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Multi-century dynamics of ant communities following fire in Mediterranean-climate woodlands: Are changes congruent with vegetation succession?

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ABSTRACT

As vegetation recovers after disturbances such as fire its composition and structure systematically changes, affecting the availability of resources for fauna and mediating physical conditions. According to the habitat accommodation model, these changes drive a succession of animal species, which enter and leave according to their habitat requirements. While the response of ants to fire has been extensively studied, studies of ant communities in biomes with long fire-return intervals have been overwhelmingly short-term in nature. Here, we explore the response of ant species, functional groups and communities to time since fire using a uniquely long-term (>300 years) chronosequence in eucalypt woodlands of south-western Australia. Marked non-monotonic vegetation structural changes occur in non-resprouting *Eucalyptus salubris*-dominated woodlands following fire, with tree and ground fuel cover peaking at intermediate periods post-fire. Hence, we predicted that changes in the occurrence of Dominant Dolichoderinae, Hot-Climate Specialist and Cold-Climate Specialist functional groups would mirror the non-monotonic changes in habitat complexity, as predicted by the habitat accommodation model. Overall ant species richness and composition did not show clear post-fire successional patterns, with extensive spatial turnover a likely factor. However, richness and abundance of ant functional groups broadly responded as predicted, with Dominant Dolichoderinae and Hot-Climate Specialists more prominent in more-open recently-burnt and long-unburnt habitat, and Cold-Climate Specialists more prominent in less open habitat at an intermediate time since fire. This matching, non-monotonic temporal pattern of changes in ant functional groups and vegetation structure suggests that ant functional group occurrence is mediated through changes in habitat, as posited by the habitat accommodation model, and not simply time since disturbance. Current fire management in *E. salubris* woodlands aims to minimise wildfire occurrence, which is consistent with the maintenance of ant functional diversity at a regional scale given the long time periods over which changes occur post-fire. The combination of recent large wildfires and predicted fire-facilitating climate changes suggest that future shifts in the relative dominance of ant functional groups are likely if fire management is unsuccessful in limiting wildfires occurring in mature woodlands.

1. Introduction

As vegetation recovers after disturbances such as fire its composition and structure systematically changes (Bond and van Wilgen, 1996; Haslem et al., 2011; Gosper et al., 2012), affecting the availability of resources for fauna and mediating physical conditions such as temperature and exposure to sunlight (Whelan, 1995). According to the habitat accommodation model (Fox, 1982), these changes drive a succession of animal species, which enter and leave according to their habitat requirements and competitive

Abbreviation: GWW, Great Western Woodlands.

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interactions. As a consequence, some animal species are characteristic of vegetation that has been recently burnt, while others prefer intermediate periods post-fire, or long-unburnt vegetation (Fox, 1982; Langlands et al., 2012; Kelly et al., 2012). The majority of studies investigating the utility of the habitat accommodation model have concerned vertebrates; however the tenets of the model are equally applicable to invertebrates.

As a globally dominant faunal group, ants have been extensively studied in relation to fire. However, much of this attention has focussed on variation in fire frequency, either in extremely fire-prone biomes such as tropical savannas (Andersen, 1991a; Parr et al., 2004; Andersen et al., 2006) or in forests subject to regular prescribed burning (Vanderwoude et al., 1997; York, 2000; Andersen et al., 2009; Wittkuhn et al., 2011). Studies in biomes with long fire-return intervals have been overwhelmingly short-term in nature (Andersen, 1988; Farji-Brener et al., 2002; Arnan et al., 2013), with relatively few looking at long-term successional patterns. Jackson and Fox (1996) found that ant communities in Australian dry sclerophyll forest continued to change in composition over a chronosequence of 1–18 years post-fire, and ant community composition had not converged to unburnt conditions in a 19-year chronosequence in Mediterranean *Pinus nigra* forests (Rodrigo and Retana, 2006). These results suggest that ant communities can undergo successional change for at least 20 years following fire. The extent of post-fire succession over much longer time periods remains largely unknown, but may be dependent on the vegetation type concerned and the post-fire recovery mechanisms of the constituent plant species (Arnan et al., 2006).

The classification of ant taxa into functional groups based on their responses to environmental stress and disturbance (Andersen, 1995, 1997; Hoffmann and Andersen, 2003) provides a basis for making predictions about long-term successional change in ant communities following fire. First, fire-induced habitat simplification can be expected to favour the highly thermophilic groups Dominant Dolichoderinae and Hot-Climate Specialists, which strongly prefer open habitats (Andersen, 1995; Hoffmann and Andersen, 2003). Conversely, the highly specialised groups Cold-Climate Specialists, Cryptic Species (cryptobiotic ants associated with complex litter) and Specialist Predators are especially sensitive to habitat disturbance (Hoffmann and Andersen, 2003; Berman et al., 2013), and typically prefer mid- to late successional habitats where ground surface cover and/or complexity is greater.

Here we explore the response of ant species, functional groups and communities to time since fire using a very long-term (>300 years) chronosequence approach in the *Eucalyptus*-dominated Great Western Woodlands (GWW) of south-western Australia. Compared to most other Mediterranean-climate biomes (Cowling et al., 1996) these woodlands rarely burn when mature due to their open canopy structure and patchy distribution of fuel, and can exist for centuries without being disturbed by fire (O'Donnell et al., 2011; Prober et al., 2012; Gosper et al., 2013a). Recent decades, however, have seen an unusually high number of wildfires that collectively have burnt a large proportion of the GWW, and this has raised concerns about their conservation status (Parsons and Gosper, 2011).

The dominant tree at sites sampled was *Eucalyptus salubris* (gimlet), which is killed by complete canopy scorch. As wildfires typically result in the death of all *E. salubris* individuals, vegetation structure and composition changes dramatically with time since fire (Gosper et al., 2013a). *E. salubris* regenerates vigorously after fire from a canopy-held seed bank, but recovery of the community after fire is slow, with centuries required for vegetation composition and structure to approach the pre-fire state (Gosper et al., 2013a,b). Particularly significant changes occur in woodlands of an intermediate time since fire (~40 to 120–200 years), when dense regeneration of dominant trees and shrubs drives shifts in plant community composition and results in peak ground fuel (litter, logs, etc.) and canopy cover (Fig. 1; Gosper et al., 2013a,b). From this time onwards competition between tree saplings likely mediates density dependent thinning such that tree density decreases but mean trunk size continues to increase (Gosper et al., 2013a).

The non-monotonic pattern of change in vegetation structure described above allows for the teasing out of confounding effects of habitat change as predicted by the habitat accommodation model, from those of time since fire *per se*. If the occurrence of individual ant species and ant functional groups changes in a monotonic fashion with time since fire, this would lend support to these changes being driven mainly by the passage of time. This might reflect the time required for re-colonisation from unburnt patches or for populations to recover to pre-fire levels after fire-induced mortality, or competitive displacement of disturbance-tolerant, but less competitive species by dominant but more fire-sensitive species. If, however, changes in ant species and functional groups are non-monotonic and match changes in vegetation struc-

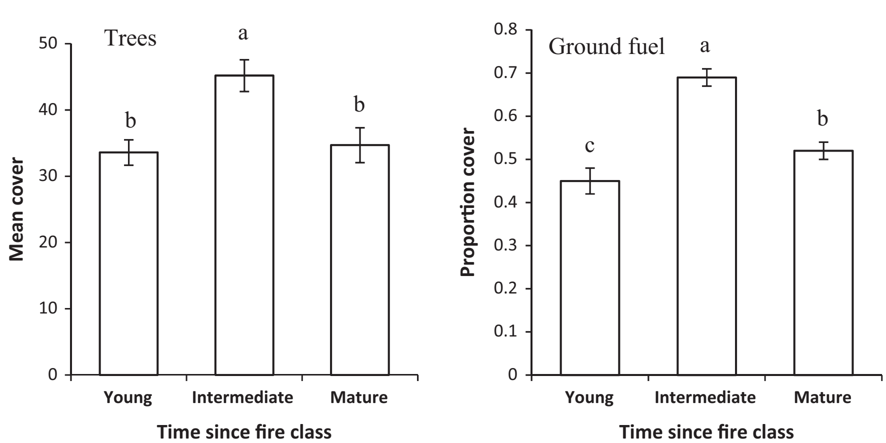

Fig. 1. Changes with Time-since-fire class of selected vegetation structural variables that are likely important habitat features for ants in *Eucalyptus salubris* woodlands. Error bars show 1 × SE, all Locations are combined, and pair-wise differences in ANOVA (see Gosper et al., 2013a,b) are shown by different superscripts. Tree cover refers to the aggregation of cover measured on an individual species basis for all species of the Tree-S plant functional type of Gosper et al. (2013b) (i.e. an index of relative cover; cover in the other plant functional type with a tree growth form was negligible). Ground fuel refers to all dead vegetation on the ground surface (litter, logs, etc.), with the remainder of ground cover being either bare ground or biological soil crust.