Insect Conservation and Diversity (2021) doi: 10.1111/icad.12493

FORUM & POLICY

Limited understanding of bushfire impacts on Australian invertebrates

MANU E. SAUNDERS,[1] PHILIP S. BARTON,[1,2] JAMES R. M. BICKERSTAFF,[3] LINDSEY FROST,[1] TANYA LATTY,[4] BRYAN D. LESSARD,[5] ELIZABETH C. LOWE,[6] JUANITA RODRIGUEZ,[5] THOMAS E. WHITE[4] and KATE D. L. UMBERS[3,7] [1]School of Environmental and Rural Sciences, University of New England, Armidale, NSW, Australia, [2]School of Science, Psychology and Sport, Federation University Australia, Mount Helen, VC, Australia, [3]Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW, Australia, [4]School of Life and Environmental Sciences, University of Sydney, Sydney, NSW, Australia, [5]Australian National Insect Collection, CSIRO, Canberra, ACT, Australia, [6]Department of Biological Sciences, Macquarie University, Sydney, NSW, Australia and [7]School of Science, Western Sydney University, Penrith, NSW, Australia

Abstract. 1. Understanding how increasing risk of frequent and severe fires affects biodiversity and ecosystem function is important for effective conservation and recovery, but large knowledge gaps exist for many taxa in many parts of the world, especially invertebrates.

2. After Australia's 2019–2020 catastrophic bushfire disaster, estimates of biodiversity loss and government priorities for post-fire conservation activities were focused on vertebrates and plants because of lack of knowledge about invertebrates.

3. Our synthesis of published evidence reveals a fragmented and ambiguous body of literature on invertebrate responses to fire in Australian ecosystems, limiting the capacity of evidence to inform effective conservation policy in response to extreme fire events. Peer-reviewed studies are available for only six of the more than 30 invertebrate phyla and 88% were on arthropods, predominantly ants.

4. Nearly all studies (94%) were conducted in terrestrial habitats, with only four studies measuring impacts in freshwater habitats and no studies of impacts on marine invertebrates. The high variation in study designs and treatment categories, as well as the absence of key methodological details in many older observational studies, means that there is substantial opportunity to improve our approach to collating meaningful estimates of general fire effects.

5. To understand the full ecological effects of catastrophic fire events, and design effective policies that support recovery of ecosystems now and in future, it is critical that we improve understanding of how fire regimes affect invertebrates. We list key priorities for research and policy to support invertebrate conservation and ecosystem recovery in the face of increasing fire risk.

Key words. Biodiversity, ecosystem function, ecosystem recovery, fire, insects, megafire, wildfire.

Introduction

Global climate change is increasing the risk of frequent, severe fires around the world (Virgilio *et al*., 2019; Goss *et al*., 2020). Understanding how fires affect biodiversity is important for effective conservation and recovery efforts, but there are significant gaps in our understanding of the taxa most at risk in many

Correspondence: Manu E. Saunders, School of Environmental and Rural Sciences, University of New England, Armidale, NSW 2350, Australia. E-mail: manu.saunders@une.edu.au

parts of the world (Driscoll *et al*., 2010). This is particularly true for invertebrates, which include a staggering diversity of species with more than 1 million known to science (Roskov *et al*., 2020), and an estimated 4 million undiscovered or undescribed (Stork, 2018). The majority of invertebrate species are critical to ecosystem function and associated ecosystem services across all biomes and in managed and unmanaged systems (Wallace & Webster, 1996; Boulton *et al*., 2008; Prather *et al*., 2013; Yang & Gratton, 2014; Saunders, 2018). Paradoxically, they are also the most understudied group of animals and large knowledge gaps about invertebrate identification, ecology and distribution limit our understanding of their responses to stochastic events and environmental change (Cardoso *et al*., 2011).

In Australia, only about 30% of the invertebrate fauna (over 320 000 species) has been described (Braby, 2018). Due to a lack of baseline knowledge for the majority of species, a very small proportion (653 species) are listed as threatened under state and Commonwealth legislation and the International Union for Conservation of Nature's Red List, the vast majority of which are land snails (Stylommatophora), crayfish (Decapoda), and butterflies and moths (Lepidoptera). Although threatened species lists are intended as a tool to prioritise conservation funding and action, such lists currently cannot account for undescribed species with unknown roles in the ecosystem until they are formally documented and recognised by science. This means that when mounting a priority-based response to catastrophic disasters, unlisted species and, moreover, unknown species, can easily be ignored. The implications of this dearth of knowledge became apparent during Australia's recent catastrophic bushfire disaster. From August 2019 to February 2020, fires burned continuously through more than 10 million hectares (approx. 25 million acres), over 80% of this area native forests, until the last fires were extinguished by heavy rainfall (Davey & Sarre, 2020). Multiple bioregions and ecosystem types were affected, including many unique Australian forests and threatened ecological communities, such as the World Heritage listed Gondwana Rainforests and Greater Blue Mountains area, grassy woodlands, alpine grasslands and meadows, and temperate rainforest (Boer *et al*., 2020; Kooyman *et al*., 2020; Lindenmayer & Taylor, 2020).

Although Australia is a fire-prone country, the unprecedented spatial and temporal scale of this fire season, and the intensity and severity of many of the burns, were unlike anything scientists and firefighting experts had experienced before (Boer *et al*., 2020; Nolan *et al*., 2020). The catastrophic event captured global attention, especially as smoke from the fires made a full circuit around the globe affecting air quality and depositing aerosols in other countries including New Zealand and on the South American continent (Seftor & Gutro, 2020). The fire event turned the spotlight on what we know, and do not know, about the ecological effects of increasing fire risk. Reports of biodiversity losses have estimated that hundreds of millions of animals have died and many threatened species may have been pushed closer to extinction (Woinarski *et al*., 2020a). Most of these estimates focused on plants and vertebrates, which dominate threatened species lists and fire ecology studies in Australia, and for which there are often baseline data available to detect population declines (Pastro *et al*., 2011; Taylor *et al*., 2012; Woinarski & Legge, 2013; Fairman *et al*., 2016; Geary *et al*., 2020). In contrast, there is little understanding of how the fire season affected Australia's unique invertebrate fauna because fundamental baseline data have not been collected in most places for most taxa. Failure to systematically collect monitoring data has left us with no meaningful ways to assess the impact of the fires on our invertebrate fauna and therefore severely limits our understanding of how critical ecosystem functions have been impacted and which recovery activities should be prioritised.

Catastrophic fire events, which are predicted to become more frequent and severe in Australia based on recent modelled climate change scenarios (Dowdy *et al*., 2019), have the potential to significantly restructure ecological communities, cause local extinctions, and disrupt ecological interactions that are essential to ecosystem recovery. The paucity of data on invertebrates leaves us with no guidelines for protecting invertebrate species in the face of increasing prevalence and risk of future bushfires. Australia's megafires captured global attention and millions of dollars were donated to bushfire recovery efforts, leaving many agencies with the question of what to prioritise. Post-fire government priorities for conservation funding targeted individual species comprising approximately 0.06% of Australia's invertebrate diversity compared to about 1.2% of Australia's vertebrates and about 1.9% of plants (Woinarski *et al*., 2020b). Listing was based on species captured in current threatened species legislation, by distribution mapping and/or collated via expert advice (Woinarski *et al*., 2020b). This approach unfortunately misses the larger majority of unstudied and undescribed species impacted by the fires and it is possible that many undescribed species may now be at risk. For example, in recent months, several new invertebrate specimens collected before the fires from fire-impacted areas have been formally described as species new to science (Lessard *et al*., 2020; Yuan & Rodriguez, 2020). This is likely to be a growing trend as more invertebrates in the estimated 70% of unknown species continue to be described from museum collections. In the meantime, current policy and decision-making to facilitate immediate and medium-term responses to fire recovery is informed by a body of knowledge that largely excludes invertebrate ecology and life histories, and could result in poor biodiversity recovery outcomes. It is unreasonable to expect rapid expansion of invertebrate threatened species lists to counter this, due to knowledge limitations and the need for formal taxonomic descriptions. A more immediate solution is to focus policy and restoration efforts on ecosystems and communities, rather than species, to limit the potential bias of decisions informed by vertebrate ecology and distributions.

In this commentary, we seek to amplify the discourse on how fire impacts biodiversity and increase focus on the neglected yet dominant group of animals that drive ecosystem function and influence ecosystem recovery. We focus on Australia, the core of our expertise, because the 2019–2020 Australian megafires were a key global event that highlighted the increasing severity and risk of fire impacts on ecosystems from anthropogenic climate change. Predicting the impact of fire on invertebrates is a complex problem because current evidence of these impacts is fragmented and often has limited relevance beyond the taxa or system of focus. There are few general literature reviews of evidence and these are decades old or specific to geographic locations (e.g. Friend, 1995; McCullough *et al*., 1998; Nunes *et al*., 2000; Swengel, 2001), limiting their application to contemporary global climate conditions, or Australian ecosystems generally. More recent reviews and opinion pieces have been published on Australian contexts (e.g. New *et al*., 2010; York & Lewis, 2018), but these have focused on particular systems or taxonomic groups and, to date, there has been no synthesis of existing relevant literature to guide a constructive path forward for research and policy.

To identify the full range of ecological effects of wildfire events, and design effective policies that support the recovery of ecosystems now and into the future, it is critical that we improve our understanding of how fire regimes affect invertebrates. An urgent first step is to collate existing empirical evidence of how fire impacts Australian invertebrates in an effort to rapidly identify knowledge gaps and guide future research and management priorities. To support our argument and inform future discussion on this important issue, we conducted a structured synthesis of published literature investigating fire effects on invertebrates in Australian ecosystems. We framed our review within the context of these questions:

1. What is the biome coverage of evidence measuring fire effects on invertebrates in Australian ecosystems?
2. For which invertebrate taxa is there available evidence measuring fire effects in Australian ecosystems?
3. How relevant is the available evidence for developing effective conservation policy and recommendations?

We synthesised the published empirical evidence of Australian invertebrate responses to fire and identified major knowledge gaps that currently hinder conservation and restoration initiatives. Due to major methodological limitations in the majority of studies and the limited and fragmented evidence, our aim here is to ignite evidence-based discussion and action rather than conduct formal meta-analysis of effects, which would provide potentially misleading results. We provide a synthesis of published peer-reviewed literature using repeatable and transparent methods to support our argument by highlighting the major knowledge gaps that hinder current understanding of bush fire impacts on Australian invertebrates. We present guidelines for consideration in effective policy and decision-making that acknowledge the significant contribution to biodiversity and essential role of invertebrates in ecosystem function and recovery.

Structured literature synthesis

We conducted a search of peer-reviewed literature in the Scopus database, using the search string: (TITLE-ABS-KEY ((burn* OR *fire)) AND TITLE-ABS-KEY ((*invertebrate OR insect OR arthropod* OR mollusc* OR platyhelminth* OR nematod* OR annelid* OR tardigrad* OR onychophor* OR acanthocephal* OR brachiopod* OR bryozo* OR cephalorhynch* OR chaetognath* OR cnidari* OR ctenophor* OR cycliophor* OR dicyemid* OR echinoderm* OR entoproct* OR gastrotrich* OR gnathostomulid* OR hemichordat* OR micrognathoza* OR myxozoa* OR nematomorph* OR nemert* OR orthonectid* OR phoronid* OR placozoa* OR porifer* OR rotifer* OR sipuncul* OR xenacoelomorph*)) AND TITLE-ABS-KEY (australia)). This search was conducted on 1 February 2020 and returned 324 results. We acknowledge that, as with any literature search method, we may have missed some unpublished works, including PhD theses, technical reports, and papers from non-indexed journals, as well as papers that use more specific taxonomic nomenclature than we covered in our search terms, but we are confident that these minor limitations are unlikely to have changed our conclusions about the overall variability among studies and key knowledge gaps. Our aims here are to ignite an important discussion on available evidence and the inclusion of invertebrates in policy decisions, not to conduct an exhaustive review of all published and unpublished data from Australian systems.

For the first stage of the review, the full set of papers was uploaded to Sysrev for abstract-only screening (project page: https://sysrev.com/u/992/p/24557). The abstract of each paper was screened by two people and included in our review if it met the following criteria: (i) it was an empirical study that measured an effect of fire on a group of invertebrates, and; (ii) the study was conducted in Australia (any continental state or territory, including offshore islands). Studies in managed systems (e.g. crops, forestry) were included, and studies focusing on non-invertebrate taxa were included if they also included invertebrate sampling in their methods (e.g. as available prey). This screening process resulted in 43 conflicts, i.e. 43 papers where the two reviewers had not agreed on whether to include the paper. A third person (ECL) not involved with the first round of screening then screened these papers to resolve the conflict. This process was completed on 9 March 2020 and resulted in a total of 91 papers (see Supplementary Data).

In the second stage of review, the 91 relevant papers were divided among the authors to screen the paper in full and extract data. The lead author assessed the whole dataset after screening to ensure consistency, fill in missing information, and remove duplication. A total of 24 papers were removed during this second stage, as they were either duplicates or found to be irrelevant after detailed reading of the full paper. This resulted in 67 total papers that met the criteria and contained the information needed to answer our questions. For each relevant paper, we extracted data on the study design and results, including: location, biome, invertebrate taxa, type of fire, fire effect (e.g. frequency, intensity, burned vs. unburned), and reported trends (see Supplementary Data). This process was completed on 27 May 2020. At this point, the search terms were refreshed in Scopus to pick up any newly published papers since the initial search occurred, but no new relevant results were found.

Ecoregion coverage of available evidence

We assessed evidence coverage across Australian ecoregions using the Terrestrial Ecoregions of The World map layer delineated by Olson *et al*. (2001) (available to download from: https://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world). Three-quarters of the studies measuring fire effects on invertebrates were conducted in two southern Australian ecoregions: Mediterranean Forests, Woodlands and Scrub, and Temperate Broadleaf and Mixed Forests (Figure 1). Two ecoregions were not represented in the available evidence: Montane Grasslands and Shrublands, and Tropical and Subtropical Moist Broadleaf Forests. Most studies were conducted in terrestrial habitats. Only four studies measured effects in freshwater

 doi: 10.1111/icad.12493

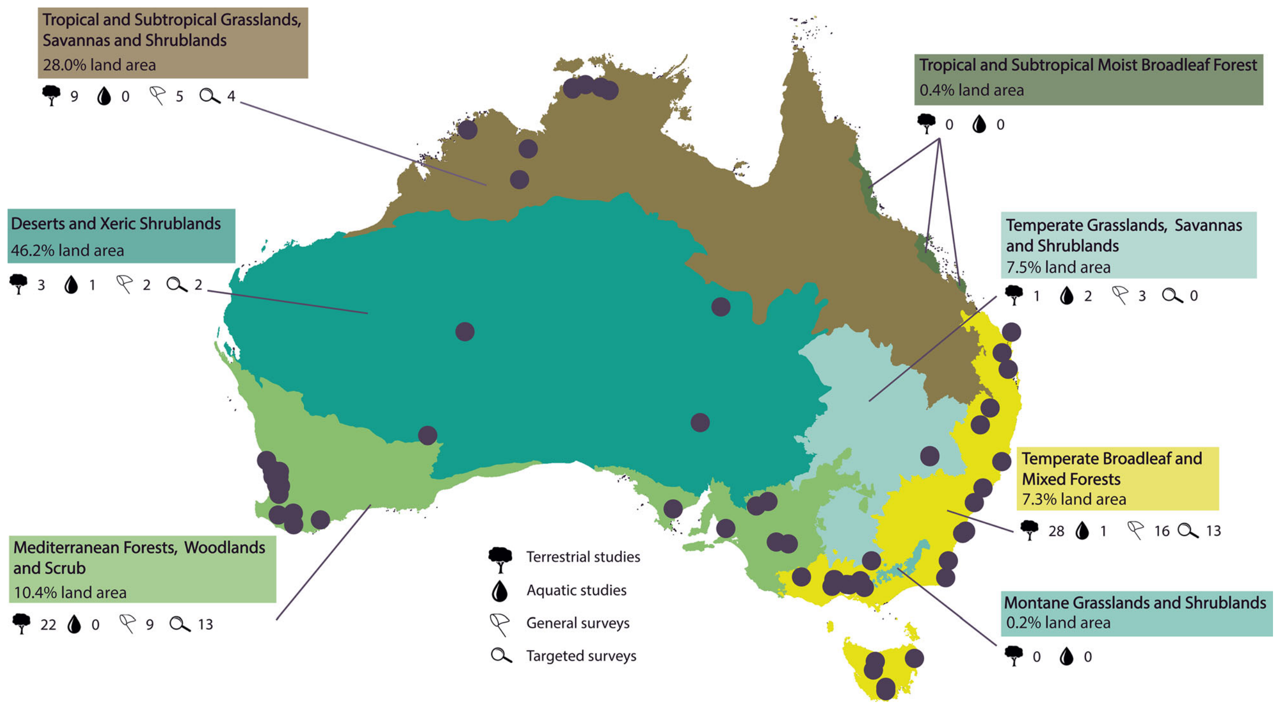

Figure 1. Summary of published studies measuring effects of fire on invertebrates in Australia. Map shows ecoregions delineated by Olson *et al*. (2001). General surveys are studies that aimed to focus any invertebrates in the study system; Targeted surveys are studies that focused on specific taxa or taxonomic groups. Full details of studies are available in Supplementary Data. [Color figure can be viewed at wileyonlinelibrary.com]

aquatic systems: two in river catchments, one in an ephemeral lake, and one in an artesian spring. No studies measured the effects of fire on marine invertebrates.

Taxonomic coverage of available evidence

The extremely high diversity of invertebrates has resulted in a variety of appropriate sampling techniques each targeting specific functional or taxonomic groups. Therefore, the aims and methodology of a given study determine how broadly the results can be applied to understanding invertebrate communities. In the majority of studies (52%), researchers stated their aims were to conduct a general survey of invertebrates at the study site (Supplementary Data - DOI 10.17605/OSF.IO/MJ8PD). However, nearly all (91%) of these studies used a sampling method that targeted invertebrates adapted to a particular habitat or substrate type, usually at ground level (e.g. pitfall traps, soil cores, leaf litter samples). Only three studies used multiple sampling techniques that would collect a broader sample of the local invertebrate community. The remaining studies were targeted at a specific species or group of invertebrates, and sampling techniques were suited to the target taxa.

Targeted studies provided evidence of effects for a total of six invertebrate phyla (there are over 30; Ruppert *et al*., 2004). Most studies (88%) focused on Arthropoda, and insects were the most common focus of these studies, predominantly ants (Hymenoptera: Formicidae). This is possibly an artefact of the high abundance and diversity of ants in Australian environments, their relative ease of sampling, and the greater historical research effort on this group relative to other Australian invertebrate taxa (Majer, 1983; Hoffman & Andersen, 2003). However, ants can be more resilient to fire than other fire-prone groups and may not represent responses of the whole invertebrate assemblage (Pryke & Samways, 2012). Two studies measured impacts on Mollusca (Gastropoda), one study focused on mammalian parasites in three phyla (Acanthocephala, Nematoda, Platyhelminthes), and one study focused on Onychophora.

The majority of studies used metrics of abundance, diversity and/or community composition to quantify invertebrates or compare sites. Nine studies measured an ecological function or interaction to quantify invertebrate presence or abundance, for example, decomposition rate, parasitism rate, and herbivory damage (Supplementary Data).

Relevance of available evidence to conservation policy

Our synthesis of published evidence reveals a fragmented and ambiguous body of literature on invertebrate responses to fire in Australian ecosystems. This is a significant finding as it limits our capacity to inform effective biodiversity conservation policy in response to extreme fire events. A major gap highlighted by our review is the lack of invertebrate studies from two ecoregions that are becoming increasingly fire-prone because of climate change (Montane Grasslands and Shrublands, and Tropical and Subtropical Moist Broadleaf Forests). Notably, all studies in this review were conducted at spatial scales vastly smaller than those at which fires burned in the 2019–2020 season. The magnitude and type of effects of fire on invertebrates varied widely across studies, and often showed complex variation for individual species or functional groups. For example, many general surveys that sampled multiple invertebrate orders showed overall neutral effects, with high variation between groups (e.g. Andersen & Müller, 2000; Robson *et al*., 2018). Even studies that focused on specific taxonomic groups showed contrasting effects at the species level (e.g. Arnold *et al*., 2017). Studies comparing effects of different types of managed burns highlighted how fire attributes, including season of burn, intensity, or frequency, can lead to different responses in the same taxonomic groups (e.g. Neumann & Tolhurst, 1991; Blanche *et al*., 2001). Some studies found immediate post-fire declines in abundance, but these population changes were not permanent (e.g. Neumann, 1991; Radford & Andersen, 2012), while other studies testing fire frequency found population declines over time associated with frequent fires in some habitats (e.g. York, 1999). Most studies (64%) identified invertebrates to higher taxonomic ranks such as Order or Class or to morphospecies, possibly to save on costs or due to a lack of taxonomic expertise, further limiting our ability to meaningfully interpret the results for policy application. Clearly, much more evidence is needed before effective policy recommendations can be made about which taxa are post-fire winners or losers, within which contexts these effects can change, and what this means for ecosystem functions.

A key limitation of the available evidence is the dearth of studies measuring impacts of severe bushfires, which limits capacity to predict invertebrate responses to the increasing fire risk and severity predicted under global change. Most studies (45%) measured the effects of managed or experimental burns, 31% measured the effects of unmanaged fires, and 22% used space-for-time substitutions to measure general effects of fire history (combined managed and bushfires) in fire-prone landscapes. A total of 10 studies (15%) were confounded by land management, with fire effects only measured in forest blocks used for timber harvesting. The high variation in study designs and treatment categories, as well as the absence of key methodological details in many older observational studies, means there is a substantial opportunity to improve our approach to collating meaningful estimates of general fire effects.

The current literature provides limited insight into how interactions between invertebrates and their habitat can influence fire behaviour and its effects on ecosystems (Foster *et al*., 2020). For example, ground and leaf litter invertebrates, especially decomposing species, can potentially influence the intensity of a fire by reducing fuel loads (e.g. Brennan *et al*., 2006). Yet few datasets are available to show how litter-dwelling invertebrate diversity translates into ecosystem resilience or recovery from fires (Arnold *et al*., 2017). Approaches to invertebrate research therefore needs to shift to incorporate their interactions with ecosystem attributes, and how this might affect fire dynamics.

Extreme fire events, such as Australia's 2019–2020 bushfires, can have large-scale and indirect effects on invertebrates that we are yet to understand. Post-fire recovery of invertebrate communities can occur via multiple mechanisms including survival *in situ*, recolonisation by dispersal or reproduction from egg banks (e.g. Munro *et al*., 2009; Robson *et al*., 2018). However, without a better understanding of the fundamental ecology of invertebrate taxa and how these mechanisms of resilience support post-fire recovery over extended spatial scales, our ability to predict and manage for recovery is limited. Critically, the lack of studies from aquatic habitats, especially marine systems, have left major knowledge gaps in our understanding of ecosystem level effects of extreme fire events. The effects of large-scale fire events, such as Australia's 2019–2020 catastrophic bushfires, can reach far beyond the burned area, including long-range transport of ash into marine systems many thousands of kilometres away (Zheng *et al*., 2020). Ash runoff can have negative impacts on a range of aquatic invertebrates (Silva *et al*., 2016; Carvalho *et al*., 2019), yet understanding of the direct and indirect effects of fires on downstream freshwater and marine ecosystems is limited (Bixby *et al*., 2015; Baumgartner *et al*., 2020).

The capacity of fire events to transfer invertebrate biomass across systems and mediate dispersal is also poorly understood. During the Australian bushfires, observations of mass wash-ups of dead insects along beaches downwind of the fires were shared on social media, suggesting that insects had been carried out to sea via firestorms associated with an upwind megafire (Figure 2). There is little explanation of this fire-related phenomenon in scientific literature, as is the case with insect wash-ups generally (Denemark & Losey, 2010). Research into these events would provide better understanding of invertebrate biodiversity losses from major fire events, as well as increase knowledge of fire-mediated energy transfer (via invertebrate biomass) and dispersal.

Insufficient evidence about invertebrate diversity and ecology, particularly their responses to fire, limit our capacity to make evidence-informed decisions about post-fire land restoration and funding priorities. In response to the 2019–2020 catastrophic fires, the Australian government established a rapid assessment process to support wildlife recovery efforts, including priority lists of threatened species to support decision-making (Woinarski *et al*., 2020b). Unsurprisingly, these lists contain few invertebrate species compared to the number of invertebrate species that exist. This is likely because the methods required to make such lists filter out species for which: (i) their susceptibility to fire is unknown, (ii) distribution records are unavailable, and (iii) they are not formally listed as threatened (Woinarski *et al*., 2020b). The consequences are that the recovery of invertebrate species receives an inadequate proportion of funding and recovery of ecosystem function is potentially compromised.

Priorities to guide research, policy and decision-making

Research:

- Systematic, ongoing invertebrate biodiversity surveys (e.g. the Australian Government sponsored BushBlitz program) should be prioritised in understudied ecosystems and bioregions and fire-prone areas, especially in collaboration with citizen science programs. Such surveys should be linked to research questions that provide clear boundaries around the monitoring goals.

  doi: 10.1111/icad.12493

Figure 2. Dead insects washed up on the beach at Bermagui, New South Wales, 24 December 2019. The closest fire at the time was the Currowan mega-fire near Bateman's Bay, about 100 km to the north. Insects shown include: Diptera (Calliphoridae), Coleoptera (Coccinellidae, Cerambycidae), Hemiptera (Pentatomoidea), and Hymenoptera (Apoidea, Formicidae, Ichneumonidae). Photo copyright: Caitlin Brown (Instagram: @bluebowerstudio), used with permission. [Color figure can be viewed at wileyonlinelibrary.com]

- Increase knowledge of invertebrate species distribution. This includes new surveys as well as support for existing datasets to be made available digitally via public biodiversity databases (e.g. Atlas of Living Australia).
- Significant investment in taxonomic research to formally describe and identify invertebrate species previously unknown to science and support to upload specimen data to biodiversity atlases (e.g. Atlas of Living Australia).
- Ecological assessment of unlisted but rare and endemic invertebrate species.
- Increase knowledge of cross-scale fire effects. For example, quantifying long-term variation in post-fire invertebrate

responses to understand how long it takes invertebrate populations to recover after fire, and how their interactions vary over time post-fire (e.g. Neumann, 1991); documenting downwind wash-ups of dead invertebrates to identify taxa most likely to be killed during fires, and to quantify potential biomass inputs for coastal ecosystems (e.g. Fig. 2).

- Quantify how terrestrial plant–invertebrate interactions (including detritivores and saproxylic invertebrates) affect fuel loads and fire intensity (e.g. Arnold *et al*., 2017).
- Increase knowledge of how different fire regimes and management strategies (including fuel reduction and mosaic burning) influence invertebrate diversity at local and landscape scales, and improve understanding of how pyrodiversity influences invertebrate biodiversity and post-fire recolonisation (e.g. Kelly *et al*., 2017).
- Increase knowledge of indirect fire effects on invertebrates, especially in aquatic systems. In particular, there is an urgent need for more research on downstream effects of fire (direct and indirect) on marine invertebrates.
- Genetic and genomic research to understand how intraspecific variation influences fire impacts, and how fire affects population dynamics over multiple spatial scales.

Policy and decision-making:

- Focus on restoring ecological communities and ecosystem function in fire recovery efforts, to limit the potential bias of decisions informed by vertebrate ecology and distributions.
- Update threatened species lists and conservation management plans by establishing more rapid and simple listing processes for potential threatened taxa for which there is limited available knowledge.
- Dedicated funding streams from relevant societies and government bodies targeting invertebrate research.
- Greater advocacy efforts from ecology and entomology relevant professional societies, including fire and conservation focused committees and opportunities for members to contribute to coordinated expert responses.

Conclusion

We have shown that major knowledge gaps hinder our understanding of invertebrate responses to increasing fire risk and severity in Australian ecosystems. We argue that lack of knowledge and limited funding for invertebrate research means invertebrates, and the ecosystems they support, face serious threats as fire severity and frequency intensifies in response to global change. Critically, our capacity to make effective decisions about ecosystem recovery and restoration funding after future fires is hampered by the lack of knowledge on how invertebrates are impacted by fire, directly and indirectly, and how invertebrate communities influence ecosystem recovery. We urge researchers, funding bodies, and policy makers to take a whole-ecosystem approach and prioritise research on invertebrates in fire-impacted and fire-prone ecosystems to increase the effectiveness of post-fire recovery actions.

Acknowledgements

The authors thank Ainsley Seago, Markus Riegler and Nathan Lo for contributing to early discussions about this project, and Laurence Packer and Raphael Didham and two anonymous reviewers for providing helpful comments on the manuscript draft.

Data availability statement

Supplementary data are deposited at Open Science Framework DOI 10.17605/OSF.IO/MJ8PD (available at https://osf.io/mj8pd/).

References

Andersen, A.N. & Müller, W.J. (2000) Arthropod responses to experimental fire regimes in an Australian tropical savannah: ordinal-level analysis. *Austral Ecology*, **25**, 199–209.

Arnold, K.T., Murphy, N.P. & Gibb, H. (2017) Post-fire recovery of litter detritivores is limited by distance from burn edge. *Austral Ecology*, **42**, 94–102.

Baumgartner, L., Doyle, K., Silva, L. G. M., Pearce, L., & Ning, N. (2020) Before and after: see how bushfire and rain turned the Macquarie perch's home to sludge. The Conversation. <https://theconversation.com/before-and-after-see-how-bushfire-and-rain-turned-the-macquarie-perchs-home-to-sludge-139919> 13th July 2020

Bixby, R.J., Cooper, S.D., Gresswell, R.E., Brown, L.E., Dahm, C.N. & Dwire, K.A. (2015) Fire effects on aquatic ecosystems: an assessment of the current state of the science. *Freshwater Science*, **34**, 1340–1350.

Blanche, K.R., Andersen, A.N. & Ludwig, J.A. (2001) Rainfall-contingent detection of fire impacts: responses of beetles to experimental fire regimes. *Ecological Applications*, **11**, 86–96.

Boer, M.M., Dios, V.R. & Bradstock, R.A. (2020) Unprecedented burn area of Australian mega forest fires. *Nature Climate Change*, **10**, 171–172.

Boulton, A.J., Fenwick, G.D., Hancock, P.J. & Harvey, M.S. (2008) Biodiversity, functional roles and ecosystem services of groundwater invertebrates. *Invertebrate Systematics*, **22**, 103–116.

Braby, M.F. (2018) Threatened species conservation of invertebrates in Australia: an overview. *Austral Entomology*, **57**, 173–181.

Brennan, K.E.C., Christie, F.J., York, A. & Lawrence, J. (2006) Fuel for thought: do litter-dwelling invertebrates mediate fine fuel loads in frequently burnt eucalypt forests? *Forest Ecology & Management*, **234**, S163.

Cardoso, P., Erwin, T.L., Borges, P.A.V. & New, T.R. (2011) The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation*, **144**, 2647–2655.

Carvalho, F., Pradhan, A., Abrantes, N., Campos, I., Keizer, J.J., Cássio, F. & Pascoal, C. (2019) Wildfire impacts on freshwater detrital food webs depend on runoff load, exposure time and burnt forest type. *Science of The Total Environment*, **692**, 691–700.

Davey, S.M. & Sarre, A. (2020) Editorial: the 2019/20 Black Summer bushfires. *Australian Forestry*, **83**, 47–51.

Denemark, E. & Losey, J.E. (2010) Causes and consequences of ladybug washups in the finger lakes region of New York State (Coleoptera: Coccinellidae). *Entomologica Americana*, **116**, 78–88.

Dowdy, A.J., Ye, H., Pepler, A., Thatcher, M., Osbrough, S.L., Evans, J. P., Di Virgilio, G. & McCarthy, N. (2019) Future changes in extreme weather and pyroconvection risk factors for Australian wildfires. *Scientific Reports*, **9**, 10073.

Driscoll, D.A., Lindenmayer, D.B., Bennett, A.F., Bode, M., Bradstock, R.A., Cary, G.J., Clarke, M.F., Dexter, N., Fensham, R., Friend, G., Gill, M., James, S., Kay, G., Keith, D.A., MacGregor, C., Russell-Smith, J., Salt, D., Watson, J.E.M., Williams, R.J. & York, A. (2010) Fire management for biodiversity conservation: key research questions and our capacity to answer them. *Biological Conservation*, **143**, 1928–1939.

Fairman, T.A., Nitschke, C.R. & Bennett, L.T. (2016) Too much, too soon? A review of the effects of increasing wildfire frequency on tree mortality and regeneration in temperate eucalypt forests. *International Journal of Wildland Fire*, **25**, 831–848.

Foster, C.N., Banks, S.C., Cary, G.J., Johnson, C.N., Lindenmayer, D. B. & Valentine, L.E. (2020) Animals as agents in fire regimes. *Trends in Ecology & Evolution*, **35**, 346–356.

Friend, G.R. (1995) Fire and invertebrates – a review of research methodology and the predictability of post-fire response patterns. *CALMScience Supplement*, **4**, 165–174.

Geary, W.L., Doherty, T.S., Nimmo, D.G., Tulloch, A.I.T. & Ritchie, E. G. (2020) Predator responses to fire: a global systematic review and meta-analysis. *Journal of Animal Ecology*, **89**, 955–971.

Goss, M., Swain, D.L., Abatzoglou, J.T., Sarhadi, A., Kolden, C., Williams, A.P. & Diffenbaugh, N.S. (2020) Climate change is increasing the risk of extreme autumn wildfire conditions across California. *Environmental Research Letters*, **15**, 094016.

Hoffmann, B.D. & Andersen, A.N. (2003) Responses of ants to disturbance in Australia, with particular reference to functional groups. *Austral Ecology*, **28**, 444–464.

Kelly, L.T., Brotons, L. & McCarthy, M.A. (2017) Putting pyrodiversity to work for animal conservation. *Conservation Biology*, **3**, 952–955.

Kooyman, R.M., Watson, J. & Wilf, P. (2020) Protect Australia's Gondwana Rainforests. *Science*, **367**, 1083–1083.

Lessard, B.D., Yeates, D.K. & Woodley, N.E. (2020) *Opaluma*: a new genus of iridescent soldier flies (Diptera: Stratiomyidae) from Australia, including seven new species. *Austral Entomology*, **59**, 467–486.

Lindenmayer, D.B. & Taylor, C. (2020) New spatial analyses of Australian wildfires highlight the need for new fire, resource, and conservation policies. *Proceedings of the National Academy of Sciences*, **117**, 12481–12485.

Majer, J.D. (1983) Ants: bio-indicators of minesite rehabilitation, land-use, and land conservation. *Environmental Management*, **7**, 375–383.

McCullough, D.G., Werner, R.A. & Neumann, D. (1998) Fire and insects in northern and boreal forest ecosystems of North America. *Annual Review of Entomology*, **43**, 107–127.

Munro, N.T., Kovac, K.-J., Niejalke, D. & Cunningham, R.B. (2009) The effect of a single burn event on the aquatic invertebrates in artesian springs. *Austral Ecology*, **34**, 837–847.

Neumann, F.G. & Tolhurst, K. (1991) Effects of fuel reduction burning on epigeal arthropods and earthworms in dry sclerophyll eucalypt forest of west-central Victoria. *Australian Journal of Ecology*, **16**, 315–330.

Neumann, F.G. (1991) Responses of litter arthropods to major natural or artificial ecological disturbances in mountain ash forest. *Australian Journal of Ecology*, **16**, 19–32.

New, T.R., Yen, A.L., Sands, D.P.A., Greenslade, P., Neville, P.J., York, A. & Collett, N.G. (2010) Planned fire and invertebrate conservation in south east Australia. *Journal of Insect Conservation*, **14**, 567–574.

Nolan, R.H., Boer, M.M., Collins, L., Dios, V.R., Clarke, H., Jenkins, M., Kenny, B. & Bradstock, R.A. (2020) Causes and consequences of eastern Australia's 2019–20 season of mega-fires. *Global Change Biology*, **26**, 1039–1041.

Nunes, L.F., Leather, S.R. & Rego, F.C. (2000) Effects of fire on insects and other invertebrates. A review with particular reference to fire indicator species. *Silva Lusitana*, **8**, 15–32.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T. H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001) Terrestrial ecoregions of the world: a new map of life on Earth. *Bioscience*, **51**, 933–938.

Pastro, L.A., Dickman, C.R. & Letnic, M. (2011) Burning for biodiversity or burning biodiversity? Prescribed burn vs. wildfire impacts on plants, lizards, and mammals. *Ecological Applications*, **21**, 3238–3253.

Prather, C.M., Pelini, S.L., Laws, A., Rivest, E., Woltz, M., Bloch, C.P., Toro, I.D., Ho, C.-K., Kominoski, J., Newbold, T.A.S., Parsons, S. & Joern, A. (2013) Invertebrates, ecosystem services and climate change. *Biological Reviews*, **88**, 327–348.

Pryke, J.S. & Samways, M.J. (2012) Differential resilience of invertebrates to fire. *Austral Ecology*, **37**, 460–469.

Radford, I.J. & Andersen, A.N. (2012) Effects of fire on grass-layer savanna macroinvertebrates as key food resources for insectivorous vertebrates in northern Australia. *Austral Ecology*, **37**, 733–742.

Robson, B.J., Chester, E.T., Matthews, T.G. & Johnston, K. (2018) Post-wildfire recovery of invertebrate diversity in drought-affected headwater streams. *Aquatic Sciences*, **80**, 21.

Roskov, Y., Ower, G., Orrell, T., Nicolson, D., Bailly, N., Kirk, P. M., Bourgoin, T., DeWalt, R. E., Decock, W., van Nieukerken, E., & Penev, L. (2020). *Species* 2000 *& ITIS Catalogue of Life, 2020-04-16 Beta*. Catalogue of Life. <www.catalogueoflife.org/col> 13th July 2020.

Ruppert, E.E., Fox, R.S. & Barnes, R.D. (2004) *Invertebrate Zoology*, 7th Edn. Thomson Brooks/Cole, California.

Saunders, M.E. (2018) Ecosystem services in agriculture: understanding the multifunctional role of invertebrates. *Agricultural and Forest Entomology*, **20**, 298–300.

Seftor, C. & Gutro, R. (2020) NASA animates world path of smoke and aerosols from Australia fires. NASA. <https://www.nasa.gov/feature/goddard/2020/nasa-animates-world-path-of-smoke-and-aerosols-from-australian-fires> 7th October 2020.

Silva, V., Abrantes, N., Costa, R., Keizer, J.J., Gonçalves, F. & Pereira, J. L. (2016) Effects of ash-loaded post-fire runoff on the freshwater clam *Corbicula fluminea*. *Ecological Engineering*, **90**, 180–189.

Stork, N.E. (2018) How many species of insects and other terrestrial arthropods are there on earth? *Annual Review of Entomology*, **63**, 31–45.

Swengel, A.B. (2001) A literature review of insect responses to fire, compared to other conservation managements of open habitat. *Biodiversity and Conservation*, **10**, 1141–1169.

Taylor, R.S., Watson, S.J., Nimmo, D.G., Kelly, L.T., Bennett, A.F. & Clarke, M.F. (2012) Landscape-scale effects of fire on bird assemblages: does pyrodiversity beget biodiversity? *Diversity and Distributions*, **18**, 519–529.

Virgilio, G.D., Evans, J.P., Blake, S.A.P., Armstrong, M., Dowdy, A.J., Sharples, J. & McRae, R. (2019) Climate change increases the potential for extreme wildfires. *Geophysical Research Letters*, **46**, 8517–8526.

Wallace, J.B. & Webster, J.R. (1996) The role of macroinvertebrates in stream ecosystem function. *Annual Review of Entomology*, **41**, 115–139.

Woinarski, J. & Legge, S. (2013) The impacts of fire on birds in Australia's tropical savannas. *Emu - Austral Ornithology*, **113**, 319–352.

Woinarski, J., Wintle, B., Dickman, C., Bowman, D., Keith, D., & Legge, S. (2020a). A season in hell: bushfires push at least 20 threatened species closer to extinction. The Conversation. <http://theconversation.com/a-season-in-hell-bushfires-push-at-least-20-threatened-species-closer-to-extinction-129533> 13th July 2020.

Woinarski, J., Nimmo, D., Gallagher, R., & Legge, S. (2020b). After the bushfires, we helped choose the animals and plants in most need.

Here's how we did it. The Conversation. <http://theconversation.com/after-the-bushfires-we-helped-choose-the-animals-and-plants-in-most-need-heres-how-we-did-it-138736> 13th July 2020.

Yang, L.H. & Gratton, C. (2014) Insects as drivers of ecosystem processes. *Current Opinion in Insect Science*, **2**, 26–32.

York, A. (1999) Long-term effects of frequent low-intensity burning on the abundance of litter-dwelling invertebrates in coastal blackbutt forests of Southeastern Australia. *Journal of Insect Conservation*, **3**, 191–199.

York, A. & Lewis, T. (2018) Understanding the effects of fire on invertebrates in Australian temperate and sub-tropical forests: the value of long-term experiments. *Australian Zoologist*, **39**, 633–645.

Yuan, D. & Rodriguez, J. (2020) Three new species of *Epipompilus* Kohl (Hymenoptera, Pompilidae, Pepsinae) from Australia. *Zootaxa*, **4743**, 575–584.

Zheng, G., Sedlacek, A.J., Aiken, A.C., Feng, Y., Watson, T.B., Raveh-Rubin, S., Uin, J., Lewis, E.R. & Wang, J. (2020) Long-range transported North American wildfire aerosols observed in marine boundary layer of eastern North Atlantic. *Environment International*, **139**, 105680.

Accepted 4 March 2021

Editor: Laurence Packer; Associate Editor: Myles Menz