

INVERTEBRATES AND FIRE—CHALLENGES AND OPPORTUNITIES FOR CONSERVING BIODIVERSITY

ALAN YORK

Forest and Fire Ecology Group, Department of Forest and Ecosystem Science,
University of Melbourne, 4 Water Street Creswick 3363, Victoria, Australia

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Fires, whether planned or unplanned, impact upon a suite of organisms in natural ecosystems. Direct (short-term) and indirect (longer term) effects influence the composition and structure of invertebrate communities through the interaction of site history, characteristics of individual fire events and species life-history traits. Prediction of fire responses based on vascular plant species life-history traits, and the development of a functional classification based on shared traits, underpins current fire management in south-eastern Australia. Can a similar approach be developed for terrestrial invertebrates, or should we focus on utilising a framework based on surrogates developed around vegetation composition and structure, or taxonomic alternatives? This paper considers whether the use of surrogates offers promise as a strategy of dealing with the complexity of invertebrate biodiversity and associated issues surrounding fire management. It proposes a functional approach, based on species' life-history traits, that can complement existing strategies; and identifies opportunities that have potential for resolving existing challenges in biodiversity conservation in fire-prone environments.

Key words: biodiversity, bushfire, fire, functional groups, invertebrates

FIRES have both direct (short-term) and indirect (longer-term) effects on organisms. Immediate impacts on individuals resulting from the fire itself may be injury or death, or survival through escape (emigration) or shelter (seeking refuge or through dormancy in a protected location). Indirect impacts result from the fire causing changes to some aspects of the environment (such as resources) which, in turn, affect the biota. Thus unsuitable conditions after a fire may lead to emigration; with persistence at that location influenced by food availability, competition and/or predation, and the capacity of an organism to reproduce or recolonise from outside the area directly impacted. Over time, responses of a population of organisms will be influenced not only by features of a particular fire (intensity, season, patchiness), but by processes occurring after the fire. These 'interval related' processes affect resource availability, with population and community (species level) responses determined by various life-history (morphological, physiological and behavioural) characteristics. These characteristics or 'traits', which allow organisms to persist in spite of fire, have been shaped over evolutionary time periods by the fire regime (Gill 1975), not just by single fires in isolation. Thus the response of an individual organism, population or community to fire will depend on the starting state, determined by the past history (e.g. time since last

fire), as well as the characteristics of the particular fire and interactions with life-history traits (Whelan 1995; Gill 2008).

A mechanistic understanding of the responses of a range of plants and animals to fire regimes represents a fundamental knowledge gap in fire management (Driscoll et al. 2010). Predicting fire responses based on species' life-history traits, and the development of a functional classification based on shared traits, provides a powerful framework supporting fire management for biodiversity conservation (Keith et al. 2002). Can such a functional approach be developed for invertebrates, or are there alternative approaches to resolve this complexity? As a group, invertebrates are numerous, diverse, and play important functional roles in ecosystems (Beattie 1995; Raven & Yeates 2007). Their abundance and diversity however also poses a major challenge. A classification based on the lack of a morphological feature (a backbone) is unlikely to provide insight into shared characteristics that might form the basis of such an approach. With their exceptional diversity compared to other groups (Fig. 1) and enormous range of life histories and morphologies, invertebrates comprise a vast and heterogeneous assemblage exhibiting often complex life-cycles. Ideally, a species-level approach to assessing biodiversity responses to fire is required, but often appears largely problematic because of the

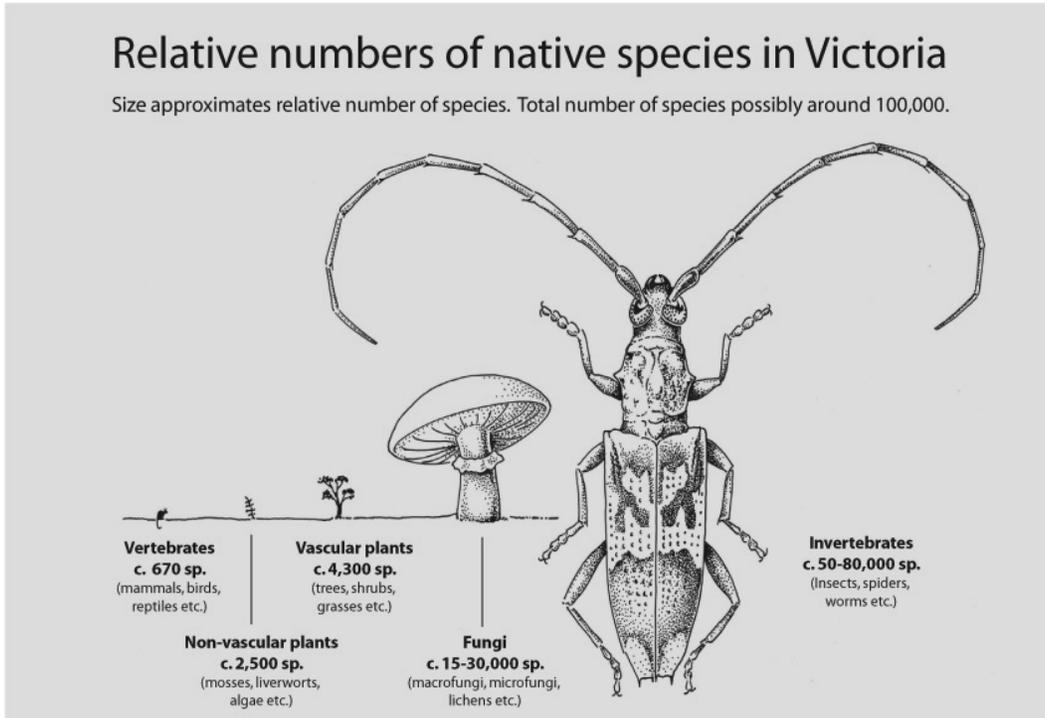


Fig. 1. A diagrammatic representation of relative species richness of major taxa in Victoria. The size of the image is indicative of the number of species in that broad taxonomic group. Source: Victorian National Parks Association.

diversity involved and poor taxonomic resolution for many groups (Austin et al. 2004; New 2009). Their associations with many other organisms, especially plants, suggest that viewing invertebrates as a group in isolation may also be unproductive.

ADDRESSING COMPLEXITY

Resolving this complexity is challenging, but complexity is the norm in environmental management (Wainwright & Mulligan 2004). In Victoria, and in other temperate areas of Australia, complex fire management issues are often addressed through the use of surrogates (Fig. 2). Vegetation is commonly mapped as associations based on floristic composition (Ecological Vegetation Class), similar responses to fire (Ecological Vegetation Division) and post-fire developmental (growth) stages (Cheal 2010). Although patterns and rates of secondary succession after fire are seldom linear (Whelan et al. 2002; Gill 2008), management agencies often use time since last fire as a surrogate for assemblage composition and stage of structural developmental (Fire Ecology Working Group 2004; Clarke 2008; Cheal 2010).

Additionally, species with known and predictable tolerances and response to fire (Key Fire Response Species) are used to inform management concerning intervals between successive fires (see below).

Similarly, surrogates have also been used to resolve complexity issues in invertebrate biodiversity conservation and management. Studies using coarse levels of taxonomic resolution (e.g. order, family), indicator groups (e.g. ants, spiders, collembola) and/or functional groups are common (e.g. Greenslade & Majer 1993; Madden & Fox 1997; Collett 1999; Abbott et al. 2003; York & Tarnawski 2004; Ribas et al. 2012). Questions relating to ecological processes (e.g. pollination, decomposition) may be best addressed using functionally important taxa (Seastedt 1984; Brennan et al. 2009; Olotu et al. 2012). Here, I discuss whether the use of surrogates offers promise as a strategy of dealing with the complexity of invertebrate biodiversity and associated issues surrounding fire management. I consider how we might develop a functional approach, based on species' life-history traits that can complement existing strategies that, generally, focus on surrogates

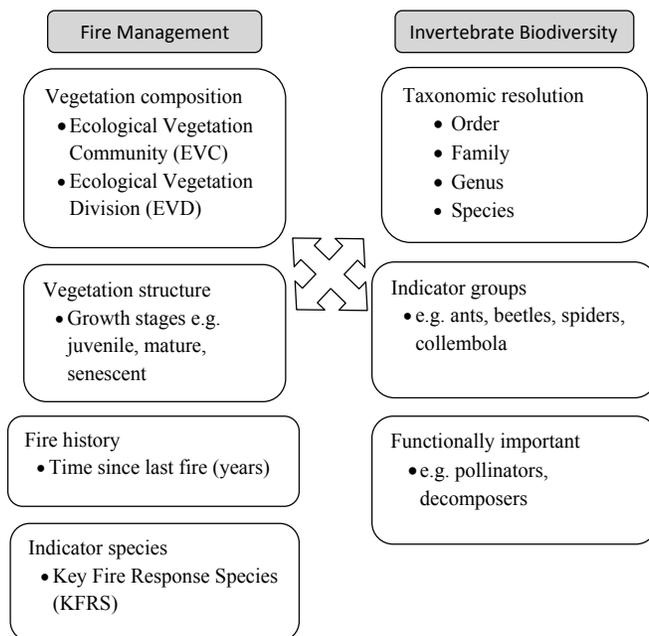


Fig. 2. The use of surrogates to address complexity is commonplace in both fire management and biodiversity conservation.

and/or listed (threatened) species. I use a number of examples from the published literature to illustrate different approaches. It is not intended as a review of the effects of fire on invertebrates (Friend 1995; Swengel 2001; Whelan et al. 2002; Van Heurck & Abbott 2003; New et al. 2011) but focuses on opportunities that have potential for resolving existing challenges.

USE OF VEGETATION COMMUNITY SURROGATES

Evidence that different plant species support particular assemblages of invertebrates (Peeters et al. 2001; Majer et al. 2003; Moir et al. 2010) and that the composition of assemblages might reflect broad vegetation (structural) associations (Yen 1987, beetles; Harris et al. 2003, spiders) provides encouragement that vegetation associations (as defined management units) might be useful surrogates for invertebrate assemblage composition. Mac Nally et al. (2002) investigated the potential for EVCs to be used as biodiversity management units in the box-ironbark ecosystem of central Victoria. They surveyed eighty sites for tree species, birds, mammals, reptiles, terrestrial invertebrates, and nocturnal flying insects. EVCs proved useful surrogates for bird, mammal

and tree communities, but not so for reptiles and invertebrates (at the ordinal level). While differences in taxonomic resolution (lack of species-level data for invertebrates – see below) may have contributed to this outcome, other studies have demonstrated that invertebrates rarely display biogeographic patterns of endemism or turnover similar to vascular plants and vertebrates (Oliver et al. 1998; Ferrier et al. 1999; Moritz et al. 2001). An alternate approach might involve the use of habitat and/or growth stages as surrogates; a method that is being developed for vertebrates (Clarke 2008; MacHunter et al. 2009) but remains largely untested for invertebrates (but see Hein et al. 2007).

COARSE TAXONOMIC CLASSIFICATION

Given the extraordinary diversity of many invertebrate groups, and associated taxonomic challenges, it is reasonable to ask whether data at a coarse level of taxonomic resolution are sufficient to answer many fire-related questions. This approach is often used for environmental monitoring (Campbell 2004) where the response of orders or families to a particular environmental variable is known and can be indicative of a change of state. As the first

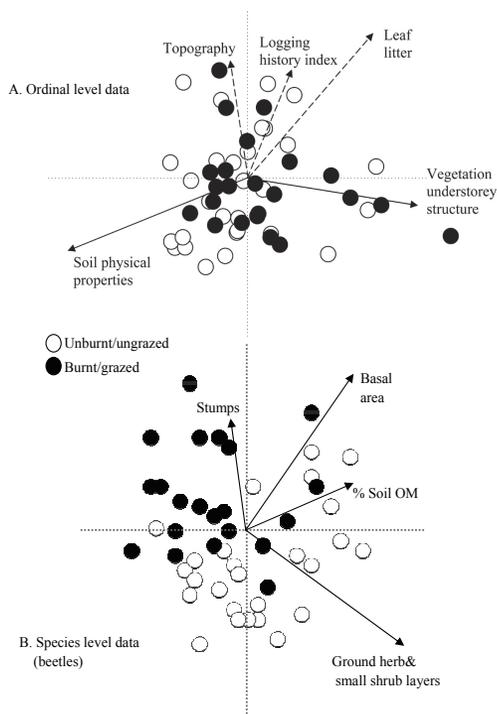


Fig. 3. Biplot from Canonical Correspondence Analyses (CCA) of (A) invertebrate abundance data – ordinal level and (B) beetle abundance data. Points represent sample sites and vectors (arrows) represent environmental variables. The length of the arrow signifies the relative contribution of that variable to assemblage composition, while the direction signifies its contribution to the difference between treatments. Solid arrows represent statistically significant vectors ($P < 0.05$) while dashed arrows represent variables that make a lesser contribution. Adapted from York 1999 and York & Tarnowski 2004.

stage of identifying material from most collections of terrestrial invertebrates involves ordinal sorting (Harvey & Yen 1997) it is worth testing the efficacy of such data to address fire management issues.

A study of terrestrial invertebrate fauna in north-eastern NSW compared sites with a history of grazing and associated burning to others without grazing and burning (York 1999; York & Tarnowski 2004). Data were analysed initially at the level of order, and then at species level for beetles (362 species). At coarse taxonomic resolution (order) there was no apparent difference in invertebrate assemblages between grazing/burning treatments (Fig 3A). The invertebrates were responding to coarse habitat features such as vegetation understory structure and soil physical properties, with no grazing/burning

signal observable. In comparison, species-level beetle data (Fig 3B) showed a clear separation of treatments in ordination space, suggesting different assemblage composition, with beetle species again responding to soil and vegetation-related habitat parameters. In particular this analysis identified that, at the species-level, changes in the amount of vegetation in the ground herb and small shrub layers (0–20 cm) was the primary determinant of assemblage composition; clearly a response to grazing and burning. Interestingly, species-level data also allowed the identification of a previous logging disturbance history (stumps) which had an interaction with the grazing/burning regime (York & Tarnowski 2004). While some similar patterns were identified for spiders at the species level (Harris et al. 2003), no grazing/burning patterns were observed for this group. This has implications for the selection of ‘indicator’ taxa for addressing particular disturbance-related questions (see below).

USE OF INDICATOR TAXA

In Victoria, the primary approach used to formulate desirable inter-fire intervals for the conservation of biodiversity is based on functional groups of plants. The desired mean fire interval is determined by monitoring plant responses of the most vulnerable types as indicators and measuring critical times in their life cycles (Gill 2008). These Key Fire Response Species (KFRS) are a central feature of the flora vital attributes model; species within an EVC whose vital attributes indicate that they are vulnerable to either a regime of frequent fires or to long periods of fire exclusion (Fire Ecology Working Group 2004). The model assumes if the fire frequency fits within the tolerable fire interval determined by the KFRS then all species of vascular flora within the area should survive. Interestingly, this assumption is a largely untested for plants (Cawson & Muir 2008), with the outcome for other groups unknown.

With invertebrates, research and inventory projects are rarely sufficiently well funded to support the sampling and identification of more than a few taxa in a given area. Usually a reduced set of taxa, or more commonly a single taxon, are sometimes used as surrogates for all taxa. These have been called variously, priority taxa (New 1998), indicator taxa (Kremen 1992; Churchill 1997), focal groups (di Castri et al. 1992), predictor sets (Kitching 1993) or target taxa (Kremen 1994; Lewandowski et al. 2010). Surrogate taxa should have known

relationships to the diversity of other taxa, or respond in a predictable way to environmental parameters or disturbance (Hammond 1994). The identification of suitable invertebrate indicator taxa for fire-related questions is beyond the scope of this paper, but it is likely that no single taxon would prove superior, and should be determined by the specific question being posed (Andersen 1999; Oliver et al. 1999). In Victoria (and elsewhere) Fire Management Plans must evaluate risks to rare and threatened species and communities against the risk to (human) life and property (DSE 2006, p.10). However, the capacity of listed invertebrate taxa to function as surrogates or indicators in fire management would seem severely constrained; primarily by their rarity and patchy distribution, and lack of knowledge with regard to fire responses, but also due to the fact that terrestrial invertebrates are currently markedly underrepresented on threatened species lists (as a proportion of their overall diversity).

A FUNCTIONAL APPROACH

There are, however, opportunities to progress this issue using a functional approach, allowing us to simplify the complexity associated with exceptional biodiversity and interpret changes in an ecologically meaningful way. I suggest that there are two main steps in this process (York 2003). Firstly, we need to define functional (target) taxa based on feeding guilds, groups that can be defined and interpreted ecologically (Krebs 1985; Schowalter 2000, p. 235). The selection of target taxa would depend upon the question being posed, the scope (timing and scale) of the investigation, and their suitability for the environment under investigation (Oliver et al. 1999). With regard to invertebrates, such guilds (with example constituent taxa from which candidate species/groups could be chosen) might involve, for example: nectar and pollen feeders (butterflies, bees), predators and parasitoids (spiders, wasps), fungal feeders (flies, beetles) or decomposers and carrion feeders (dung beetles). Secondly, within such a functional classification, we then need to define groups based on their habitat utilisation so as to predict (and interpret) their response to disturbance by fire. Extending the model proposed by Warren et al. (1987) for grassland invertebrates, such response groups could be defined as: flying surface dwellers, non-flying surface dwellers, litter dwellers, soil dwellers, bark dwellers and saproxylic (associated with dead and decaying wood).

Within this scheme, a subset of response groups within functional target taxa, with known sensitivities to aspects of the fire regime, could be identified and effectively function as KFRS. Using an appropriate sampling methodology (Southwood & Henderson 2000; Lovell et al. 2010), data collected could be utilised to address particular management questions. For example, if the management issue concerned the impact of a particular fire regime on litter decomposition and nutrient cycling, then litter- and soil-dwelling organisms from the decomposer functional guild would be the appropriate target taxa. Target species could vary between locations as it is function and response that are the key indicator attributes. An understanding of the mechanisms underlying observed response patterns would need to be developed through focussed research with an adaptive management framework (Di Stefano & York 2012). Once the links between taxa and the ecological functions that they facilitate are better understood, monitoring of selected functions (rather than the invertebrates themselves) could be used to assess the impact of altered fire regimes (herbivory–Christie & York 2009, decomposition–Brennan et al. 2009).

CONCLUSIONS

To incorporate invertebrates effectively in fire management we need firstly to routinely include them in surveys and monitoring. The development of rapid biodiversity protocols (see Oliver and Beattie 1996), improved and widely available on-line taxonomic keys (e.g. Ants Down Under, <http://anic.ento.csiro.au/ants/>), novel approaches such as DNA barcoding (Smith et al. 2005), and improved ways of dealing with taxonomic uncertainty in data analyses (Cayuela et al. 2011), now makes routine inclusion a realistic proposition.

Given the widespread and systematic use of surrogates in fire management (e.g. EVCs, KFRS, vegetation growth stages based on time since last fire) it is worthwhile considering whether these approaches are appropriate to address management issues relating to diverse invertebrate assemblages. As invertebrate distribution patterns manifest themselves at different spatial scales to vertebrates and vascular plants, exhibiting narrow distributions and high species turnover, vegetation mapped at coarse scales (e.g. EVC) is unlikely to prove a useful substitute. The use of habitat models as surrogates for broad invertebrate assemblages has

greater promise (Hein et al. 2007), and aligns with approaches being developed for vertebrates (Clarke 2008; MacHunter et al. 2009; Di Stefano et al. 2011). Additionally, while the use of coarse level taxonomy (e.g. order) is potentially more cost-effective, the utility of this approach is limited to coarse-grained landscape questions (York & Tarnowski 2004), with species-level resolution usually required to detect fire responses (Friend & Williams 1996).

For many fire management related issues the use of surrogate approaches such as these has limited utility, with broad-scale non-targeted surveys also likely to be unproductive and expensive. A more achievable and informative approach could involve focussed surveys of representatives from functional groups which best address explicit management questions. In Western Australia, a subset of invertebrates are regularly monitored as part of the FORESTCHECK program in jarrah forests (Abbott & Burrows, 2004), <http://www.dec.wa.gov.au/content/view/5605/2290/>). To progress this approach and gain wider acceptance of the need to include invertebrates in fire management, we must develop a functional classification of invertebrates utilising target taxa with known ecological roles. Within this framework we can use known life history attributes to describe responses to disturbance, define thresholds (e.g. acceptable population fluctuations) and thereby develop 'indicator' criteria which can be used to monitor responses to fire. By using species groups with known attributes in this way we can explain trends rather than just describe them, and make testable predictions about the consequences of alternate fire management strategies. Identification and understanding of fire-response patterns of target taxa will facilitate the prediction of the outcome of a particular fire regime in much the same way as life-history and vital attribute models have been developed for vascular plants. Recent studies with freshwater invertebrates (Menezes et al. 2010) and spiders (Langlands et al. 2011) have demonstrated that trait-based approaches can be successfully used to predict how species assemblages respond to disturbance.

With growing concern about the potential impacts of altered fire regimes on invertebrate diversity in Australian temperate forests (New et al. 2010) and uncertain impacts of global change (York et al. 2012), it is essential that we better understand the diversity and functional roles of invertebrates in fire-prone environments. While the routine inclusion of this

diverse group presents a number of challenges to fire management, there are a range of new approaches that currently present exciting opportunities to address and resolve what has previously been often regarded as an intractable problem.

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