



A palaeontological perspective on the proposal to reintroduce Tasmanian devils to mainland Australia to suppress invasive predators

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ABSTRACT

The diversity of Australia's mammalian fauna has decreased markedly since European colonisation. Species in the small-to-medium body size range have been particularly badly affected. Feral cats and foxes have played a central role in this decline and consequently strategies for reducing their numbers are being evaluated. One such strategy is the reintroduction to the mainland of the Tasmanian devil, *Sarcophilus harrisii*. Here, we provide a palaeontological perspective on this proposal. We begin by collating published records of devil remains in Quaternary deposits. These data show that the range of devils once spanned all the main ecological zones in Australia. This indicates that they are capable of coping with a wide range of climatic and environmental conditions, and suggests that they could conceivably be reintroduced much more widely than has been thought possible hitherto. Subsequently, we examine fossils and coprolites from two sites in the Willandra Lakes Region World Heritage Area. These specimens not only support the suggestion that devils have wide ecological tolerances, but also suggest that devils can coexist with native small-to-medium species over long periods of time, which addresses one of the major concerns about the proposed reintroduction. We believe these two sets of palaeontological observations add substantial weight to the idea of reintroducing devils to the mainland as a way of suppressing cat and fox numbers.

1. Introduction

Biodiversity is declining rapidly in many parts of the world (Rockstrom et al., 2009; Barnosky et al., 2012) and some of these losses are likely to have disproportionate impacts on ecosystem function (Ritchie and Johnson, 2009). Removal of top-predators, in particular, commonly leads to marked changes in the abundance of species at lower trophic level (Estes and Duggins, 1995; White et al., 1998), which in turn can have major impacts on the rest of the ecosystem (MacArthur and Wilson, 1963; Terborgh, 1988; Terborgh et al., 2001; Ritchie et al., 2012). When the loss of native top-predators coincides with the arrival of invasive predators, native prey populations can be irrevocably disrupted (Wallach et al., 2010).

Australia is a case in point. The diversity of Australia's mammalian

fauna has declined markedly since European colonisation, with at least 30 species and subspecies suffering extinction and many others experiencing substantial decreases in both range area and population size over the same time period (Ceballos and Ehrlich, 2002). In some regions of Australia, current terrestrial mammal diversity is estimated to be < 50% of that prior to the 18th century (McKenzie et al., 2007). The majority of mammal species that have been lost or experienced sizeable population declines are in the so-called 'critical weight range' (CWR), which is 35 g to 5500 g (Burbidge and McKenzie, 1989). Most of Australia's CWR species are adapted to arid or semi-arid environments. They include native rodents, small-bodied macropods, bandicoots, dasyurids, and potoroids.

There is general agreement that most of the losses of Australian CWR species are due, at least in part, to the introduction of invasive

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placental predators, especially feral cats (*Felis catus*) and red foxes (*Vulpes vulpes*) (Johnson et al., 1996; Moseby et al., 2011; Woinarski et al., 2014). In terms of mammalian predators, cats and foxes are second in body size only to the dingo (*Canis dingo* (Crowther et al., 2014) or *Canis familiaris* (Jackson et al., 2017)), which is itself an invasive placental predator, albeit one that was introduced ca. 3500 years ago (Milham and Thompson, 1976). Cats and foxes are thought to be a more significant problem for CWR species than dingoes partly because they often kill prey beyond their immediate needs (Short et al., 2002), and partly because dingoes are excluded from a large section of the country's southeast by the 'Dingo Fence,' which runs for 5631 km from the Darling Downs in the east to the Great Australian Bight in the south (Glen and Short, 2000).

The dominance of predatory placental mammals in Australia is a relatively new phenomenon on the geological timescale. For most of the past 25 million years, the apex mammalian predators were the marsupial lions (Thylacoleonidae), some of which were as large as a female African lion. Thylacoleonids went extinct sometime during the late Pleistocene (Wroe et al., 2013). After their disappearance, the largest mammalian predators were the marsupial wolf or thylacine (*Thylacinus cyanocephalus*) and the Tasmanian devil (*Sarcophilus harrisii*) (Wroe, 2003). These species disappeared from the mainland ca. 3500 years ago, possibly due to competition from newly-arrived dingoes (Johnson and Wroe, 2003). The thylacine persisted on the island of Tasmania into the early 20th century, when they were driven to extinction as a result of anthropogenic pressures including hunting. Devils still occur throughout Tasmania.

Recently, the reintroduction of native top-predators to Australian environments has been proposed as a way of preventing further losses of native prey species and of reinstating the function of disrupted ecosystems (Ritchie and Johnson, 2009; Louys et al., 2014). The idea here is that where a non-native meso-predator impacts lower trophic order species, the reintroduced top-predator will function as a 'biological control' (Murdoch, 1992) by suppressing the meso-predators (Ritchie and Johnson, 2009; Ritchie et al., 2012). Perhaps the best known case in which the reintroduction of predators has helped restore a semblance of former ecosystem function is that of the wolf translocation program in Yellowstone National Park in the US (Fortin et al., 2005).

In the Australian context, most attention has focused on the proposal to reintroduce the dingo to the country's southeast (Johnson and Wroe, 2003; Dickman et al., 2009; Letnic et al., 2009a, 2009b; Letnic and Koch, 2010; Letnic and Dworjanyan, 2011; Brook and Kutt, 2011; Allen and Fleming, 2012; Fleming et al., 2012; Letnic et al., 2012a, 2012b; Newsome et al., 2015). Two studies found that CWR species were in greater abundance and diversity outside the Dingo Fence, which is consistent with the hypothesis that dingoes are able to suppress cats and foxes (Pople et al., 2000; Travouillon and Legendre, 2009). But concerns have also been expressed about the proposal (e.g. Allen et al., 2013; Hayward and Marlow, 2014). One obvious issue is that dingoes are known to prey on some CWR species (Paltridge, 2002; Brook and Kutt, 2011), particularly smaller macropods (Paltridge, 2005; Augusteyn et al., 2010). Thus, the reintroduction of the dingo could exacerbate the very problem it is designed to solve. Another major issue is that dingoes are regarded as a major pest by the farming industry because of their significant impact on sheep (Allen and West, 2013). Given this, it seems likely that any attempt to increase their abundance on the inside of the Dingo Fence would be met with considerable resistance.

The reintroduction of Tasmanian devils to mainland Australia has been proposed as an alternative means of controlling cat and fox numbers (Johnson and Wroe, 2003; Hunter et al., 2015). There is evidence that devils play a role in suppressing feral cats on Tasmania (Hollings et al., 2014). In recent years, devils have experienced a severe decline due to Devil Facial Tumour Disease and feral cats have moved into areas relinquished by devils but the nature of the shifting predator

regime is far from clear (Fancourt et al., 2015). This implies that devils had previously prevented cats from expanding. Equally important for present purposes, devils do not naturally prey upon livestock, and have a more positive relationship with farmers when compared to dingoes. Devils also appear to have a minimal impact on CWR species in Tasmania, with no decline in the diversity of CWR fauna documented (as it has been on the mainland, see Burbidge and Manly, 2002). It is of course expected that devils will hunt some CWR species (and indeed exotic animals such as rabbits), but their impact will likely be minimal on the mainland when compared to foxes. Thus, reintroducing them has the potential to address at least part of Australia's invasive predator problem without the most obvious downside of reintroducing dingoes to eastern Australia. There are, however, some questions that need to be answered before such a proposal can be evaluated properly.

One of the most important of these questions is, which areas on the mainland are suitable for devils? Hunter et al. (2015) used computer modelling to predict the habitats into which devils could potentially be reintroduced in southeast Australia, but some of the assumptions they made in the modelling process have been challenged (Fancourt and Mooney, 2016). Also, by only using contemporary occurrence data from Tasmania, it is possible that Hunter et al. (2015) may have underestimated the range of mainland habitats that are suitable for devils. Here, we report work in which we approached the task of identifying potential mainland habitats for devils from a different perspective—that of palaeontology. Firstly, we reviewed and collated palaeontological records for Tasmanian devils on the mainland of Australia with the goal of establishing the species' range of environmental and climatic tolerances. Subsequently, we analysed palaeontological data from the Willandra Lakes World Heritage Area that provide a deep-time perspective on the interaction between devils and CWR species.

2. The fossil record of devils in Australia

We conducted a thorough review of the published archaeological and palaeontological literature to identify devil fossils from Quaternary sites in Tasmania and mainland Australia. The taxonomy of Quaternary devils was debated for a number of years because morphological variation among fossil specimens exceeds that of modern Tasmanian populations. Some authors recognized only one species, *Sarcophilus harrisii* (= *S. lanarius* of Werdelin, 1987; see also Groves, 2005), while others argued for three species (*S. harrisii* and larger, extinct species including *S. lanarius* and *S. moornaensis* (e.g. Crabb, 1982; Dawson, 1982). Today, most authorities accept the one species hypothesis (Jackson et al., 2017). In our review of the literature, we included Quaternary specimens originally assigned to *S. harrisii* and specimens that were initially assigned to *S. lanarius* and *S. moornaensis*.

We identified > 120 Quaternary-aged deposits that have yielded fossil devil remains (Fig. 1 and Table S1). The majority of these deposits are located in the southern half of the continent, particularly in the southeast. Although Quaternary sedimentary deposits represent the dominant surface geology across Australia, those from the southern part of the continent have been surveyed for fossil vertebrates much more extensively than those in the north (Horton, 1984). Thus, the distribution of devil fossils likely reflects a collecting bias rather than a 'true' biologic pattern. In line with this, recent excavations in previously under-explored regions in the north (e.g., Broken River) have produced the fossilized remains of a variety of Quaternary species, including devils (Price et al., 2017). Such research highlights how poorly the northern half of the continent has been explored for Quaternary vertebrates. An important implication of this for present purposes is that it is likely that devils were even more widespread during the Quaternary than Fig. 1 suggests.

Although many of the fossil specimens lack reliable dates, it is clear that both size classes of devils overlapped temporally and spatially during the Quaternary, which suggests that they shared similar ecological and climatic tolerances (see also Reed and Bourne (2009) and

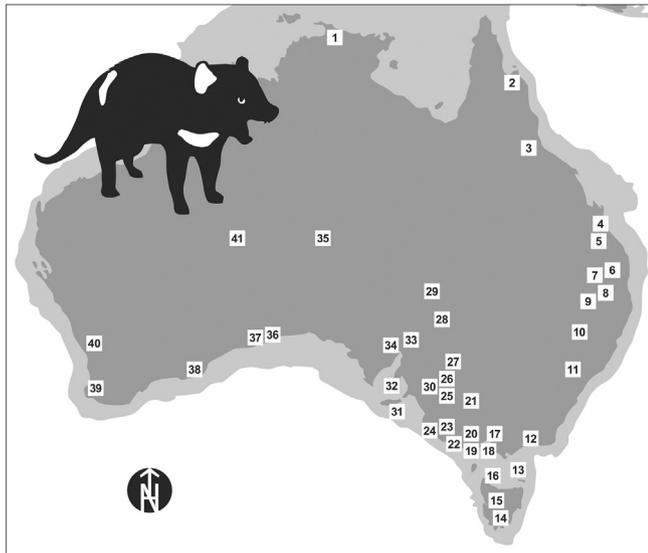


Fig. 1. Distribution of the known fossil record for Tasmanian devils, based on the fossil record that has been collected to date. The bias towards the southeast is likely to be at least partly due to the fact that considerably more fieldwork has been conducted there than in the rest of the country.

Price et al. (in press)). It is also clear from specimens recovered from unambiguously Holocene sites that devils occurred in a wide range of climate areas just prior to their mainland extirpation, including the central desert zone (Mygoora Lake), the temperate south (Belfast Coastal Reserve, Greenhead, Karridale, Pilliga, Princess Margaret Rose Caves, Scott River, Woorndoo, Yallingup, and Yanchep), southern grasslands (Mundrabilla), and the northern tropical savanna (Pady-padiy and Laura). Crucially, current ecological and climatic conditions at these sites are not markedly different than in earlier parts of the Holocene (Reeves et al., 2013). This suggests that it may be possible to re-introduce devils to a much wider range of mainland habitats than recent modelling work suggests (e.g., Hunter et al., 2015).

3. Devils and CWR species in the Willandra Lakes

In this part of the study, we focus on fossils and coprolites from the Willandra Lakes Region World Heritage Area. Established in 1981, the Willandra Lakes Region World Heritage Area is located in New South Wales, approximately 900 km west of Sydney, 350 km northwest of Melbourne, and 400 km northeast of Adelaide (Fig. 2). It covers around 2400 km² and has multiple fossil-bearing lakes within its boundaries. The main ones are, from north to south, Lake Mulurulu, Lake Baymore, Lake Pan Ban, Lake Garnpung, Lake Leaghur, Lake Gogolo, Lake Mungo, Lake Arumpo, and the Prungle Lakes. The Willandra Lakes Region was recognized as a World Heritage Area on the basis of the early modern human fossils and archaeological sites that have been discovered there, but it is also a rich source of palaeontological data (Hope, 1978; McIntyre and Hope, 1978; Johnston and Clark, 1998; Westaway et al., 2017).

The majority of fossils and coprolites discussed here come from two sites, GL13 and GG16. The locations of these sites relative to Lake Garnpung, Lake Leaghur, and Lake Mungo are shown in Fig. 2. As can be seen, the sites are in the Garnpung-Leaghur interlake area, which is one of the richest fossil areas in the Willandra. Some of the fossils we will discuss were collected by Mr. Michael McIntyre in the late 1970s and early 1980s. These specimens were analysed by Dr. Ken Aplin and then reported by Fuller (1986). The remainder of the fossils was recovered by our team in 2013, as were the coprolites; these specimens are reported here for the first time.

We will begin with the fossils. McIntyre collected over 600

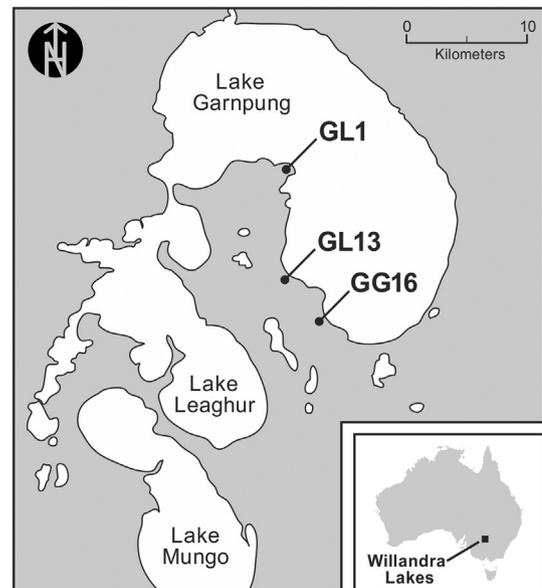


Fig. 2. The Willandra Lakes World Heritage Area and location of fossil sites investigated in this study.

specimens at GL13 and GG16, while our work at the two sites yielded over 350 specimens. The majority of the nearly 1000 specimens were recovered from the surface; only a few were obtained via excavation. McIntyre found GL13 to be markedly more fossil-rich than GG16, and so did we. Of the 354 fossil specimens we obtained during our fieldwork in 2013, 341 come from GL13 and only 13 from GG16.

Table S2 lists the taxa identified by Aplin, as reported by Fuller (1986), and the taxa we identified in our sample. The GL13 fossils are quite taxonomically diverse. They can be assigned to at least 25 different genera. Importantly for present purposes, the genera include *Sarcophilus* and several in the CWR. The latter include *Bettongia*, *Isoodon*, *Macrotis*, *Perameles*, and *Hydromys*. Taxonomic diversity at GG16 is markedly lower than at GL13, but the site has also yielded *Sarcophilus* remains and fossilized skeletal elements that belong to three CWR genera, *Bettongia*, *Onychogalea*, and *Pseudomys*.

While there are multiple genera represented at GL13, the majority of specimens (196 of the 341) belong to *Bettongia*. Of these, 34 can be confidently assigned to *B. lesueur*, the burrowing bettong. We suspect that most, if not all, the *Bettongia* specimens are actually burrowing bettongs and that we have simply run up against the limits of taxonomic identification for the specimens in question. Fuller (1986) reached the same conclusion regarding the *Bettongia* remains recovered by McIntyre. Based on the prevalence of *B. lesueur* remains, we think it likely that most of the fossils recovered from GL13 eroded out of old *B. lesueur* burrows. Consistent with this, Fuller (1986) reported that several complete burrowing bettong skeletons were recovered from in-filled burrows in the early 1980s, and we found another such specimen during our fieldwork. Because burials, fireplaces, shell middens, and artefacts have been found at GL13, Fuller (1986) concluded that it is an archaeological site. However, we think it is more likely that the archaeological material and the *Bettongia* fossils are not directly associated. Unfortunately, the GG16 fossil material is too limited to say anything about the nature of the site.

We obtained dates on some of the fossils we collected from GL13 and GG16. Radiocarbon dating proved impossible, so we employed U-series dating, which can provide minimum estimates. Details of the methods we employed and the specimens we analysed are given in the Supplementary Materials (S3). We were able to obtain just one date for our GG16 material. This came from a thylacine mandible and suggests that the specimen is at least 4000 years old. GL13 is better dated, because we were able to obtain dates from five bettong fossils. The age

estimates for these specimens range from 36,000 years ago (kya) to 6 kya, which suggests that GL13 may span as much as 30,000 years. In addition, we dated a Tasmanian devil fossil from the site of GL1, which is located ~10 km to the north of GL13 (Fig. 2). This specimen was recovered by National Parks and Wildlife employees in the course of their day-to-day work. It returned an age estimate of > 5100 kya.

We will now turn to the coprolites. We recovered a large number of these ($n = 172$) during our fieldwork at GL13 and GG16. For the purposes of the present study, we selected 32 relatively complete specimens that had dimensions consistent with those reported for devil scats (Triggs, 2004a, 2004b; Rose et al., 2017). We then used an ultrasonic bath and probe techniques to retrieve bone fragments without damaging them (Miscamble and Manne, 2016). Subsequently, the bone fragments were examined for taxonomic identification using a $\times 2$ magnification lamp. Lastly, we sought to identify the signatures of dasyurid consumption outlined by Miscamble and Manne (2016). This was carried out with a light microscope at magnifications between $\times 6.7$ and $\times 30$.

Many of the bone fragments obtained from the coprolites have tooth and digestion markings that are consistent with bone consumption by dasyurids, which supports the hypothesis that the coprolites were produced by devils. The taxa represented among the identifiable bone fragments recovered from the coprolites are listed in Table S4. The majority of the fragments ($N = 26$) are from burrowing bettongs. Given that the coprolites were likely deposited by devils, the bones recovered from them suggest that burrowing bettongs may have been the key prey species for devils in the Willandra.

Fig. 3 compares key elements of the Late Pleistocene-early Holocene food web based on the fossil specimens recovered from GL13 and GG16 with a food web for the Willandra constructed from data obtained in the last few decades by National Parks and Wildlife (Jo Gorman and Ray Dayman, pers. comm.). The different coloured lines indicate the relationships between predators and their common prey. It is obvious that there have been major changes in both species richness and taxonomic composition. At the top of the food web, the native predators have been replaced by cats and foxes. There have also been significant changes at lower trophic levels. Most obviously, native CWR species been replaced by the European rabbit (*Oryctolagus cuniculus*). The only native lower-trophic-level animals to survive are large macropods and a few small-bodied marsupial and rodent species. The former are too large for cats and foxes to hunt. Presumably the latter are able to evade predation due to their nocturnal behaviour and the survival of remnants of their preferred habitats.

Taken together, the fossils and coprolites from GL13 and G16 indicate that in the past devils not only lived in the Willandra but also preyed on CWR species, especially burrowing bettongs. At this stage, it is not possible to give a precise estimate of the length of time that devils and CWR species coexisted in the Willandra but the dated fossils suggest that it may have been > 30,000 years. This supports Hunter et al.'s (2015) suggestion that devils can be expected to have relatively weak impacts on CWR species. In addition, the date range for GL13 encompasses at least two periods of major climatic change—the Last Glacial Maximum (ca. 21 kya; a time of widespread aridity in Australia) and the Pleistocene-Holocene transition (ca. 20–11 kya; a period of significant global warming). This adds further weight to the suggestion that devils are able to cope with a wide range of environmental conditions.

4. Summary and conclusions

It has been suggested that Tasmanian devils should be reintroduced to mainland Australia as a way of countering the negative effects of invasive placental mammals (Johnson and Wroe, 2003; Hunter et al., 2015). A key question concerning this proposal is, which areas of the mainland are suitable for devils? A recent ecological modelling study suggested that devils could be introduced to southern Victoria and the

highlands of northeast New South Wales (Hunter et al., 2015), but some of the assumptions made in the course of that study have been challenged (Fancourt and Mooney, 2016). A key question is whether the study by Hunter et al. (2015) is too conservative regarding the areas of the mainland that are suitable for devils. We decided to tackle the problem of assessing where in mainland Australia devils could be successfully reintroduced in a different way—we turned to the palaeontological record for guidance.

We began by collating published records of devil fossils from Tasmania and mainland Australia. The resulting dataset suggests that Hunter et al.'s (2015) ecological modelling study is indeed too conservative. The devil fossils that have been recovered to date indicate that their range once incorporated all key environments in Australia, including at the time immediately prior to their mainland extirpation. This suggests that devils are able to cope with a wide range of environmental conditions and could conceivably be reintroduced into many of Australia's ecosystems. Subsequently, we analysed fossils and coprolites from sites in the Willandra Lakes World Heritage Site. The results suggest that devils likely coexisted with a number of CWR species for a long time in the Willandra, possibly as long as 30,000 years. The results also suggest that devils survived through two major episodes of climatic change when they lived in the Willandra, which further supports the idea that they are able to cope with a wide range of environmental conditions.

The case for reintroducing devils to mainland Australia to control the abundance of invasive predators can be summarized as follows:

- Feral cats and foxes have had, and continue to have, a major impact of native CWR species; there is an urgent need to reduce their numbers.
- Suppressing cats and foxes by reintroducing dingoes inside the Dingo Fence might be counterproductive and would almost certainly be unpopular because dingoes cause problems for farmers.
- Reintroducing Tasmanian devils to the mainland may be a viable alternative.
- Contemporary data from Tasmania suggest that devils are able to exclude cats from the habitats they occupy.
- It is unlikely to pose as great a threat to the pastoral industry as reintroducing dingoes; Tasmania shows that sheep farming is able to flourish in the presence of sizeable devil populations.
- Ecological modelling suggests that devils could be successfully reintroduced to southern Victoria and the highlands of northeast New South Wales, while devil fossils indicate that the reintroduction could actually be successful in many other parts of Australia.
- Palaeontological evidence also suggests that devils are able to coexist with CWR species over the long-term.

Needless to say, there are still issues to be investigated. For example, the evidence that devils can suppress cat numbers is circumstantial, and we currently do not have any data on the interaction of devils and foxes (Hunter et al., 2015). However, we are of the opinion that there are now adequate grounds for carrying out a program of carefully controlled field experiments on the mainland. These experiments should be designed to shed light on the impact of devils on cat and fox numbers and the nature of the interaction between the three species. They should also be designed to be informative regarding the potential success of devils in areas that have been heavily affected by agricultural practices compared to areas that have been less heavily impacted by farming. Given the results of the Hunter et al.'s (2015) ecological modelling and those of the present study, southeast Australia would seem to be the best focus for an initial program of experimental work.

In recent years a number of researchers have argued that the fossil record can provide a deep-time understanding of prehistoric food webs and interactions across trophic levels that are useful for conservation (Louys, 2012; Lyman, 2015; Boivin et al., 2016; Westaway and Lyman, 2016). The analyses reported here support this suggestion. The fossil

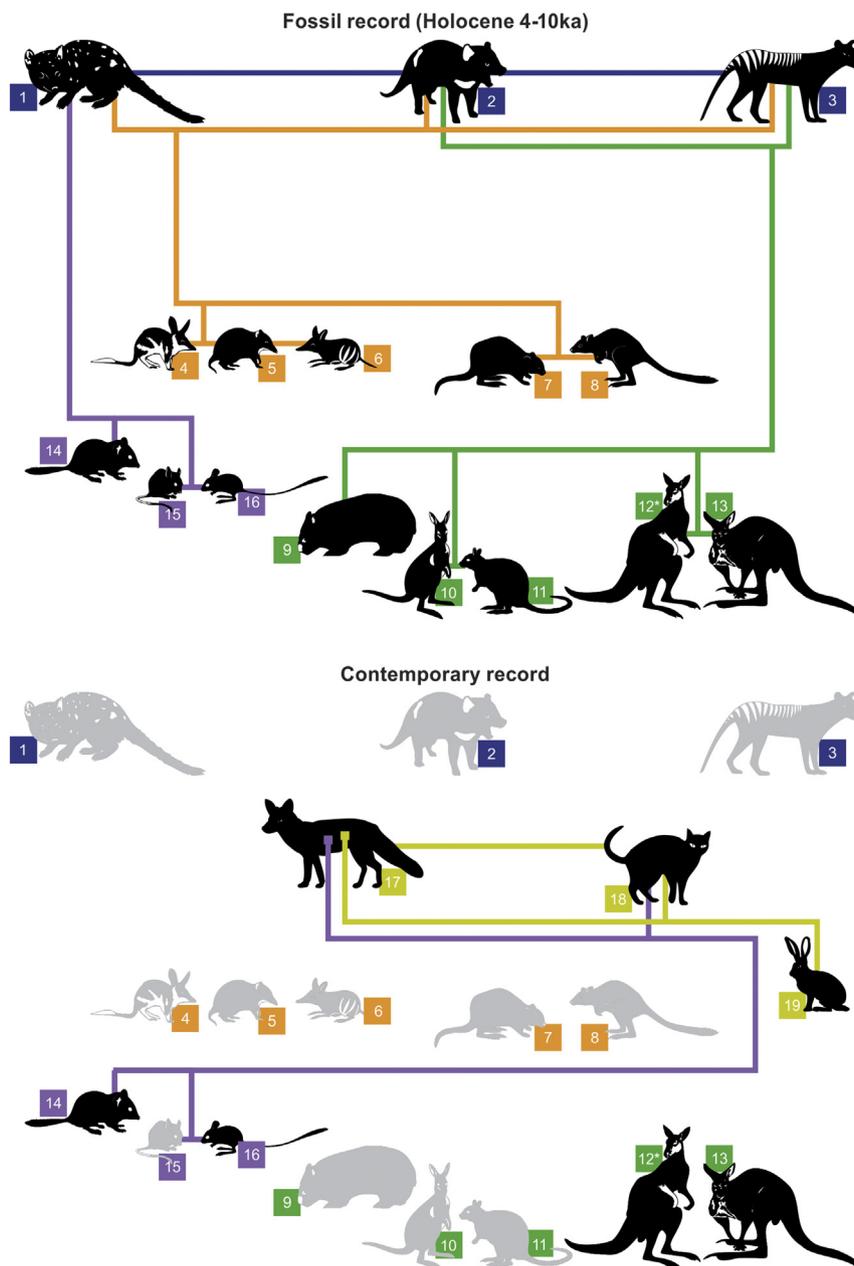


Fig. 3. Comparison of key elements from the faunal community at Willandra Lakes illustrating the dramatic change between recent prehistory to the contemporary record.

data we have discussed not only indicate that the potential mainland range of Tasmanian devils is dramatically larger than ecological modelling work has indicated, but also provide insights about the interaction of devils and CWR species. These represent, we believe, important contributions to the debate about how to tackle the problem of invasive predators and foster the recovery of native species and ecosystems in Australia.

Impact statement

We report analyses of fossil data that support a proposal to reintroduce Tasmanian Devils to mainland Australia as a way of reducing the impact of invasive predators.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2019.02.002>.

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