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Review

Coextinction of *Pseudococcus markharveyi* (Hemiptera: Pseudococcidae): a case study in the modern insect extinction crisis

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Abstract The majority of modern insect extinctions are likely unrecorded, despite increasing concern for this hyperdiverse group. This is because they are either yet to be discovered and described, their distributions and host associations are poorly known, or data are too sparse to detect declines in populations. Here, I outline the likely extinction of an Australian mealybug, *Pseudococcus markharveyi* Gullan 2013, which was discovered and described less than 15 years ago but was highlighted recently as one of five most threatened invertebrates in Australia from recent bushfires. The synergistic threats of dieback disease (*Phytophthora cinnamomi* Rands 1922) and inappropriate fire regime as a consequence of climate change have decimated host plant populations of the critically endangered *Banksia montana* (George 1996) Mast & Thiele 2007 and the montane habitat of both organisms, thereby leading to the coextinction of the mealybug. Its loss occurred despite attempts at conservation management and illustrates the general insect extinction crisis that Australia, and the world, is facing. The majority of Australian mealybugs are not receiving the same attention as *P. markharveyi*. Many poorly known species either remain undetected, without formal names, or data on their distribution, abundance and critical habitat are too scant to assess their conservation status. I also discuss the diversity of Australian mealybugs more generally and their need for conservation.

Key words climate change, coextinction, inappropriate fire regime, insect Armageddon, insect–plant interactions, Stirling Range National Park.

INTRODUCTION

The majority of invertebrate extinctions are almost certainly unrecorded, despite increasing concern for this hyperdiverse group as a major part of the sixth mass extinction (Dunn 2005; Braby 2019; Sanchez-Bayo & Wyckhuys 2019; van Klink *et al*. 2020). Régnier *et al*. (2015), for example, demonstrated that we may have already lost 7% of all land snail species, two orders of magnitude greater than the officially recorded 0.04% of the current IUCN Red List. This is because they remain undiscovered, their ecologies are poorly known, spatial and temporal survey data are inadequate to record declines in populations, or current threat assessment criteria are not easily applied to the data that are available (Cardoso *et al*. 2011a, 2011b; Moir & Brennan 2020). This bias means that declines in common widespread species are being used to highlight the potential mass extinction, particularly for insects (Sanchez-Bayo & Wyckhuys 2019; Wagner 2020; Sánchez-Bayo & Wyckhuys 2021).

Some invertebrates have the additional misfortune of being considered expendable by humankind, for example, the parasites of mammals (see Carlson *et al*. 2020). This misfortune is the case for the mealybugs (Hemiptera: Pseudococcidae), insect herbivores, which are most familiar for their pest status on domesticated plants (Miller *et al*. 2002; Hardy *et al*. 2008). The family certainly contains many economically important pest species such as the cotton mealybug, *Phenacoccus solenopsis* Tinsley 1898, long-tailed mealybug, *Pseudococcus longispinus* (Targioni Tozzetti 1867), and citrus mealybug, *Planococcus citri* (Risso 1813), and so are often targeted for control (e.g. Moore 1988). Rarely are mealybugs considered in the context of conservation, yet some species are threatened with extinction. Two Hawaiian mealybug extinctions have been documented, likely due to reductions in host plant densities (IUCN 2020). Mealybugs also provide important ecological roles through the provision of excreted honeydew, which is an energy rich food for many other invertebrates (Moir *et al*. 2018) and fungi. For example, the critically endangered South African butterfly *Chrysoritis dicksoni* (Gabriel) depends on a dual mutualism between ants and Coccomorpha (scale insects), including several species of Pseudococcidae, for honeydew, which is essential for its survival (Giliomee & Edge 2015).

In this overview, I outline the Pseudococcidae diversity in Australia and detail a likely third global recorded mealybug extinction from this fauna – *Pseudococcus markharveyi* Gullan. This small pinkish mealybug was discovered as recently as 2007 (Moir *et al*. 2012) and described 6 years later (Gullan *et al*. 2013). In 2019–2020, it likely suffered coextinction (loss of a dependent species with loss or reduction in host species populations), a mere 13 years after its discovery. Following the example of *P. markharveyi*, I consider the threatened status of Pseudococcidae in Australia.

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PSEUDOCOCCIDAE DIVERSITY IN AUSTRALIA

The pseudococcid diversity of Australia consists of 210 described species, about 10% of the global fauna of 2143 described species (Deng *et al*. 2016; García Morales *et al*. 2016). However, only 171 of the 210 are native to Australia, as the remaining 39 species (18.5%) are potentially introduced (Fig. 1). Interestingly, the first documented incursion of an exotic species was *Pseudococcus viburni* (Signoret) (obscure mealybug or tuber mealybug) found on Dahlia tubers (Fig. 2). Once considered an Australian species, later assessment of its natural parasitoids indicates that it is of South American origin (Charles 2011). The early finding of *P. viburni* on the tubers of an exotic plant underscores the cryptic nature of many Pseudococcidae, which increases their potential to be transported and introduced anthropogenically to new regions (Miller *et al*. 2002; Hardy *et al*. 2008), but also has implications for their detectability during surveys of native habitats.

Discovery rates of new taxa are dictated by the quantum of species remaining to be found, as well as the effort devoted to collecting and describing them (Bebber *et al*. 2007). The largest descriptive contribution to the Australian pseudococcid fauna occurred when Williams (1985) described 124 native species. In the prior 130 years, only 34 Australian species had been described (Fig. 2). Thus, one dedicated taxonomist can greatly increase the rate of species descriptions in a short period of time, a phenomenon that appears common with Pseudococcidae; for example, in New Zealand, 67 new species were added to the 47 known species in a single publication (Cox 1987). These peaks in species descriptions are problematic for estimations of the true diversity of a region. Both prior to and after 1985, descriptions of Australian pseudococcids were plateauing, suggesting that the diversity had mostly been described (Fig. 2). The prior attenuation was clearly false, being an artefact of the relative paucity of taxonomic work (e.g. Polhemus & Polhemus 2007). However, it is likely that the post-1985 plateau may also be misleading, with many more undescribed species existing due to both a lack of a dedicated taxonomist and under-collecting (see impediments to invertebrate knowledge outlined by Cardoso *et al*. 2011b). In fact, an estimated one-third of all Coccoidea remain undescribed (Deng *et al*. 2016), extrapolating to approximately 1070 undocumented Pseudococcidae species globally.

Collecting facilitates the 'discovery' of new species. If common and abundant species have a higher detection probability than rare or restricted species (McCarthy *et al*. 2013), then the 171 native Australian species described to date are more likely abundant, polyphagous, or encompass broad geographical ranges (e.g. Collen *et al*. 2004). To find the rarer species, well-designed surveys temporally, spatially, considering ecological niches and utilising a variety of collection methods need to be employed. Studies of other rare taxa demonstrate that modifications to typical biodiversity surveys are required to increase the likelihood of detection, for example, using detection dogs to locate rare plants (Bennett *et al*. 2020). The remaining undescribed Pseudococcidae are likely rarer taxa from the understudied regions of the Palaeotropics and Southern Hemisphere (Hardy 2013). Indeed, during a 4-month survey of 104 plant species which uncovered *P. markharveyi* in the biodiversity hotspot of the south-west of Australia, a total of 21 pseudococcid species were found, of which 90% (19 species) were undescribed (Moir, unpublished data).

PSEUDOCOCCUS MARKHARVEYI

Distribution, biology and critical habitat

Pseudococcus markharveyi (Fig. 3b,c) is a short-range endemic species restricted to its host plant *Banksia montana* (Gardner ex George) Mast & Thiele (Fig. 3a). *Banksia montana* is a large shrub that is confined to the high summits (>900 m above sea level) of the eastern massif of the Stirling Range National Park in the south-west of Australia (Fig. 4). Due to multiple threats including an inappropriate fire regime and the exotic root pathogen

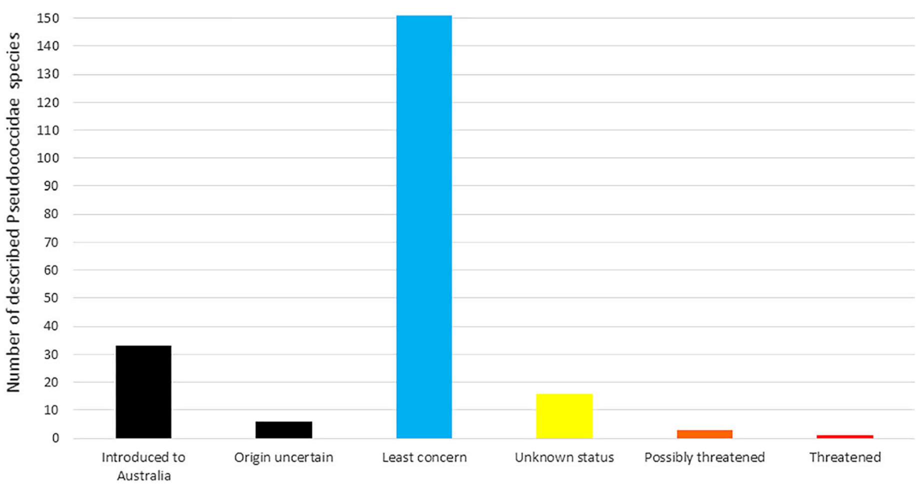

Fig 1. The likely conservation status of described species of Pseudococcidae present in Australia. Black columns represent potentially exotic species.

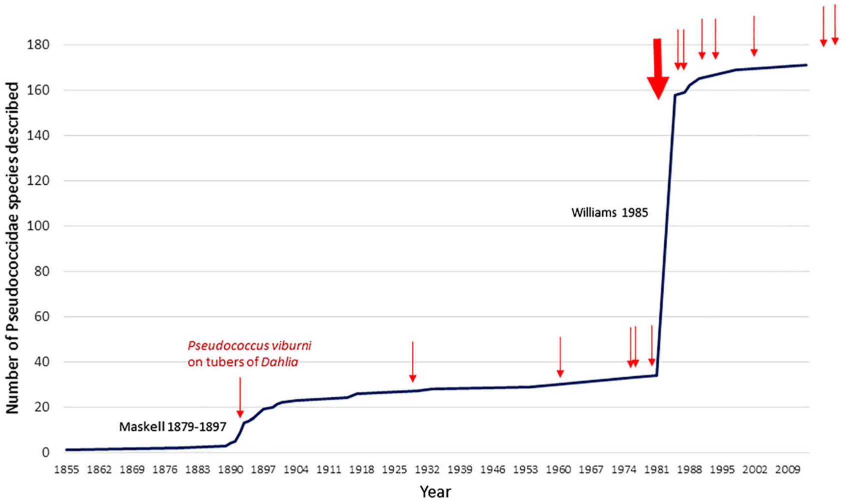

Fig 2. Cumulative native Australian Pseudococcidae species descriptions over time. Red arrows indicate a new record for an exotic species of Pseudococcidae in Australia. The taxonomists responsible for the largest increases in descriptions are listed in black. Data from García Morales *et al* (2016).

Fig 3. The study organisms of (a) an isolated individual of *Banksia montana*, the host of *Pseudococcus markharveyi*, on Bluff Knoll, November 2007; (b and c) *Pseudococcus markharveyi* photographed within insect bags on recipient *B. montana* at the translocation site, October 2014.

Phytophthora cinnamomi, *B. montana* is classified a critically endangered species and exists within a critically endangered threatened ecological community (Western Australian *Biodiversity Conservation Act 2016*). This banksia is an obligate seeder, which is killed by fire and relies on seeds in the seedbank to replenish populations (Gilfillan *et al*. 2008). Known as the '*Banksia montana* mealybug', *P. markharveyi* overwinters as eggs, with first instar nymphs emerging in September–October (spring), and adult females evident by December (summer). A second generation possibly occurs in late summer to autumn, but this requires confirmation. Males are unknown.

In 2007, mealybugs were found on one population of *B. montana* at Pyungorup Peak (on 6 of 9 plants examined) and from a single old large isolated *B. montana* on Bluff Knoll (on 1 of 7 plants examined; Fig. 3a) (Moir 2015; Moir & Leng 2015). Surveys of the Hemiptera of *Banksia* over 18 years in the south-west (including the only two sister taxa of *B. montana*: *Banksia pseudoplumosa* (George 1996) Mast &

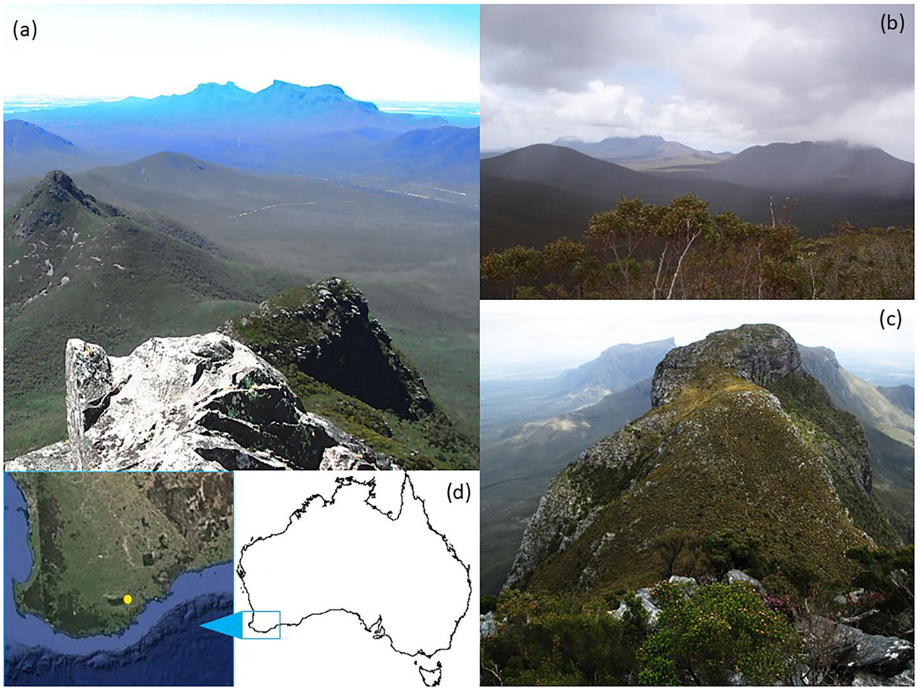

Fig 4. The Stirling Range National Park, Western Australia showing (a) the eastern massif in the far distance, the peaks of which feature the globally restricted distribution of *Banksia montana* and *Pseudococcus markharveyi* (taken from Mt Toolbrunup, 2015); (b) the eastern massif in the far distance with the peaks shrouded in cloud demonstrating how the montane habitat maintains higher levels of humidity than the surrounding areas (taken from Mt Hassel, 2013); and (c) the view on the eastern massif from Ellen Peak (2015), the easternmost peak. Pyungorup is the rounded dome in the foreground, and Bluff Knoll is the sharp triangular peak at the top left. (d) The location of the eastern massif represented by a yellow dot, within Australia (Google Earth 2020).

Thiele 2007 and *Banksia plumosa* (R.Br. 1810) Mast & Thiele 2007) and in the eastern states of Australia have failed to locate any further host species (e.g. Vesk *et al*. 2010; Moir *et al*. 2011a; Moir *et al*. 2012). The mealybug was initially detected on Bluff Knoll, residing deep within developing flower heads of *B. montana*, alerted by the proliferation of predatory ladybird beetles (Coccinellidae) that were attracted to the flower heads and feeding on the mealybug. The discovery was fortuitous as a project to document the insect communities of threatened plants using vacuum sampling had not detected *P. markharveyi*, evidently because they were unable to be dislodged by vacuuming.

The two populations of the mealybugs on Bluff Knoll and Pyungorup Peak were approximately 7 km apart, across the eastern massif ridge (Fig. 4c), and there were no genetic differences between them based on the mitochondrial CO1 gene (Gullan *et al*. 2013). The populations were likely once part of a continuous thicket of montane heath, which stretched across the eastern massif of the Stirling Range. Plant dieback, caused by the oomycete *P. cinnamomi*, and fire have recently (~20 years) further fragmented the vegetation (Barrett & Yates 2015), and small stands or single *B. montana* individuals remain scattered across the peaks between Bluff Knoll and Pyungorup Peak (Gilfillan *et al*. 2008). After a fire event, it can take 30 years for the montane thicket to return to its former height and density (Monks *et al*. 2019) and at least 9 years for plants of *B. montana* that have germinated after the fire to reach maturity (Gilfillan *et al*. 2008). The recommended fire interval for *B. montana* is at least 18 years (Gilfillan *et al*. 2008), which coincides with other estimates for lowland biodiverse heathlands of the southwest, with some regions such as the Fitzgerald River National Park estimated to have had much longer intervals between fire before the arrival of humans, including aboriginal people (Bradshaw *et al*. 2018).

By the time of its discovery in 2007, the distance between extant populations of *P. markharveyi* was likely preventing dispersal of individuals between them. Indeed, at Bluff Knoll, the mealybug remained on the oldest *B. montana*, which had escaped the last fire in 2000 (i.e. Monks *et al*. 2019). Presumably, *P. markharveyi* was not able to colonise younger host plants on Bluff Knoll, despite the time that had lapsed since the last fire and the relatively small interplant distance (90–250 m; see Fig. 3a). Despite the scattered individual plants remaining across the eastern massif, only the populations at Bluff Knoll and Pyungorup Peak were surveyed for *P. markharveyi* before 2019.

Gullan *et al*. (2013) suggested that another population of *P. markharveyi* may occur in the Fitzgerald River National Park, approximately 135 km to the east, represented by specimens collected in 1985 on *Banksia heliantha* Mast & Thiele. Multiple attempts between 2012 and 2020 to recollect Fitzgerald River specimens for molecular work did not yield adult specimens; however, some Pseudococcidae nymphs were recovered from *B. heliantha* in the same area as the 1985 collection. A genetic comparison of these nymphs with *P. markharveyi* indicated that they were different species, based on molecular markers from both mitochondrial and nuclear DNA (L Cook pers. comm. 2020). Resampling of adult female Pseudococcidae from *B. heliantha* is still required to rule out a third population of *P. markharveyi*.

Conservation status and management

By 2012, *P. markharveyi* (then designated as *Pseudococcus* sp. 15) was identified as likely cothreatened (Moir *et al.* 2012), and plans were underway to translocate it to a new site approximately 30 km south of the Stirling Range National Park for conservation management, despite active efforts to maintain populations *in situ* (for a summary of these actions, see Fig. 5). *Banksia montana* had been established at this location 9 years prior to the translocation of *P. markharveyi* and were large healthy plants (Moir et *al.* 2012). In October 2012, translocations of first and second instar mealybugs into insect rearing bags on *B. montana* occurred from the source population at Bluff Knoll (Moir & Leng 2013). The recipient plants were first vacuumed of all invertebrates to remove competitors, parasitoids and predators before the bags were placed on branches. The insect bags served the dual function of protecting *P. markharveyi* from predators and parasitoids and confining them to allow easier detection in future surveys. Two months after the translocation, when the mealybugs should have become adult females, no specimens were found, and the initial translocation using early instars was deemed a failure. It was possible that the early instars were more prone to desiccation and could not adapt to the drier

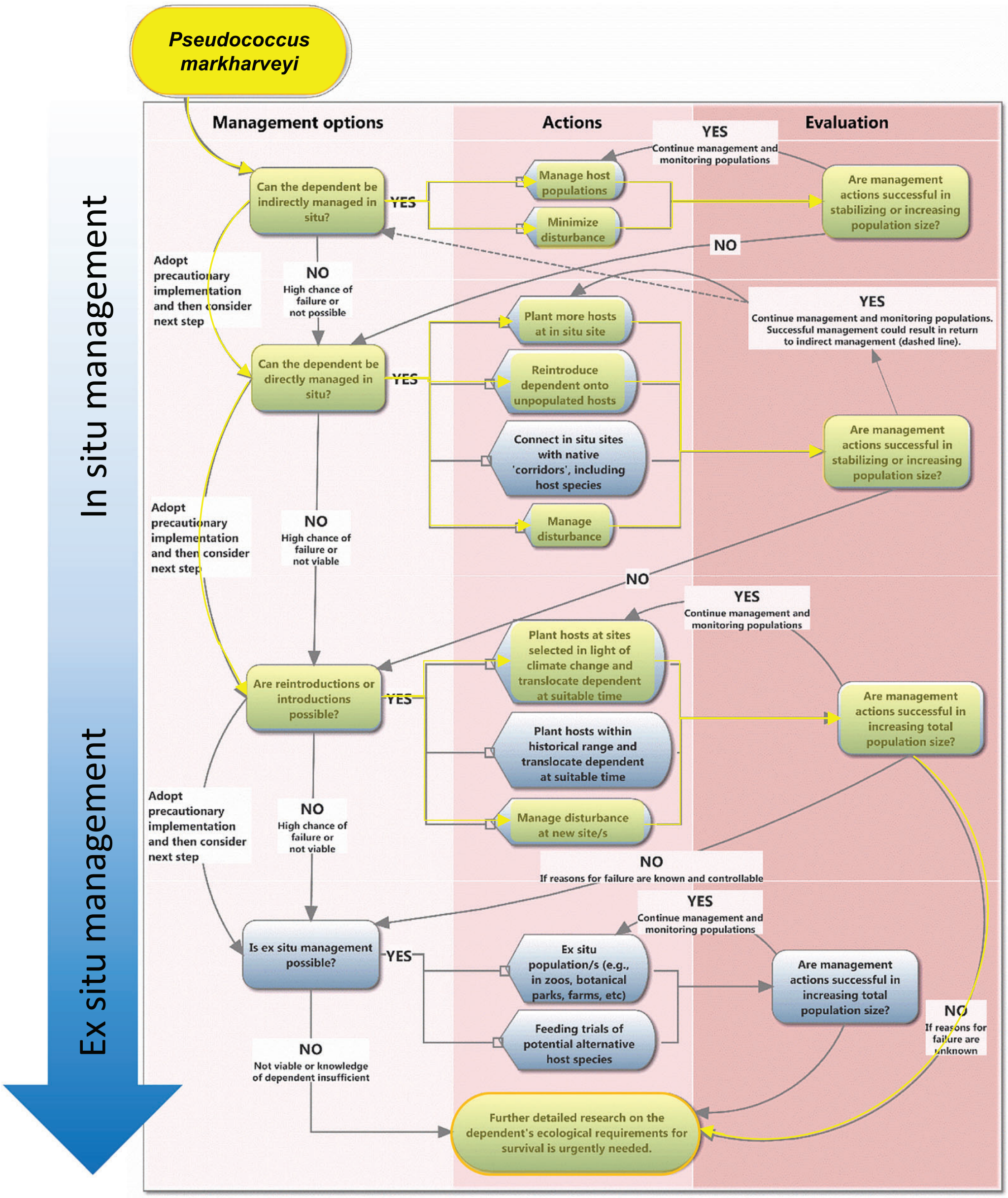

Fig 5. Conservation management framework for threatened plant-dwelling invertebrate species (adapted from Moir & Leng 2013), with the management efforts undertaken for *Pseudococcus markharveyi* highlighted in yellow.

environment at the lowland translocation site, after being sourced from the moister, more benign environment of the montane heathland (Moir & Leng 2013).

In December 2012, in the hope that adults would prove hardier, a second translocation occurred with females collected from both source populations at Pyungorup and Bluff Knoll and again confined in insect rearing bags on recipient *B. montana* (Moir & Leng 2013). Initial results from October to November 2014 showed that the translocation was successful. Many individuals were observed in at least 40% of insect bags, which were then removed to allow the mealybugs to disperse over and across the plants, as there was concern their density might become too high in confinement (Moir 2015). Unfortunately, these translocations appeared to have failed 12 months after the bags had been removed (October 2015). No *P. markharveyi* were located in surveys in 2015, 2017 or 2019. In 2015, the parasitised exoskeletons of some individuals remained on the plants, suggesting that parasitoids had played some role in their extirpation.

While attempting management through translocations in 2012–2013 and liaising with Coccomorpha expert Penny Gullan to secure its taxonomy with a species description and name, efforts were made to have *P. markharveyi* formally recognised as threatened. The species (as *Pseudococcus* sp. 15) was successfully listed in 2013 as critically endangered under the Western Australian *Wildlife Conservation Act 1950* and internationally on the IUCN Red List based on its restricted host breadth, poor dispersal capabilities and the multiple threats to its host plant (Moir & Leng 2015). It was subsequently listed by the Australian Government as critically endangered in 2018 via a memorandum of understanding with the state governments designed to ensure consistent threatened species lists between the jurisdictions.

Threatening processes leading to coextinction

On 24 May 2018, wildfires that escaped from prescribed burns, which were implemented to reduce fuel loads and lessen wildfire risk, in the south-east of the Stirling Ranges burnt a large extent of the eastern massif (Office of Bushfire Risk Management 2018; Monks *et al*. 2019). In evaluating the impact of this wildfire on the mealybug, a helicopter-assisted survey was undertaken across the eastern massif the following year (November 2019). As *B. montana* is killed by fire (Gilfillan *et al*. 2008), *P. markharveyi* are also either killed by the fire front or cannot survive afterwards without a host plant. On Pyungorup, several *B. montana* plants had escaped the fire. Of these, two *B. montana* plants (Nos 6 and 7) had thriving populations of immature *P. markharveyi* hidden within new plant growth. A third plant (No. 8) also had much new growth but was approximately 6 m away from the first two plants, but no mealybugs were present. This supported previous assumptions that *P. markharveyi* requires the canopy of host plants to touch to be able to move between hosts. I therefore translocated an individual mealybug from each of plants Nos 6 and 7 onto plant No. 8 to facilitate dispersal across plants in case one of the remaining plants died. Three individuals of *B. montana* (Nos 11, 13 and 14) were very tall, with new growth, and it was difficult to examine the canopy without damaging the plants. However, a single mealybug on plant No. 13 was sighted, and it was likely that *P. markharveyi* occurred across these three plants as the branches were touching. No other mature *Banksia* were found, although multiple seedlings that had emerged since the May 2018 fire were examined, but no *P. markharveyi* were detected on them.

Ladybird beetles (Coccinellidae) may have contributed to population declines of *P. markharveyi*, particularly within more open habitats. In 2012, I noted that the native ladybird beetle *Coccinella transversalis* Fab. 1781 and the introduced *Coccinella undecimpunctata* L. 1758 were voracious predators of *P. markharveyi* on Bluff Knoll, despite both species being considered specialist aphid feeders (Pope 1988). Although ladybird beetles facilitated the discovery of *P. markharveyi* in 2007 on Bluff Knoll, their presence and appetite for *P. markharveyi* was one reason why insect bags were necessary during translocations of the mealybug. On Pyungorup Peak in 2007, 2012 and 2015, ladybird beetles were uncommon. In contrast, in November 2019, *C. transversalis* was in high abundance across plants and on the ground on Pyungorup. The level of predation was not quantified, and their overall impact remains unknown. There is a precedence of ladybird beetles harming rare Pseudococcidae; the critically endangered St Helens mealybug *Ripersiella mediatlantica* Matile-Ferrero 1976 is threatened by introduced Coccinellidae ladybird beetles (Pryce & Dutton 2018).

On the peak of East Bluff (approximately 700 m east of Bluff Knoll), one remaining *B. montana* that had not previously been surveyed for mealybugs was examined, but no *P. markharveyi* were observed. The old *B. montana* on Bluff Knoll that was host to a large thriving *P. markharveyi* population, leading to the initial 2007 discovery of the mealybug, had been killed by the 2018 fire. Thus, by November 2019, it was likely that *P. markharveyi* only existed on six plants at a single site (Pyungorup).

From 26 December 2019, multiple large fires burnt over 40 000 ha of the Stirling Range National Park, including parts of the eastern massif that had escaped the fires in 2018. All six *B. montana* plants hosting *P. markharveyi* on Pyrungorup were burnt (S Barrett pers. comm. 22 January 2020). The risk posed to *P. markharveyi* specifically by these fires has been highlighted by its recent selection as one of five Australian invertebrates requiring urgent intervention to save it from extinction (Department of Agriculture, Water and the Environment 2020). Unfortunately, it may be too late. All individual plants that were known to host *P. markharveyi* have been extinguished, and the mealybug is now likely to be extinct.

DISCUSSION

Along with many other insect groups in Australia (Braby 2018; Taylor *et al*. 2018), mealybugs are overlooked in conservation threat assessments. *Pseudococcus markharveyi* is the only conservation-listed mealybug from the 210 described species present in Australia, and the only one that has been formally assessed. Yet utilising the information collated in García Morales *et al*. (2016) and the protocol of Moir *et al*. (2011b), a preliminary assessment of the threat status of Australian pseudococcids can be attained. Three species, *Phenacoccus cassiniae* Williams 1985 (Victoria), *Dysmicoccus insulae* Williams & Watson 1988 (Norfolk Island) and *Odacoccus anaclastus* Williams & Watson 1988 (Lord Howe Island), should be formally assessed immediately given their habitat and host restrictions (= 'possibly threatened', Fig. 1). The lack of basic information on a further 16 species means that no recommendation can be reached (= 'unknown status', Fig. 1). The majority of described native mealybugs are projected to be 'least concern' (88% or 151 species), with this figure likely to rise once the species of unknown status are investigated more thoroughly. This basic evaluation does not, however, replace a more rigorous approach, but it does triage species towards formal assessment.

The original survey that discovered *P. markharveyi* could be used as a baseline indication of the conservation status of the undescribed Australian fauna. Eight of 21 mealybug species (including *P. markharveyi*) require an assessment of their threat status due to their associations with host plant species that are already listed as threatened in Western Australia (Moir, unpublished data). The proportion of mealybugs requiring assessment represented 38% of the total mealybug fauna in the survey, which is remarkably close to the estimate by Deng *et al*. (2016) of one-third of all mealybugs being undescribed globally. Extrapolating from the survey of Pseudococcidae of south-west Australia to a continental scale, there is high likelihood that the remaining undescribed endemic mealybugs are predominantly rare and require some form of conservation management. One-third of Australian mealybugs equates to ~85 species, but it is very probable that Australia has more than 100 undescribed species because (1) as mentioned above, most of the ~1070 undescribed species likely occur in the understudied Palaeotropics and Southern Hemisphere (Hardy 2013); (2) a single effort to treat all Australian Pseudococcidae by Williams (1985) more than quadrupled the total known fauna; (3) when the mealybugs of individual plant genera are investigated, at least several new species of pseudococcids are added to the fauna, even after the work of Williams (1985) (e.g. *Xanthorrhoea* (Asphodelaceae) – three undescribed species Qin & Gullan 1989); and (4) Australia has approximately 20 000 native plant species (Australian National Botanic Gardens 2012), of which many are potential host plants of undescribed species. Given that 19 undescribed Pseudococcidae were collected from 104 plant species in south-west Australia, many hundreds of new species could be discovered more widely on native Australian plants. These estimates may of course be moderated because south-west Australia represents an area of diversification for various biota (e.g. plants – Hopper & Gioia 2004; frogs – Slatyer *et al*. 2007; millipedes – Moir *et al*. 2009; Edward & Harvey 2010; Migidae trapdoor spiders – Harvey *et al*. 2015), as reviewed by Rix *et al*. (2015). Driving diversification is a long history of climatic and landscape stability, small geographic ranges due to steep environmental and climatic gradients and isolation (e.g. Cook *et al*. 2015). Thus, pseudococcid diversification may also have occurred in the south-west, but further investigation is required because the family remain relatively understudied here.

The fate of *P. markharveyi* underscores the need to discover and describe these rarer taxa before they are lost to coextinction so that we can fully understand the extent of species loss (Costello *et al*. 2013). By refining where to search for potentially threatened species, we can be more efficient in both time and resources. There are examples of herbivorous insects that were possibly once widespread or common being threatened with extinction despite their host remaining widespread because the threatening process does not impact the host plant as severely (e.g. Lord Howe Island stick insect *Dryococelus australis* (Montrouzier 1855)). However, for those species threatened with coextinction, higher concentrations of cothreatened insects are likely where taxa are geographically restricted and environmentally adapted, such as mountainous regions, freshwater systems, coastal habitats and islands (Moir *et al*. 2014). The four current IUCN-listed mealybugs reflect associations with these habitats. The extinct Hawaiian mealybugs *Phyllococcus oahuensis* (Ehrhorn) and *Clavicoccus erinaceus* Ferris were known from mountains on islands; the critically endangered St Helens mealybug *R. mediatlantica* is also restricted to higher altitudes on a small island; and *P. markharveyi* was confined to mountain ridges (Moir & Leng 2015; Pryce & Dutton 2018; IUCN 2020). The highest priority for survey of pseudococcids should, therefore, be high altitude regions and island systems. Further refining the search within these regions to plants and habitats that are already conservation listed should increase efficiencies in detecting coextinction risk.

CONCLUSION

Despite insects comprising the bulk of terrestrial fauna diversity, for the majority of insect families, there are few well-documented examples of modern extinctions (Dunn 2005), particularly within the Southern Hemisphere (e.g. Woinarski *et al*. 2019). The general consensus among conservation biologists and entomologists is that this does not indicate a lack of extinctions, rather that the extinctions are going undetected or are not being documented or listed on conservation schedules (Fonseca 2009; Braby 2019; Sanchez-Bayo & Wyckhuys 2019). There have been several documented extinctions of Pseudococcidae in recent history with that of *P. markharveyi* likely to have occurred in the last 12 months. Significantly, the coextinction of this species occurred despite both *in situ* and *ex situ* interventions over 8 years. As one of the very few well-documented modern insect extinctions in Australia, the likely extirpation of *P. markharveyi* is a clear example of the extensive undocumented losses that may be occurring among Australia's small cryptic plant-dwelling insects, in association with a multitude of interacting disturbances and threats such as invasive predators and competitors, inappropriate fire regimes including escaped management burns, climate change and plant diseases.

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