) due to higher moisture levels and deeper, more nutrient-rich soils (Gibbons and Rowan, 1993). The understorey in gullies is dominated by mesic shrubs such as musk daisybush (*Olearia argophylla*), hazel pomaderris (*Pomaderris aspera*) and prickly currant-bush (*Coprosma quadrifida*), along with tree ferns (*Dicksonia antartica*, *Cyathea australis*). While the distribution of slope/gully vegetation is largely governed by topographically related moisture availability, there is a tendency for the more mesic ‘gully’ species to gradually spread upslope as time-since-fire increases.

2.2. Study design

The study took advantage of the natural topographical variability and the heterogeneity in fire severity within and adjacent to the 2009 fire complex. Ninety-one sites were selected, following stratification to four levels of fire severity and two levels of fire history (Table 1). In addition, we included unburnt reference sites located in extensive forest more than 1.2 km beyond the fire boundary; this was to examine whether unburnt vegetation within the fire complex provided similar habitat to that beyond the fire boundary. Sites were located such that fire history and severity were consistent over an area of ~5 ha. Each site contained two sub-sites: a gully paired with a slope, spaced ~100 m apart and of similar distance to patch edge (Fig. A1). As far as possible, sites within treatments were dispersed across the study area in order to minimise regional bias. In general, sites were greater than 1500 m apart, although in a few cases it was necessary to relax this rule to achieve sufficient replication of fire history/severity combinations (minimum site separation = 440 m). Moran's index of autocorrelation indicated no spatial autocorrelation of species richness or abundance amongst sites.

Within the wildfire complex, fire severity was categorised as unburnt, ground burnt, crown scorched or crown burnt forest (Table 1). Fire severity categories were determined using landscape-scale severity layers (DSE, 2009b), supplemented with interpretation of fine-scale 15 cm aerial photography (DSE, 2009a) and verified on ground. Unburnt and reference sites were characterised by a structurally complex understorey of deep litter, shrubs and small trees. In ground burnt sites, the understorey was simplified with less structural complexity across all height categories, especially in the mid-tall range. Crown scorch and crown burnt sites commonly had dense regeneration of eucalyptus seedlings and bracken fern (Fig. A2).

Fire history prior to the 2009 wildfire was defined as either ‘short’ (<3 years) or ‘long’ (>20 years) (Table 1). Time-since-fire was used to describe fire history classes for sites that remained unburnt in 2009 while inter-fire interval was a more appropriate term for sites burnt in