


# Accounting for the neglected: Invertebrate species and the 2019–2020 Australian megafires

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## Abstract

**Aim:** Invertebrates make up the vast majority of fauna species but are often overlooked in impact assessment and conservation response. The extent to which the 2019–2020 Australian megafires overlapped with the range of vertebrate species has been well documented; consequently, substantial resourcing has been directed towards their recovery. Here, we attempt to document the extent of overlap of these megafires with invertebrate species. In doing so, we seek to demonstrate that it is possible and worthwhile to assess the effect of a catastrophic event on a large number of poorly known species.

**Location:** Temperate and subtropical Australia.

**Time period:** 2019–2020.

**Major taxa:** Australian invertebrates.

**Methods:** We adapted a published analytical pathway for the assessment of distributional fire overlap on vertebrate species. Overlaps with fire for 32,163 invertebrate taxa were determined using point records and polygons.

**Results:** We found that 13,581 invertebrate taxa had part of their range burnt in the 2019–2020 Australian megafires. Of these, 382 taxa had the whole of their known range burnt, and a further 405 taxa had 50–99.9% of their range burnt. Five examples are described.

**Main conclusions:** Poorly known groups of biodiversity can be impacted significantly by major disturbance events, but such impact is often overlooked. This oversight has the consequences of under-estimating the magnitude of impacts and the potential failure to direct conservation responses to those species most in need of them. Our analysis demonstrates that the 2019–2020 megafires burnt  $\geq 50\%$  of the known range of nearly 800 Australian invertebrate taxa, a tally far higher than for vertebrates (19 taxa). Assessment of the real impact (i.e., beyond simply overlap with fire) requires more consideration of susceptibility and/or post-fire survey and monitoring. The magnitude of overlap of the 2019–2020 megafires on invertebrate species justifies a conservation response that is less biased towards iconic vertebrate species.

## KEYWORDS

data deficiency, ecological disturbance, extinction, fire, threatened species

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## 1 | INTRODUCTION

Climate change is driving increasingly rapid gradational changes in many environmental factors, in addition to increasing the incidence and severity of major disturbance events (Canadell et al., 2021; IPCC [Intergovernmental Panel on Climate Change], 2022). To anticipate and try to mitigate or adapt to the ongoing effects of climate change on biodiversity, it is important to document the impact of major events as comprehensively as possible. In southern and eastern Australia, the series of mega-fires in 2019–2020 were unprecedented at the national and global scale (Boer et al., 2020; Bowman et al., 2020; Collins et al., 2021; Filkov et al., 2020). Notwithstanding their exceptionalism, the 2019–2020 fires formed part of a temporal pattern of increasing fire extent and severity in Australia and globally, with this pattern being linked to climate change (Canadell et al., 2021).

The 2019–2020 wildfires burnt large proportions of the ranges of many Australian plant and animal species and, because of direct mortality in fires and reduction in habitat suitability post-fire, it is likely that many of these species were severely impacted. For species with very high fire overlap, a large proportion of the population might have been killed and/or a large proportion of their habitat made unsuitable for surviving individuals and post-fire recovery, with responses to fire likely to vary among species. To date, such evidence has been documented mostly for vertebrates (Legge et al., 2021, 2022; Ward et al., 2020) and plants (Gallagher et al., 2022; Gallagher, Allen, et al., 2021). For example, Ward et al. (2020) compared the fire extent with the distributions of all 1,511 Australian vertebrate taxa occurring in a 2.2 million km<sup>2</sup> study area (defined by the exceptional extent of the 2019–2020 wildfires; Figure 1) and reported that 70 of these vertebrate taxa (including 21 already listed as threatened) had ≥30% of their distributional extent burnt by these fires. Based on such large distributional overlaps with fire, they concluded that these wildfires might have caused the imperilment of many vertebrate species not previously considered threatened.

In this paper, we seek to complement previous broad-scale assessments of the potential impacts of these fires on Australian plants and vertebrate species by providing a comparable assessment of the overlap of these fires with the far larger number of Australian invertebrate species. Relative to plant and vertebrate species, invertebrates are typically neglected in assessments of such major disturbance events, in part because they typically have a low public profile, because the number of species involved makes analyses formidable and because there are many major knowledge gaps (including taxonomic, ecological and distributional information) that constrain analyses and interpretation. However, we consider that it is important to attempt such an assessment for invertebrates because it allows for a far more comprehensive evaluation of the potential magnitude of impacts of the disturbance event and because, without such an assessment, conservation responses might be prioritized suboptimally to better-known species that have less conservation need. One of the outcomes we seek is to provide a listing of those invertebrate species that might have been most affected by these fires (here, in

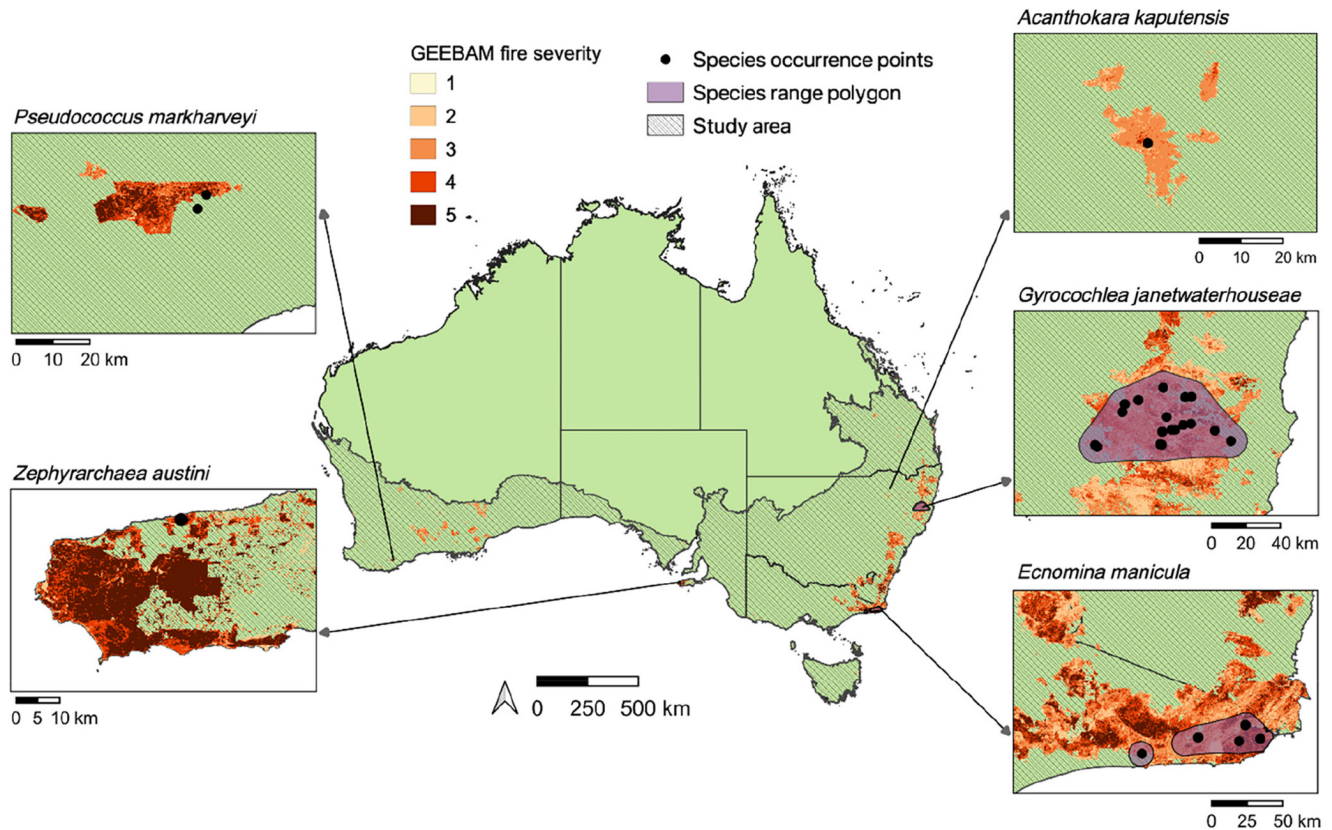
terms of distributional overlap) and therefore might be most in need of conservation responses. Our assessment is focused on the exceptional Australian wildfires of 2019–2020, but we consider that it can provide an example that can be applied for consideration of poorly known species in other major disturbance events.

There have been some published accounts of the intersection of the 2019–2020 megafires on Australian invertebrates; however, these have been restricted thus far to assessing fire overlap on limited subsets of invertebrate fauna, such as: 553 species of Australian bees (<.2% of the Australian invertebrate fauna) (Dorey et al., 2021); one genus of spiny crayfish, *Euastacus* spp. (57 species, <.02% of the Australian invertebrate fauna), within an assessment that focused mainly on vertebrates (Legge et al., 2021, 2022); 733 species across several invertebrate groups in New South Wales (.2% of the Australian invertebrate fauna) (Hyman et al., 2020); and 451 species listed as threatened under Australian national and state/territory legislation or by the IUCN (<.2% of the Australian invertebrate fauna) (Legge et al., 2021). Here, we replicate the vertebrate study by Ward et al. (2020) to conduct a large-scale assessment of fire overlap on Australia's invertebrate species, compare tallies of potentially fire-affected vertebrate and invertebrate species and note characteristics that might render invertebrates more likely to have been affected.

We expect that the magnitude of impact of these megafires might be greater for invertebrate fauna than for vertebrates. The number of invertebrate species in Australia (c. 320,000 species) far exceeds the number of vertebrates (c. 7,400 species) (Chapman, 2009); therefore, all else being equal, it is likely that far more invertebrate species would have their distribution overlapping with the 2019–2020 fires. Furthermore, many Australian invertebrate species are short-range endemics (Harvey, 2002; Harvey et al., 2011) and, being highly localized, might be particularly susceptible to having most or all of their range encompassed by a major disturbance event.

Consistent with the now widely recognized biases and shortcomings affecting knowledge and conservation of invertebrates globally (Cardoso et al., 2011; Régner et al., 2009, 2015) and in Australia (Braby, 2018; Taylor et al., 2018), there are numerous caveats to our assessment. First, knowledge of invertebrates suffers acutely from the "Linnean shortfall", which is the disparity between the number of formally described species and the number of species in existence (Lomolino et al., 2010). Most (c. 90%) of Australia's vertebrate species have been named, whereas only about one-third of Australia's invertebrate species have been described (Chapman, 2009). Hence, our assessment inevitably under-estimates the number of invertebrate species likely to have been overlapped by fire.

Second, much less is known about the distributions of invertebrate species than for vertebrate species (the "Wallacean shortfall"; Lomolino, 2004; Riddle et al., 2011). For example, we note that (as of January 2022) the average number of occurrence records per species in Australia's national biodiversity distributional database, the Atlas of Living Australia, is 42 for invertebrates versus 66,159 for birds. This paucity of records for invertebrate species adds substantial uncertainty and imprecision to our modelled distributions, hence to our estimates of their fire overlap.



**FIGURE 1** Map of the study area (shaded) defined as the bioregions that experienced exceptional wildfires in 2019–2020 (Ward et al., 2020). The map shows the fire extent, with severity indicated by increasingly darker shading (categories: 1 = no data; 2 = unburnt; 3 = low- and moderate-severity fire; 4 = high-severity fire, in which the vegetation is mostly scorched; and 5 = very high-severity fire, in which the canopy is consumed), and examples of fire overlap for four invertebrate species: *Acanthokara kaputensis* (a velvet worm), *Ecnomina manicula* (a caddisfly), *Gyrocochlea janetwaterhouseae* (Macleay Valley pinwheel snail), *Pseudococcus markharveyi* (*Banksia montana* mealybug) and *Zephyrarchaea austini* (Kangaroo Island assassin spider).

Third, although we follow Ward et al. (2020) in including a separate analysis for fire overlap of threatened species (recognizing that fire impacts might magnify pre-existing conservation insecurity for threatened species), our analyses do not adequately encompass the majority of imperilled invertebrate species. This is attributable to pervasive biases against the listing (as threatened) of Australian invertebrate species, with consequently, a very low proportion of invertebrate species being listed as threatened (Walsh et al., 2013). Furthermore, even among listed invertebrates, there is a general bias towards better-known or more charismatic taxa (Braby, 2018).

Fourth, there are major gaps in knowledge of the ecology of most Australian invertebrate species (the “Hutchinsonian shortfall”; Mokany & Ferrier, 2011). Although there is a substantial evidence base describing the response of Australian vertebrate species to fire (Whelan et al., 2002), far less is known about how fire affects invertebrate species (Saunders et al., 2021). Not all species are equally susceptible to fire, and there is likely to be marked variation among individual invertebrate species in their response; some might be far more susceptible and suffer greater impact, whereas others might benefit from fire (e.g., Bickel, 1996; Henry et al., 2022). We acknowledge that we limit our consideration explicitly to the extent of fire overlap in this study, rather than impact per se, which

we will consider further in a subsequent assessment. However, we note that many Australian invertebrate species are likely to be highly susceptible to severe wildfires because many occur in and are dependent upon highly flammable microhabitats (such as leaf litter and hollow logs) and because many have limited capability to escape fire (Moir, 2021; New, 1995). Furthermore, some phylogenetically ancient groups of invertebrates are characterized by species with now highly localized relictual distributions associated with habitats that typically provide refuge from fire (and many such areas were burnt in the 2019–2020 wildfires) (New, 1995; Rix & Harvey, 2012). Such fire-sensitive invertebrate species might not recover for many decades, if at all, following fire (Henry et al., 2022).

In this study, we describe an approach towards assessing the intercept of one exceptional season of fires on the distributional range of a large number of poorly known species. However, we acknowledge that species respond not only to single fire events but also to fire regimes (the temporal and spatial patterning of fires of varying intervals, extent, timing and severity). We restrict our consideration here to the single set of 2019–2020 megafires because we seek to counterpoint previous assessments of the extent of distributional overlaps of vertebrate species with these fires (Legge et al., 2021, 2022; Ward et al., 2020) and to address the need to

inform conservation response for supporting species recovery after the 2019–2020 wildfires. In doing so, we evaluate the total number of invertebrate taxa and the number of threatened invertebrate taxa whose distributions were burnt in the 2019–2020 wildfires and compare these tallies with those for vertebrate taxa. We also list invertebrate taxa with high distributional overlap with fire ( $\geq 50\%$  overlap with any fire, or  $\geq 30\%$  overlap with high-severity fire), as an initial step towards prioritizing conservation responses. We also provide some examples of species with high fire overlap and provide some interpretation of the potential consequences of such overlap.

## 2 | METHODS

### 2.1 | Species data

We collated records of terrestrial or freshwater invertebrates across a suite of distributional databases, including the Atlas of Living Australia, five state/territory databases, two museum databases and private data holders. Duplicate records arising from this collation were filtered out and taxon names matched to those given in the Australian Faunal Directory (AFD). We included specimen-based records only, because observational records have unacceptably low reliability for many taxa.

Similar to the approach taken by Ward et al. (2020) for vertebrate analyses, subspecies were included if these were recognized by the AFD, given that Australia's legislation for threatened species allows for listing of subspecies. Subspecies made up only a small proportion (1.7%) of the invertebrate taxa included in our assessment. We included undescribed taxa if these were classified to morphospecies and linked to specimens in a museum collection. These too made up only a small proportion (5.6%) of the taxa considered.

Records pre-dating 1990 were removed if a species had at least three post-1990 records, partly because earlier records typically lacked locational precision, and because we sought to consider only those records that were most likely to reflect current distributions (e.g., to avoid previously occupied sites from which native vegetation has subsequently been cleared). Owing to the limited number of records for most species, we accepted all valid records post-1990, notwithstanding differences in their locational precision. Records with more locational uncertainty are likely to have led to some reduction in the accuracy of our fire overlap assessments, although they will not have introduced any systematic bias.

This collation and sifting resulted in a dataset of 238,633 records of 32,163 taxa within the study area identified by Ward et al. (2020) and Legge et al. (2021), which encompassed regions with exceptional fire extent and severity in 2019–2020 (Figure 1). About half of the taxa for which we had records within the study area were represented by only one (11,749 taxa or 36.5% of all considered taxa) or two (4,671 taxa, 14.5%) records. Sixty-four terrestrial and freshwater invertebrate taxa are listed as threatened under Australia's national environmental legislation, of which 45 occur in the study area, and 41 of these had acceptable records in our cleaned dataset.

For the 15,743 taxa with three or more records, we fitted alpha hulls around records, with  $\alpha = 2$  (Burgman & Fox, 2003; IUCN Standards and Petitions Subcommittee, 2017), using the ConR package in R (v.1.3.0) (Dauby et al., 2017), and calculated the total area of this polygon. Note that records outside the study area were considered when creating the polygons such that a polygon described the entire Australian range of a taxon.

As further context for comparing the characteristics of fire overlap for invertebrate and vertebrate species, we compared polygon sizes for invertebrate taxa with those provided by Ward et al. (2020) for vertebrate taxa in the study area, using a Kolmogorov–Smirnov test. This comparison has some caveats, notably that vertebrate ranges were constructed using species distribution models rather than as alpha hulls and that the average number of records per vertebrate species is higher than for invertebrates. As a result, the estimated size of vertebrate ranges is likely to be larger than that of invertebrates. Conversely, many of the invertebrate taxa with fewer than three records, for which alpha hulls could not be created, are expected to have small ranges.

### 2.2 | Fire overlap

Fire severity obtained from the Australian Google Earth Engine Burnt Area Map (GEEBAM) (Department of Agriculture Water and the Environment, 2020) categorized the severity of the 2019–2020 wildfires into five classes, based on the extent to which the canopy was burnt: 1 = no data, 2 = unburnt, 3 = low- and moderate-severity fire, 4 = high-severity fire, in which the vegetation is mostly scorched and 5 = very high-severity fire, in which the canopy is consumed. The layer was resampled to 250m resolution and in Albers equal Area 137 projection (<https://spatialreference.org/ref/sr-org/australia-albers-equal-area-conic-134/>) and clipped to the study area, of which a total of c. 97,000 km<sup>2</sup> was burnt in the 2019–2020 fires (Ward et al., 2020). Although some invertebrate species do use cleared vegetation, many do not, and we restricted our analyses to consider impacts of fire only in areas of native vegetation. In order to do this, the GEEBAM layer was masked using the National Vegetation Information System (NVIS) dataset on the extent and distribution of vegetation types in Australian landscapes (Commonwealth of Australia, 2020). Following Legge et al. (2021), we calculate species distributional overlap with all fire categories (i.e., classes 3–5) and also with “high-severity” fire (classes 4 and 5) only. We undertook these two calculations (i.e., overlap with all fires and overlap only with fires of high severity) on the basis that some species might be affected by any fire (even mild fires), whereas others are likely to be impacted only (or much more so) by high-severity fires.

For taxa with more than two records, fire overlap was calculated using both point data (including records outside the study area; i.e., the total Australian range) and polygons. There are different assumptions and biases in the use of point data or polygons to estimate fire overlap. For example, point records might be greatly influenced by biases in collecting effort and are likely to represent a subsample of a

species' distribution. In contrast, polygons are likely to be less influenced by sampling biases but might encompass areas that are not occupied by the species, such as areas of unsuitable habitat. Polygons also cannot be calculated for species with only one or two records. We attempted to balance these biases by calculating fire overlap for points and for polygons and then averaging these overlap values. Although both approaches are imperfect, there is no a priori reason that they would introduce systematic biases in estimates of overlap with fire. We report on the extent to which fire overlaps calculated by points and by polygons are correlated across species. For taxa with only one or two records, we simply intercepted those point records with the fire coverage. For invertebrate taxa with at least three records, we also compare the overlaps estimated using point records and the overlaps using polygons, to investigate whether our consideration of point records in determining overlap might have led to biases that constrain comparison with the previous analyses of fire overlap for vertebrate species (Legge et al., 2021; Ward et al., 2020), which used polygons only rather than points.

### 3 | RESULTS

Fire overlap values calculated for individual species using their point records were highly correlated with corresponding values derived from their polygons ( $r = .73$ ,  $p < .0001$ , for all species with more than three records). Fire overlap values based on polygons were, on average, marginally larger than those derived for the same species using point records (mean overlap of 7.2 and 5.5%, respectively, across all species with more than three records), and this difference was highly significant (Wilcoxon matched-pair test,  $z = 52$ ,  $p < .0001$ ), with this significance largely attributable to the many more species with zero overlap in the points analysis.

A total of 13,581 species (42% of all invertebrate species considered in this study; i.e., with records in the study area) had at least some of their range burnt in the 2019–2020 Australian megafires. The entire known range of 382 species (1.2%) was burnt, with 193 of these entirely within the high-severity fires. It is important to note, however, that all these species were represented by only one or two records in our dataset. A further 31 species (.1%) had 80–99.9%

of their known ranges burnt (all of these being species with more than two records); 331 species (1.0%) had 50–79.9% of their known range burnt; and 489 species (1.5%) had 30–49.9% of their range burnt. Overlaps of species distributions with fire are summarized in Table 1, and species with >30% overlap are listed in the Supporting Information (Table S1). Examples of species with high fire overlap are illustrated in Figure 1.

Vastly more invertebrate species had high fire overlap than those reported for vertebrate taxa by Ward et al. (2020): of 1,511 vertebrate taxa in the study area, one taxon (.07% of all vertebrate taxa considered) had its entire known range burnt; two (.13%) had 80–99.9% of their range burnt; 16 (1.1%) had 50–79.9% of their range burnt; 51 (3.4%) had 30–49.9% of their range burnt; and 762 (50.4%) had some but <30% of their range burnt; and a total of 832 taxa (55.1%) had some overlap with fire. Invertebrate taxa had significantly smaller ranges (mean polygon size of 21,490 km<sup>2</sup>; median 3,286 km<sup>2</sup>) compared with vertebrate taxa (mean polygon size of 773,506 km<sup>2</sup>; median 204,020 km<sup>2</sup>) (Kolmogorov–Smirnov statistic,  $D = .575$ ,  $p < .0001$ ).

Of the 41 invertebrate taxa listed as nationally threatened and with records in the study area, two species [*Trioza barrettae* (*Banksia brownii* mealy bug) and *Pseudococcus markharveyi* (*Banksia montana* plant louse)] had 50–79.9% of their range burnt, three [*Bertmainius colonus* (Eastern Stirling Range pygmy trapdoor spider), *Leioproctus (Andrenopsis) douglasiellus* (a short-tongued bee) and *Euastacus dharawalus* (Fitzroy Falls crayfish)] had 30–49.9% burnt, 12 had some but <30% of their range burnt, and 24 had no fire overlap on their range. [Note that this assessment of overlap for *Pseudococcus markharveyi* was lower than the actual value (100%) because our analysis included some post-1990 records from locations at which the species was extirpated before the 2019–2020 wildfires.] These tallies are appreciably less than the overlaps reported by Ward et al. (2020) for the much larger number (243) of threatened vertebrate taxa in the study area, although the proportions are comparable: two threatened vertebrate taxa had 80–99.9% of their range burnt, nine had 50–79.9% burnt, 10 had 30–49.9% burnt, and 87 had some but <30% of their range burnt.

Invertebrate species with >30% of their range burnt belonged to a wide range of taxonomic groups, including ≥55 orders (Table 2;

TABLE 1 Tallies of distributional overlaps with fire of any severity and with high-severity fire for invertebrate taxa in the study area

Percentage overlap with all fire	Percentage overlap with high-severity fire						Number of taxa
	100	80–99.9	50–79.9	30–49.9	>0–29.9	0	
100	193 (0)	0	23 (0)	0	0	166 (0)	382 (0)
80–99.9	–	0	19 (19)	10 (10)	2 (2)	0	31 (31)
50–79.9	–	–	125 (23)	83 (83)	66 (66)	100 (0)	374 (172)
30–49.9	–	–	–	81 (81)	408 (408)	0	489 (489)
>0–29.9	–	–	–	–	11,272 (11,272)	1,033 (1,033)	12,305 (12,305)
Number of taxa	193 (0)	0	167 (42)	174 (174)	11,748 (11,748)	1,299 (1,033)	13,581 (12,997)

Note: Tallies in parentheses are for taxa with more than two records. Note that the percentage overlap bounds correspond nominally to proportional loss thresholds for listing of species under various conservation statuses.

TABLE 2 Taxonomic groups with  $\geq 20$  taxa that had  $\geq 30\%$  distributional overlaps with fire

Class	Order	Number of taxa with $\geq 30\%$ fire overlap
Insecta	Coleoptera	334
Insecta	Diptera	243
Insecta	Lepidoptera	241
Arachnida	Araneae	186
Insecta	Hymenoptera	128
Gastropoda	Stylommatophora	79
Insecta	Hemiptera	45
Insecta	Trichoptera	37
Diplopoda	Polydesmida	34
Arachnida	Trombidiformes	25
Oligochaeta	-	21
Insecta	Plecoptera	20

Supporting Information Table S1). The insect orders Coleoptera, Diptera, Lepidoptera and Hymenoptera and the arachnid order Araneae had the highest number of species with a high overlap with fire.

## 4 | DISCUSSION

Our analysis demonstrated that most of the known distributions of many hundreds of invertebrate species were burnt, often at high severity, in the Australian 2019–2020 megafires. For many of these species, it is likely that such extreme disturbance caused major population losses. This analysis suggests that the potential magnitude of the impacts of these fires on biodiversity was far larger than that reported based on assessments of better-known taxonomic groups alone. Therefore, the allocation of conservation (recovery) resources mostly to fire-affected species in such better-known groups might not reflect the highest priority conservation needs. We consider it likely that this might be typical of conservation assessment and recovery in the wake of any major disturbance event: poorly known species tend to be neglected, but might well have suffered the greatest impact and might most need conservation support.

This was evident in the wake of the catastrophic 2019–2020 Australian megafires. Rapid assessments undertaken soon after the fires demonstrated potentially major impacts on many Australian vertebrate species (Legge et al., 2021; Ward et al., 2020). That documentation, and widespread public concern about impacts on iconic wildlife species, stimulated urgent conservation responses by governments and non-government organizations to implement recovery efforts for prioritized vertebrate species. For example, the Australian government contributed AUD12 million specifically towards the recovery of fire-affected populations of the koala, *Phascolarctos cinereus*, for which fire overlapped 17% of its distribution (Legge et al., 2021), and a further AUD 10 million to the recovery

of another set of 10 prioritized vertebrate species (Block et al., [In press](#)). Undoubtedly, such responses have conservation benefits. However, the response for the entire set of fire-affected invertebrate species has been far less substantial. It is likely that such relative neglect is pervasive for all poorly known taxa and for those with limited perceived public appeal, in general and after catastrophic events specifically. We cannot estimate reliably how much allocation is needed to support the recovery of all the invertebrate species most affected by the 2019–2020 wildfires. However, we note that some relevant projects funded by the Australian government include c. AUD270,000 for management responses for a set of three stonefly species, c. AUD 100,000 for one bee species, c. AUD340,000 for a set of 18 land snail species, and c. AUD 145,000 for one fire-affected butterfly species. These resource contributions will provide significant conservation benefits for these fire-affected species and can be used to provide a very crude estimate of how much might be required to support the conservation of all fire-affected invertebrate species. If the average of c. AUD 37,000 per species included in these projects represents what might be needed for the most fire-affected species, and we found that 787 species had most of their range burnt (and might therefore have been substantially affected), then c. AUD300 million might be required to recover the full set of these invertebrate species, a tally far higher than the total allocated to biodiversity recovery after these fires. Of course, we recognize this figure is highly conjectural, and there are probably many efficiencies that can be made through conservation management of co-occurring species.

We show that, potentially, far more invertebrate than vertebrate species were affected by the 2019–2020 fires, with many more of these invertebrate species having all or most of their known range burnt. These results are consistent with, and provide a substantial expansion from, previously published studies on smaller subsets of the Australian invertebrate fauna (Dorey et al., 2021; Hyman et al., 2020). Furthermore, given that most Australian invertebrates are undescribed, hence not included in our assessment, it is likely that the number of invertebrate species affected by these fires is much higher than the tally we derived.

We also found that the use of point records (solely for species with fewer than three records, or averaged with polygon overlaps for species with more than two records) in our calculations of fire overlap is unlikely to have inflated the number of fire-affected invertebrate species relative to fire-affected vertebrate species [for which previous analyses used only modelled (polygon) distributions to calculate overlap], given that, across species, we found overlap values based only on point records to be significantly less than those based only on polygons.

Why is it that many more invertebrate species were impacted by these fires than vertebrate species? A simple reason is that there are far more invertebrate species. Additionally, the number of invertebrate species with  $\geq 50\%$  of their range burnt (787) represents a higher proportion of the tally of invertebrate species with records in the study area ( $787/32,163 = 2.4\%$ ) than is the case for vertebrates ( $19/1,501 = 1.3\%$ ). For some species, this apparent range

restriction is likely to be an artefact of collection effort or because species are hard to find (e.g., cryptic species, species with life stages beneath ground, or seasonally inactive species). However, short-range endemism is a characteristic of many Australian invertebrates (Harvey, 2002; Harvey et al., 2011; Taylor et al., 2018), and for such species, a disturbance event is more likely to encompass all or a substantial proportion of a species' range than for those with larger ranges.

The Australian 2019–2020 megafires burnt many important known centres of endemism for Australian invertebrates (Harvey et al., 2011), in addition to many sites known to be important refugial areas for species with marked susceptibility to fire. These include the Stirling Range in Western Australia, the Gondwanan rainforests of eastern Australia, Kangaroo Island, and isolated altitudinal refuges, such as Mount Kaputar and parts of the Australian alpine region. Given that many fire-sensitive invertebrate species are restricted to such centres of endemism and that many of these areas were extensively burnt in the 2019–2020 wildfires, there is now an urgent need to safeguard such areas better, in order to maintain and protect any unburnt patches and to reduce the likelihood that they will be affected extensively by comparable fires in the future.

Many of the invertebrate species that we found to have very high fire overlap were those with apparently restricted ranges. An extreme example of the impact of fire on a short-range endemic species is the *Banksia montana* mealybug, *Pseudococcus markharveyi*, whose entire population immediately before the 2019–2020 wildfires was restricted to six shrubs of its host plant species on one hilltop in south-western Australia (Figure 1). All these shrubs were killed by the 2019–2020 wildfires, leading to the presumed extinction of this host-plant-specific invertebrate species (Moir, 2021). Relative to most other Australian invertebrate species, this was a well-studied species subject to some conservation management. There is considerable risk that many of the more poorly known species, which our analyses found to have had the whole of their known range burnt by the 2019–2020 wildfires, might also have become extinct.

Before the 2019–2020 fires, the Kangaroo Island assassin spider, *Zephyrarchaea austini*, was known from only one site on Kangaroo Island, South Australia, which was impacted in its entirety in 2019 by high-severity fire (Figure 1). The species lives in leaf litter suspended in low-level vegetation, a feature of long-unburnt vegetation and a habitat that is highly flammable. Extensive targeted post-fire surveys have so far located only one surviving population, in an unburnt remnant c. 4 km from the original site (Marsh & Glatz, *In Press*). The species has since been listed as Critically Endangered under the Australian Federal Government's Environment Protection and Biodiversity Conservation Act (EPBC Act).

We know much less about most of the other species illustrated in Figure 1, further constraining our assessment of these species and hampering conservation response. The velvet worm *Acanthokara kaputensis* (Phylum Onychophora) is a narrowly endemic species known only from Mount Kaputar, New South Wales, an extinct volcano recognized as an isolated, high-elevation climatic refuge and an important hotspot for many narrowly endemic invertebrate species

(Murphy et al., 2019). Our analysis showed that its single known locality was burnt at high severity in the 2019–2020 wildfires. Little is known of its ecology other than that it has been recorded only from rotting logs (Reid, 1996), a microhabitat very likely to be destroyed in wildfires. Furthermore, the post-fire habitat is likely to offer little shelter for any individuals that might have survived the fire, and onychophorans might be particularly susceptible to burnt landscapes because they are prone to desiccation (Ruhberg & Hamer, 2005). As a group they also have very limited dispersal ability (Ruhberg & Hamer, 2005); therefore, even if any individuals survived in unburnt patches their recovery back to burnt areas is likely to be very slow.

Although not so localized as the previously discussed species, the land snail *Gyrocochlea janetwaterhouseae* also has a restricted distribution. We found that 63% of its range was burnt (with 25% at high severity). It shelters under logs, hence some populations might have survived mild fires, but probably not high-severity fires.

The caddisfly *Ecnomina manicula* (Trichoptera) occurs in a restricted area in Victoria. Our analyses showed that 75% of the species range was burnt (21% at high severity). Like most caddisflies, nymphs are aquatic and adults terrestrial. Fires impact freshwater systems through sedimentation, increased nutrient input, phytoplankton growth and eutrophication, and these effects can spread beyond the area directly impacted by fire (New, 2020).

Although the examples described above indicate that many species with high fire overlap are likely to have been severely impacted by these fires, this is not necessarily the case for all species. Some invertebrate species might benefit from fire or be unaffected by it (Bradstock, 2008; Saunders et al., 2021) and, as such, high fire overlap does not necessarily represent cause for conservation concern. Although our results demonstrate the potential impacts of these wildfires on many Australian invertebrate species, further survey, research and assessment are needed to provide a more robust assessment of impact and to provide insights for conservation planning to help recover the most fire-affected species. Such considerations are summarized in Table 3 and in some recommendations below in light of our findings (see also Table 3). We note that these issues related to defining and responding to impact are likely to apply to comparable conservation situations globally.

First, we note that the responses of individual species to fire and to fires of varying severity are related to ecological and life-history characteristics of the species, and several studies have used frameworks of traits to evaluate the likely impacts of fires on plant species (Gallagher et al., 2022; Gallagher, Allen, et al., 2021; Gallagher, Butt, et al., 2021) and vertebrate species (Legge et al., 2021). Therefore, for invertebrate species with high fire overlap, we recommend the development and application of a trait database that can be used to evaluate species' relative susceptibility to fire, hence (when combined with fire overlap) to provide a more robust assessment of the likely impact of the fires. We acknowledge that building a trait database will be challenging for many invertebrate species that have no relevant ecological studies, but we argue that such an assessment can be used to highlight these knowledge gaps and aid the prioritization of research. Given predictions of increasing fire severity with

**TABLE 3** Beyond assessment of fire overlap alone: A framework of actions to improve assessment of, and responses to, the impacts of catastrophic disturbance events on poorly known species

Action	Rationale
Develop and apply a species database of ecological and life-history traits that can be used to infer likely responses of (impact on) species to disturbance	Species will vary in their responses to any disturbance event, with such variation mostly attributable to characteristics of their ecology and life history. When combined with data on the range overlap with a disturbance event, such trait information can be used to estimate the impact and might also help to provide direction for conservation management responses
Undertake targeted surveys to refine estimates of population losses and to attempt to locate any important surviving populations	Extinction might be averted if, after severe disturbance events affecting most of the population of a species, any surviving population is located and protected. Such survey effort might also help to clarify and refine estimates of impacts
List the severely affected species as threatened, where appropriate using the precautionary principle for poorly known species	Listing as threatened those species that have been severely affected by a major disturbance event helps to recognize formally the magnitude of impacts and might proffer some conservation recognition and benefit to the affected species
Implement conservation management responses for affected species	Species severely affected by a major disturbance event might need targeted management response to enable recovery
Undertake targeted research to fill key knowledge gaps	Knowledge acquisition from targeted research (before and after disturbance) on poorly known species will allow for more informed assessments of impacts and will also help to guide and assess post-disturbance recovery
Identify and increase protection for areas where many susceptible species co-occur, such as centres of endemism for short-range endemics and refugial areas	Some locations are likely to be critical for the survival of many poorly known species, and such sites should be managed appropriately to try to reduce the likelihood of major disturbance events
Help engender more public support for the conservation of poorly known and uncharismatic species that might have suffered severe impacts	Recovery efforts after disturbance will continue to be biased to more charismatic species, hence suboptimal, if there is not more public and political recognition that poorly known species have also been affected

climate change (Canadell et al., 2021), it is likely to become increasingly important that we also gain a better understanding of the varying effect of fires of different severity on taxa.

Second, we recognize that there is considerable uncertainty in our evaluation of fire overlap for invertebrate species with few records. Further surveys are a priority for such species, targeting unburnt areas that are comparable to the burnt areas in the 2019–2020 wildfires. Surveys of burnt areas to establish whether specific populations have survived the fire are also needed urgently for all species showing high overlap in our analyses.

Third, many of the species most affected by the 2019–2020 wildfires were short-range endemic species that might well have been imperilled before the 2019–2020 fires and are now much more likely to be so after the fires. However, recognition of threatened status for invertebrates has been much neglected, in part because of data deficiencies. Listing is currently being implemented for many vertebrate species affected by the 2019–2020 Australian wildfires (Legge et al., 2022) and for a small number of the invertebrate species showing high fire overlap in our study. Listing provides recognition of conservation concern and some possibility of prioritization for conservation response, and we therefore recommend a far more comprehensive consideration of listing for the vastly greater number of invertebrate species likely to have been affected by these fires. For species likely to have suffered severe impacts in catastrophic events such as the 2019–2020 wildfires, but for which the knowledge base

is very limited, the precautionary principle should be applied, rather than ignoring potentially affected species owing to data deficiencies.

Notwithstanding the paucity of ecological knowledge for many fire-affected invertebrate species, we propose that there are clear and urgent management actions that can be implemented and that need to be implemented now to support species recovery. For those species shown here to have had much of their range burnt (1,426 with >30% of their range burnt) in the 2019–2020 wildfires, there is an urgent need to reduce the risks of subsequent fire within known burnt ranges and to provide protection for any unburnt patches. For species for which other threats are known to compound the impacts of fire (such as habitat degradation owing to exotic weeds; e.g., Marsh, 2021), targeted actions to mitigate these threats are required, and the implementation of such actions should be accompanied by monitoring programmes that can evaluate and hone those actions.

Our assessment demonstrates that it is possible to undertake some analysis of the magnitude of distributional overlap with a major disturbance event across a large number of poorly known species. However, we recognize that more information on taxonomy, distribution and ecology would allow for a more robust evaluation. Data-deficient species are challenging to conserve (Jetz & Freckleton, 2015), and an obvious response is to support further targeted research that addresses key knowledge gaps.

We also note that our assessment is focused on individual species, but there is likely to be considerable efficiency in managing



groups of species and habitats, especially where many short-range endemic species co-occur, and in areas that normally provide some refuge from disturbance. Severe disturbance events in such areas might have disproportionately large impacts on many co-occurring species because the entire populations might be narrowly confined in such areas. We suggest identifying, formally protecting and intensely managing such areas as a conservation priority.

As is typical of conservation efforts generally, the conservation response to the 2019–2020 wildfires in Australia was biased to iconic species and those with wide public appeal. The better inclusion of a greater component of biodiversity will require resourcing, and this figure will need to be commensurate with the task required. We argue that the potential magnitude of the impacts of the 2019–2020 wildfires on invertebrate species justifies such resourcing and a more comprehensive and encompassing response, in order to include all severely affected species that are now rendered most imperilled by these fires.

We recognize that any such conservation actions taken to recover invertebrates affected by these megafires will deliver benefits. However, such actions might be futile if comparable severe fires recur before recovery can be achieved. In such case, losses will not be transient, but rather compounding and enduring. Climate change is leading to an increased frequency of such megafires (Canadell et al., 2021) and other catastrophic disturbance events. It is important that there is some accounting of the costs of such events on all components of biodiversity. Losses of the magnitude indicated here will become more frequent unless climate change can be constrained.

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## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available on Zenodo at <https://doi.org/10.5281/zenodo.6395707>. GitHub

repository for R scripts used for the analysis is available at <https://doi.org/10.5281/zenodo.5775361>.

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## BIOSKETCH

**Jessica R. Marsh** (lead author) is a researcher with interests in the fields of arachnology, entomology, taxonomy, invertebrate fire ecology and conservation biology. Her current research focuses on the use of trait-based systems to predict invertebrate susceptibility to fire and on the taxonomy and systematics of spiders.

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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