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PERSPECTIVE

Reconstructing mechanisms of extinctions to guide mammal conservation biogeography

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Abstract

An emerging research program on population and geographic range dynamics of Australia's mammals illustrates an approach to better understand and respond to geographic range collapses of threatened wildlife in general. In 1788, Europeans colonized an Australia with a diverse and largely endemic mammal fauna, where many species that are now extinct or threatened were common and widespread. Subsequent population declines, range collapses and extinctions were caused by introduced predators and herbivores, altered land use, modified fire regimes and the synergies between these threats. Declines in population and range size continue for many Australian mammals despite legislative protection and conservation interventions. Here, we propose an approach that integrates museum data and other historical records into process-explicit macroecological models to better resolve mammal distributions and abundances as they were at European arrival. We then illustrate how this integrative approach can identify the likely synergistic mechanisms causing mammal population declines across these and other landscapes. This emerging research approach, undertaken with fine temporal and spatial resolution, but at large geographic scales, will provide valuable insights into the different pathways to, and drivers of, extinction. Such insights may, in turn, underpin conservation strategies based on a process-explicit understanding of population decline and range collapse under alternative scenarios of impending climate and environmental change. Given that similar information is available for other regional biotas, the approach we describe here can be adapted to conserve threatened wildlife in other regions across the globe.

KEYWORDS
conservation biogeography, extinction, geographic range collapse, mammals, palaeoecology, process-explicit modelling, species recovery

1 | INTRODUCTION

Biogeography holds a central place in understanding patterns in biological diversity across space and time (Lomolino & Heaney, 2004; Wilson, 1999). The field's applied subdiscipline, conservation biogeography, uses the principles and tools of biogeography to preserve the distributions and, in turn, the ecological and evolutionary contexts of threatened species (Lomolino et al., 2017). Knowledge of species' distributions is fundamental to conservation biogeography, and has rapidly improved over recent decades (Jetz et al., 2012; Staniczenko et al., 2017). To be successful, however, geographically explicit conservation strategies require a much more thorough understanding of the dynamics of geographic ranges; in particular, the patterns and causal forces of early stage population declines and eventual geographic range collapse (Beissinger, 2000; Channell & Lomolino, 2000; Lomolino & Channell, 1998).

The drivers of population decline and geographic range collapse are likely to be complex and to vary among regions, time periods and focal taxa. Fortunately, the biogeographer's tool kit now includes process-explicit models (Connolly et al., 2017), which can simulate the typically multifactorial and synergistic drivers of distributional and demographic dynamics that generally operate over a broad range of spatial and temporal scales (Fordham et al., 2021, 2022; Rangel et al., 2018). When coupled with information on the historical distributions of focal taxa, environmental associations and temporal dynamics in climatic and other key environmental factors, these process-based approaches enable us to advance from phenomenological and inferential biogeography to process-explicit strategies for mitigating, and possibly redirecting declines of highly threatened species (Fordham et al., 2016).

Our purpose here is to describe a new research program in conservation biogeography—one that marshals insights from a diversity of disciplines to develop a more comprehensive and mechanistic understanding of the geographic signature and drivers of the historical and ongoing range collapse of native faunal assemblages. We illustrate this process-explicit (theory- and data-driven) macroecological approach by focusing on one of the world's most thoroughly researched, but highly threatened assemblages of native animals, the endemic mammals of Australia. We note that the approach we describe could also be applied to enhance the conservation of many other threatened taxa elsewhere. We first review previous episodes of mammalian extinctions across Australia, along with the ongoing extinction crisis and the current state of our knowledge on the patterns and drivers of geographic range collapse. We then show how these lines of research can advance conservation biogeography, providing an exemplary case study demonstrating how process-explicit models can be used to: (i) reconstruct past (pre-European) spatiotemporal abundances; (ii) identify the likely drivers of population decline and range contraction; and (iii) optimize conservation strategies to prevent future extinctions.

2 | EXTINCTIONS OF AUSTRALIAN MAMMALS

2.1 | Extinction episodes of Australian mammals

Australia has a unique mammal fauna that includes an ancient lineage of monotremes, as well as marsupials and eutherians (Holt et al., 2013). However, Australia's extant mammal fauna is just a shadow of what existed about 60 ka, which then included an estimated 55 additional species that vanished after Australia was first colonized by humans (Johnson, 2006). The most plausible reconstruction of Late Pleistocene extinctions in Australia indicates an initial phase of large herbivore extinctions (ca. 61–51 ka) with extinctions peaking ca. 45–35 ka with the losses of both small and large herbivores, along with Australia's largest predators (Saltré et al., 2016). Given that these extinctions closely followed the first arrival of people in Australia (Flannery, 1994), humans probably played a role in the Late Pleistocene collapse of Australia's marsupial megafauna (Johnson et al., 2016; Saltré et al., 2016), possibly driven by the synergistic effects of overharvesting, habitat transformation (including the use of fire) and natural climate change (Johnson et al., 2023; Saltré et al., 2019).

European colonization of Australia in 1788 triggered a further, accelerated wave of mammal extinctions, beginning in south-eastern Australia in the 1840s, then moving north and west through the 20th century (Burbidge et al., 1988; Johnson, 2006; Woinarski et al., 2011). Again, the geographic signature of this historical wave of extinctions appears consistent with the dynamic geography of human-induced impacts, namely the spread of invasive species and habitat conversion across the continent. Since 1788, 33 mammal species have gone extinct (Woinarski et al., 2019), with recognized historical extinctions increasing in recent decades. The latter extinctions likely involved extinction debts from a legacy of historical drivers (Kuussaari et al., 2009), and may have been exacerbated by the emerging impacts of anthropogenic climate change (Waller et al., 2017); with additional extinctions tallied based on taxonomic revisions (McDowell et al., 2015; Travouillon & Phillips, 2018). Compared to the earlier waves of extinctions, the species involved in post-1788 extinctions were smaller and more concentrated in arid and semi-arid Australia, and their population declines and range collapses were more rapid (Burbidge & McKenzie, 1989).

Many of the now extinct mammals, or those that persisted and are now threatened, were abundant species; many having near continent-wide ranges when Europeans colonized Australia (Hanna & Cardillo, 2013). The broad, pre-European distributions of these species is evident from fossil and subfossil remains (Westaway et al., 2019), ecological knowledge of Aboriginal people (Burbidge et al., 1988; Ziembicki et al., 2013), the historical accounts of 20th century naturalists (Dahl, 1926; Finlayson, 1961; Short & Calaby, 2001) and specimens in museum collections (Helgen et al., 2012). However, this historical information on distributional dynamics and local extirpations of native mammals in Australia remains geographically and temporally sparse and spatially biased (Figure 1). Therefore, it is difficult to determine patterns, timing and causes of range collapses using these records alone (Caughley, 1994). Halting and reversing the erosion of mammal diversity in Australia is more than a moral imperative, however, since native mammals provide critical ecological services, such as pollination (Goldingay et al., 1991), seed dispersal (Chapman, 2015; Dennis, 2003) bioturbation and increased soil fertility (Elliott et al., 2020; James et al., 2011; Valentine et al., 2018).

2.2 | The current extinction crisis

Knowledge of biological events of the past is essential for contextualizing the present, predicting population trajectories of key wildlife species, and guiding conservation strategies far into the future (Fordham et al., 2016; Nogués-Bravo et al., 2018). The timing of post-European mammal extinctions in Australia is most closely correlated with the spread of invasive cats (*Felis catus*) and red foxes (*Vulpes vulpes*) across the continent, and with altered fire regimes (Johnson, 2006; Stobo-Wilson et al., 2020; Woinarski et al., 2019). However, with few exceptions (Abbott, 2008a; Menkhorst, 2009), there is little information on how the spatial dynamics of these threats interacted with the ecology of Australian mammals to cause their rapid population declines and extinctions (Fisher et al., 2014). This knowledge gap is handicapping efforts to avert future declines in mammals and other components of Australia's unique biodiversity (Woinarski et al., 2019), partly because drivers of early-stage population declines can be very different from those that maintain rarity (Caughley, 1994).

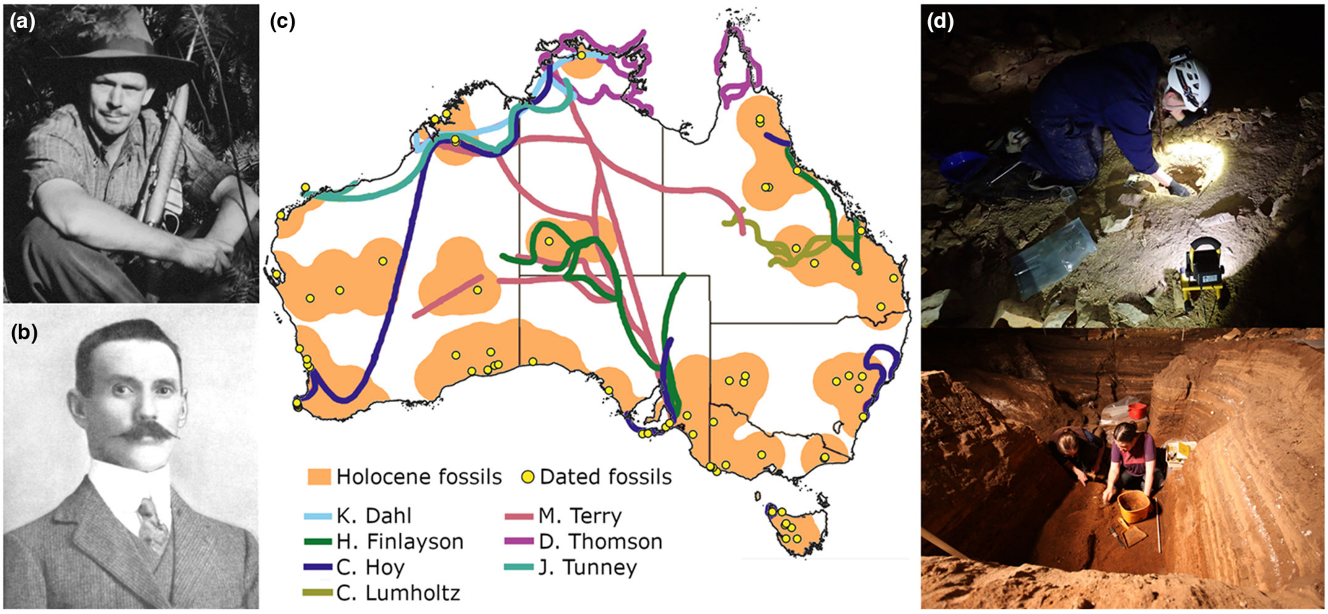


FIGURE 1 Palaeo-archives and early sighting records can complement contemporary records on species distributions. Early sighting records from Australia come from 20th century naturalists, including Hedley Finlayson (a), John Tunney (b), and numerous others, whose explorations of remote Australia (c), detailed by the coloured lines, provide early records of Australian mammal distributions. Since the late 20th century, these records have been supplemented by recovering and studying subfossil and fossil remains (d) of extant and now extinct species, many of which were once widespread and common. Image credits: National Library of Australia, E. Reed.

For many threatened species, a limited understanding of their current and potential distributions in the absence of environmental threats often limits the scope of conservation activities to a subset of the historical range, ignoring key regions and habitats where the species may have once flourished. This is evident in the spatial clumping of occurrence data for Australia's most threatened species (Figure 2), which represent only a fraction of the area that these species once inhabited (Hanna & Cardillo, 2013). For example, the Endangered mountain pygmy possum, *Burramys parvus*, is currently largely restricted to habitats above the snowline in the Australian Alps (Archer et al., 2019; Heinze et al., 2004), and faces substantial conservation threats from the combined effects of climate change, introduced predators, habitat loss and increased incidence and intensity of wildfire (Broome et al., 2012). While reintroduction efforts have focused only on alpine habitats, fossil evidence suggests that the current alpine distribution represents a stranding of the species in suboptimal conditions (Archer et al., 2019). Thus, the persistence of the mountain pygmy possum in the face of 21st century climate change may benefit from translocations to a broader range of habitats. This assertion is further supported by the recent discovery of some populations in locations with very different habitat characteristics (Hawke et al., 2019).

Halting the current extinction crisis in Australia (and elsewhere) will, in part, require historically informed conservation programs that are large-scale, long-term and informed by the temporal and spatial dynamics of the primary drivers of range collapse and extinctions (Barnosky et al., 2017; Figure 3). Fortunately, for at least some species, the requisite information on past distributions and key extinction processes is now available. Ecological requirements and likely past distributions can be reconstructed from fossil and historical sighting records using palaeo- and historical simulations of past (pre-European) climatic and environmental conditions. This can be done statistically by capturing the environmental conditions and resources that enable a species to persist through time (Maiorano et al., 2013; Nogués-Bravo, 2009). Detailed spatiotemporal records of the spread of some invasive species and other threatening processes exist for Australia (Abbott, 2008b; Fairfax, 2019; Power et al., 2008; Stodart & Parer, 1988). Synthesizing this information in process-explicit macroecological models can provide ecological baselines needed to direct conservation efforts where and when they will be most effective in halting geographic range collapses of threatened species (Fordham et al., 2020).

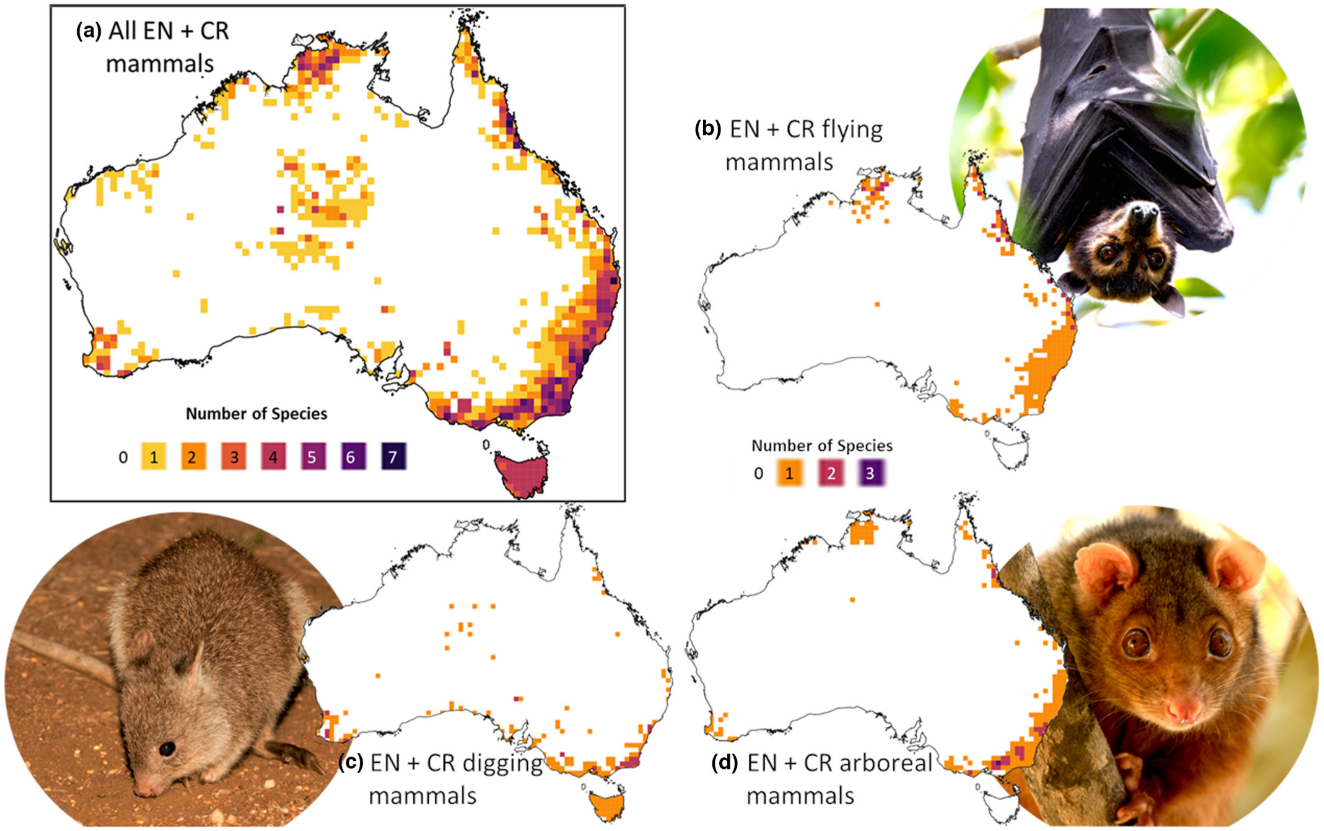


FIGURE 2 Recent spatial distribution of highly threatened (Endangered [EN] or Critically Endangered [CR]) mammal species in Australia. Maps are for: (a) all EN + CR mammals; (b) EN + CR flying mammals (bats); (c) EN + CR burrowing mammals; and (d) EN + CR arboreal mammals. Threat status is based on the Australian Commonwealth *Environmental Protection and Biodiversity Conservation (EPBC) Act 1999* (Australia, 2021). Counts of species are based on the Atlas of Living Australia (http://www.ala.org.au. Accessed 18 January 2021) records (post-1950) in 50 × 50 km grid cells. Image credits: David Paul (Museums Victoria), Kazredracer@Flickr, Andrew Mercer@Flickr, licensed under Creative Commons.

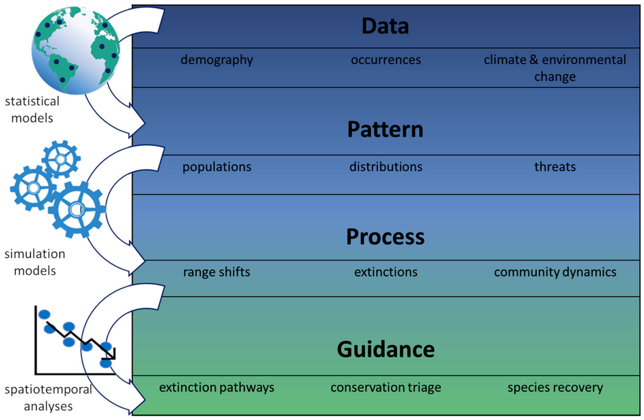


FIGURE 3 A protocol for mitigating, re-directing and possibly reversing geographic range collapses of threatened species. This approach integrates information from contemporary, historical and palaeo-archives (Data) using statistical models to reconstruct species population structure, distributions and potential threatening processes (Pattern). This information is then used to train simulation models that reconstruct the spatiotemporal dynamics of range expansion and contraction, extinction and ultimately community structure (Process). Post-hoc analysis of these process-explicit models can provide guidance to conservation practitioners to better predict extinction patterns, prioritize (or triage) conservation expenditure, and ultimately plan species recovery (Guidance).

2.3 | Geographic range collapse

Conservation biology traditionally focuses on rare species, which seems appropriate because they are often at most immediate risk of decline and extinction (Caughley, 1994). However, threatening processes generally first erode populations and ranges slowly, remaining inconspicuous until populations decline to a critical threshold beyond which they rapidly disappear (Soule, 1983). These lags, or extinction debts, between the onset of population decline and rapid range contraction are often prolonged (Kuussaari et al., 2009; Tilman et al., 1994), obscuring evidence for pathways to extinction (Lindenmayer et al., 2011), and emphasizing the need for an historical context in current-day conservation planning.

Current efforts to conserve mammals in Australia are focused primarily on protecting small populations that have already experienced large declines, with less focus on identifying, understanding and managing species that are currently wide-ranging and abundant but experiencing initial stages of population decline. The greater bilby *Macrotis lagotis* (Abbott, 2001), woylie *Bettongia penicillata* (Wayne et al., 2015) and several species of quolls *Dasyurus* spp. (Peacock & Abbott, 2014) are prime examples of how apparently stable species can undergo rapid decline, often decades after the onset of the threatening processes. More recently, populations of previously common mammal species in Australia's north have declined rapidly, with some studies predicting extinctions of some species before 2050 (Geyle et al., 2018; Woinarski et al., 2011). While this new phase of rapid decline could suggest a change in the dynamics of threatening processes, there is little evidence of influence by altered fire regimes or expanding land use change (Woinarski et al., 2011). It is therefore possible that we are now witnessing a phase shift between the early, slow decline of mammals following European arrival in northern Australia and a tipping point of imminent acceleration when 'extinction debts' are paid.

Initial research on geographic range collapse (Channell & Lomolino, 2000; Lomolino & Channell, 1995, 1998) indicated that the spatial dynamics of species ranges across Australia and other continents reflected that of the underlying extinction forces—with the salient pattern being that of persistence of the most isolated populations last to be impacted (i.e. those along an isolated edge of the range, on islands or in high, alpine reaches). Subsequent research indicates that the spatiotemporal signatures of geographic range collapse of mammals are likely to have varied substantially across regions of Australia following European colonization (Evans et al., 2011; McKenzie, 1981; Smith & Quin, 1996). For example, the extinction crisis that played out in the Australian interior in the early to mid-20th century (Finlayson, 1961) owing, in part, to red foxes, probably differs fundamentally from that currently occurring in northern Australia, where red foxes are absent (McKenzie, 1981; Smith & Quin, 1996). A better understanding of the potential ecological pathways to extinction will require a greater focus on the demographic traits, ecological processes, and geographic dynamics of threats and environmental conditions that have combined to drive population declines since European colonization. This research is likely to identify key metrics that signal the early stages of decline in species' abundances and distributions, as well as an improved understanding of extinction dynamics in general (Davidson et al., 2009).

Research on geographic range collapse has now advanced from its initial, descriptive phase thanks to recent advances in palaeo- and historical-ecology. Reconstruction of past distributions is now a common tool for understanding the fragmentation, isolation and refugia of plants and animals, often producing hindcasts of the dynamics of historical and ancient distributions that closely match reconstructions based on population genetic patterns (Knowles et al., 2007; Nevill et al., 2014). At the core of these projections are correlative species distribution models, built using contemporary records of occurrence and projected back in time (Ryeland et al., 2021). The approach identifies potential critical habitats based on statistical descriptions of climatic and environmental associations of species (Elith & Leathwick, 2009). The addition of historical and ancient records for remnant species can expand estimates of the breadth of climate and environmental conditions in which the species can persist, providing a closer approximation of the fundamental (rather then realized) niche of the species (Nogués-Bravo et al., 2018). This multi-temporal approach can improve model projections (Goring & Williams, 2017; Teresa et al., 2014) and therefore the utility of species distribution models for conservation planning.

Limitations to the initial phenomenological approaches of range collapse research include an inability to causally link current patterns to the past events that produced them, a failure to account for synergistic drivers of global change and an inability to directly model spatiotemporal abundance and extinction risk (Fordham et al., 2013). In contrast, the process-explicit modelling framework that we advocate (Figure 3) and describe below, provides a deeper, mechanistic understanding of the chain of causality leading to dynamics in biodiversity across space and time. Here, we will show how process-explicit macroecological models can be used to identify the key drivers of post-European mammal declines in Australia, how these drivers interact synergistically, and what ecological requirements are essential for developing successful programs to conserve persisting native mammals long into the future.

3 | EMERGING RESEARCH PROGRAM IN CONSERVATION BIOGEOGRAPHY

3.1 | Determining drivers of species' declines

Analytical advances in the use of process-explicit models to reconstruct and dissect extinction dynamics have recently been reported in detail (Fordham et al., 2021, 2022). These simulation-based approaches, which explicitly model ecological responses of species to environmental changes (Pilowsky, Colwell, et al., 2022), provide important historical insights into the dynamics of biodiversity change (Colwell & Rangel, 2010; Fordham et al., 2022; Knowles & Massatti, 2017). Consequently, these modelling approaches also offer substantial potential to improve conservation management and policy (Fordham et al., 2020) and to guide conservation activity.

The thylacine (*Thylacinus cynocephalus*), for example, experienced rapid decline and extinction when faced with novel threats of land use and persecution as European settlers spread across Tasmania (Bulte et al., 2003; Prowse et al., 2013). However, process-explicit spatial models of the extinction pathway for thylacine, validated against natural history records (observations and bounty counts), were needed to disentangle the complex drivers and demographic processes of extinction. They were also needed to identify rates and directions of range contraction and the location of the last refugia (Fordham et al., 2021). Although such insights came too late to conserve the Thylacine, if applied more broadly, our process-explicit modelling approach could be used to reveal chains of causality and trajectories of declines in the population abundance and range size of extant threatened species. This is likely to provide critical information needed to manage the drivers that underpin population declines and extinctions of wildlife (Fordham et al., 2020). Reconstructions of historic distributions and abundances of threatened species generated by process-explicit models could also be fed into existing systematic conservation planning algorithms (Ringma et al., 2019) and conservation criteria (Grace et al., 2019), thus enabling conservation efforts to be focused where they are most needed (Perry et al., 2016).

The specific process-explicit modelling architecture that we advocate follows precedents with demonstrated success in modelling the range and extinction dynamics of northern hemisphere megafauna using fossil records, palaeoclimatic data and new simulation and inference methods (Canteri et al., 2022; Fordham et al., 2022; Pilowsky, Haythorne, et al., 2022). The approach uses spatially explicit population models (SEPMs; Hanski, 1998) and pattern-oriented modelling methods (Grimm & Railsback, 2012) to integrate historical information into simulations of historic changes in species distributions and abundances. Figure 4 illustrates how this could be done for an exemplar Australian mammal, the numbat (*Myrmecobius fasciatus*), which the IUCN ranks as Endangered, and is classified as having a Vulnerable conservation status under the Australian *Environment Protection and Biodiversity Conservation Act 1999*.

Model development and application is broken into three stages:

Stage 1 is to reconstruct ecological requirements and extinction threats. This can be done using multitemporal calibration to intersect projections of past climates and vegetation structure with fossil and historical records to approximate the species' fundamental niche (Maiorano et al., 2013; Nogués-Bravo, 2009) from which estimates of the realized niche can be generated and later tested in the SEPM using pattern-oriented modelling methods (Fordham et al., 2022). The timing of arrival and spread of post-European threatening processes, such as introduced predators (cats and foxes), are available for continents such as Australia, having already been mapped using 19th and 20th century documents (Abbott, 2008b; Fairfax, 2019). Other threatening processes, such as expanding land conversion to agriculture are available globally at a coarse scale. Because Australia has a relatively short history of destructive land-use impacts (Bradshaw, 2012), finer scale spatiotemporal reconstructions of land-use intensity could potentially be generated using land purchase records. The approach is analogous to how archaeological evidence has been used to map the footprint of ancient human populations through space and time (Goldberg et al., 2016).

Stage 2 is where the SEPMs are built and optimized. These are used for reconstructing the timing, scale and processes underlying population declines and range contractions of threatened mammals. The demographic components of the simulation models are parametrised using published estimates or by using publicly available time series and trait databases (PanTHERIA, PHYLACINE and the Open Traits Network. Gallagher et al., 2020). Demographic models are coupled with time series of spatial projections of ecological requirements developed in Stage 1, making the models spatially explicit, allowing metapopulation processes to be simulated. Predation by introduced species can be simulated in the SEPM for Australian mammals as a product of the time of arrival of cats and foxes in a grid-cell, their upper and lower abundances, and their predation rates, drawn from published estimates (Murphy et al., 2019; Stobo-Wilson et al., 2022). Uncertainty in model parameters is captured by varying estimates across wide but plausible ranges using a robust coverage of multi-dimensional parameter space (Latin hypercube sampling; Fordham et al., 2021), producing thousands of conceivable models.

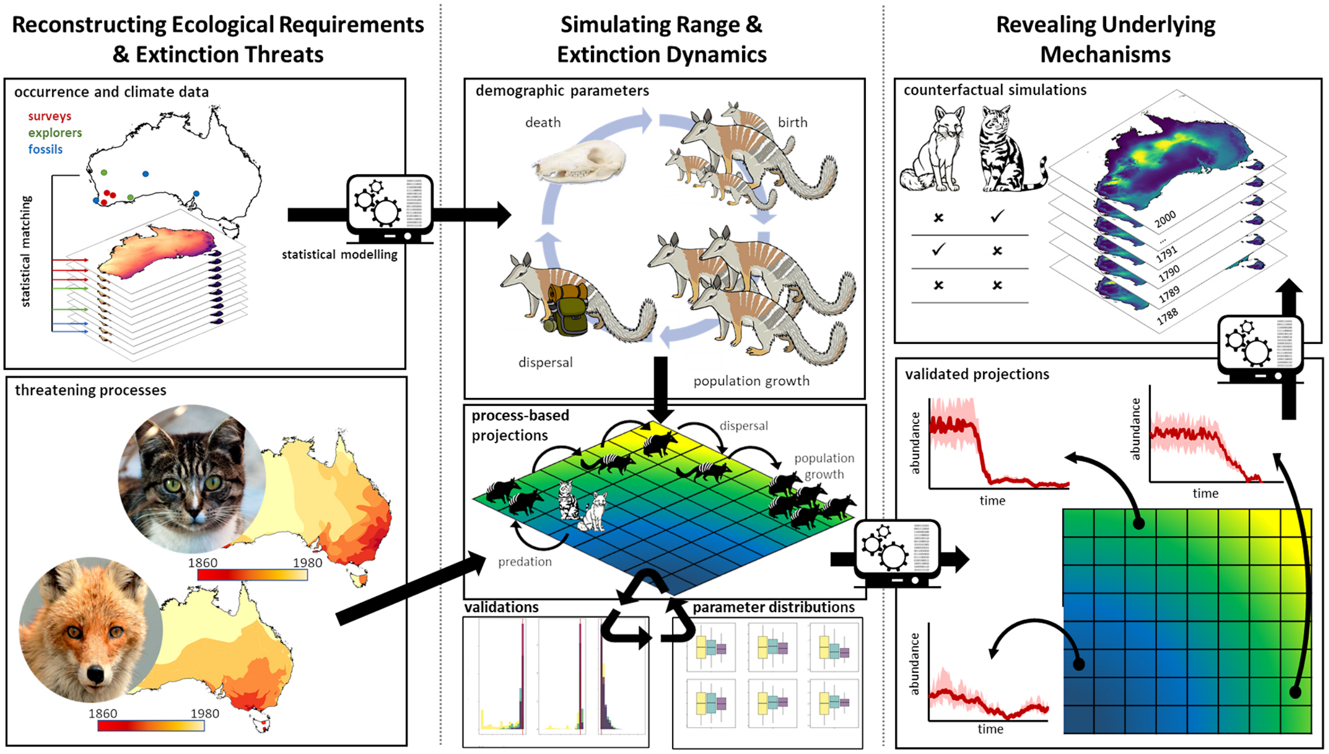


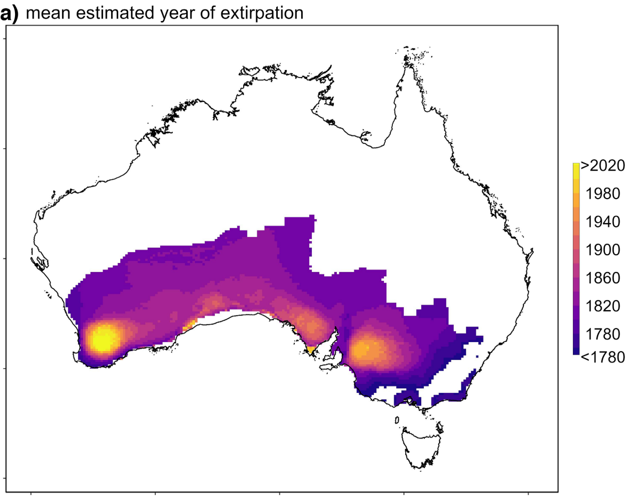
FIGURE 4 Integrated modelling framework for simulating pathways to population decline in changing environments. The three stages of model development and application are: (1) reconstructing ecological requirements and environmental threats; (2) building and simulating process-based spatially explicit population models with pattern-oriented validation; and (3) identifying ecological and environmental mechanisms of demographic change and testing these with counterfactual scenarios. Image credits: Jude@Flickr, Radovan Václav@Flickr, licensed under Creative Commons.

Pattern-oriented modelling methods (Grimm & Railsback, 2012) are then used to reject simulation models that do not closely replicate spatiotemporal patterns of demographic change inferred from palaeo- and neo-ecological data (Fordham et al., 2021, 2022), resulting in a subset of 'best' performing models based on the distance between inferred and simulated demographic change. Targets for pattern-oriented modelling can include inferences of regional extirpation events, spatiotemporal occupancy or change in abundance (Fordham et al., 2021, 2022).

Stage 3 identifies the causes of initial population declines and later extinctions. This is done by analysing simulation outputs from the 'best' SEPMs, using spatiotemporal statistical techniques that allow the role of environmental threats on change in occupancy and abundance to be disentangled spatiotemporally (Zamberletti et al., 2022). Causal explanations regarding the isolated or interactive effects of these threatening processes on emergent patterns can be further tested using counterfactual scenarios (Figure 4), whereby combinations of drivers of environmental change are switched off, while keeping all other parameters fixed (Fordham et al., 2021, 2022).

Applying this modelling framework to the numbat allowed us to reconstruct 230-years of geographic range dynamics for an ecologically and evolutionary distinct Australian mammal that declined substantially following European settlement (Figure 5). Since the decline of numbats in Australia has been linked, at least in part, to predation by feral cats (Friend, 1990), we modelled the effects of cats on the biogeography of numbats since the former's introduction into Australia in 1820 (Abbott, 2008b). We then asked where it would be appropriate to reintroduce numbats in the absence of cat predation. To do this, we quantified the ecological niche of the numbat, constructed a SEPM and optimized its ecological parameters, including rates of predation by cats and ran counterfactual scenarios.

Occurrence records were sourced from early naturalists (dating back to the 19th century) and more recent sightings. They were intersected with past climatic data describing total annual average rainfall, the average monthly temperatures for the warmest 3 months (January, February and March) and the average monthly temperatures for the coolest 3 months (June, July and August) to estimate the numbat's niche (Stage 1). Although we intersected our occurrence records with spatiotemporal data on changing climates, in theory, other spatiotemporal environmental layers could have been used, including modelled reconstructions of vegetation change from dynamic global vegetation models (DGVMs). Demographic parameters in the SEPM were based on observed numbat population dynamics (Friend, 1990, 1994; Vieira et al., 2007), while existing data on cat invasion and predation (Abbott, 2008b; Murphy et al., 2019) were used to simulate numbat-cat interactions (Stage 2). Three targets were simultaneously used for pattern-oriented model validation: (i) spatiotemporal occurrence, where numbats had to at least occur in grid cells until the date of the most recent observation; (ii) the ability of


(a) mean estimated year of extirpation

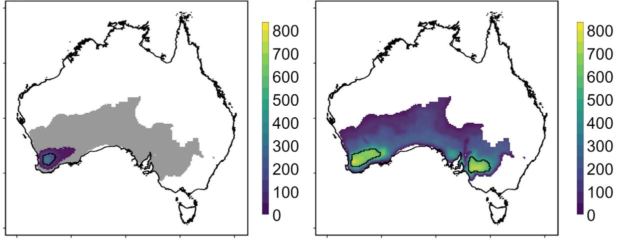

(b) estimated abundance (2020) **(c)** counterfactual abundance (2020)

FIGURE 5 Range collapse of numbat (*Myrmecobius fasciatus*) following European settlement of Australia. (a) Simulated extirpation year for numbat populations as a function of predation by cats (*Felis catus*). (b) Simulated current size and location of numbat populations. (c) Location of potential reintroduction sites, identified by black polygons (highest 10th percentile of abundance), based on simulations of numbat abundance in the absence of predation. Counterfactual simulations, where cat predation was removed, indicate potential for high population densities across much of southern Western Australia and in eastern South Australia, suggesting that these regions should be targeted for reintroduction into predator-free safe havens.

the models to recreate the extirpation pattern of numbats across the landscape; and (iii) final persistence within a 100 km radius of contemporary populations in the southwest of Western Australia. The SEPMs were built in the Program R packages *'PaleoPop'* (Haythorne, Pilowsky, et al., 2021) and *'poems'* (Haythorne, Fordham, et al., 2021). The model is fully described in the Supporting Information and supporting code can be downloaded from here: https://doi.org/10.6084/m9.figshare.16713874.

Simulations from the 'best' numbat SEPMs—those with the closest match to validation targets—did well at reconstructing occurrence and timing of regional extirpation (based on 19th and 20th century sightings), and location of last persistence (Figure 5). The models also did well at estimating numbat abundance in 2020. Simulating these inferences of historic range collapse and current day occurrence and abundance required a highly constrained set of environmental attributes (climatic requirements) and demographic traits (Supporting Information, Figure A5). In particular, low population growth rate and short-range dispersal were needed to reconcile validation targets, suggesting that these traits made numbats particularly vulnerable to introduced predators. The pre-European range of numbats and the direction and speed of their contraction following cat invasion of Australia is shown in Figure 5.

This success of our model in matching our validation targets suggests that the SEPM is well equipped to reconstruct the past range dynamics of numbats in response to cat predation. We therefore also constructed versions of the best SEPMs using an alternative (counterfactual) scenario where cats never invaded Australia. Doing this revealed that numbats are likely to attain high population densities across much of southern Western Australia and in eastern South Australia in the absence of this invasive predator, and possibly others as well. These, therefore, are regions most suitable for numbat reintroductions, if invasive species are managed at low numbers.

This proof-of-concept example shows how integrating process-based approaches into conservation biogeography can provide an improved understanding of causal agents of population declines and range contractions, providing important conservation recommendations that could not be attained from simpler correlative approaches. Moreover, it also shows the importance of accounting for multifactorial and synergistic drivers of distributional and demographic dynamics. It is possible that the numbat model overpredicts persistence at least in some regions, probably because it does not include the potential impacts of multiple invasive predators or the loss of native vegetation (Friend, 1990; Friend & Page, 2017).

The modelling framework developed here provides a potentially powerful tool for understanding why and how many Australian mammals declined in range and ultimately became extinct. However, it will not be applicable to all species. For some species, there are too few occurrence records or other data to support the modelling and validation. Nevertheless, a modelling approach focused on simulating the decline of numerous carefully chosen species that comprise diverse but representative members of a regional biota, capturing variation in life histories, and ecological guilds, will produce valuable insights and generalities for conserving native wildlife across Australia and other regions as well (Chichorro et al., 2019; Fisher & Owens, 2004).

3.2 | Increasing the effectiveness of conservation

It is now widely accepted that conservation planning will benefit from a better integration of the spatiotemporal dynamics of threatening processes into conservation decision making (Evans et al., 2011; Geyle et al., 2018). While it is often advocated that using current or future threats is more informative than a focus on past threats to prioritize conservation action (Watson et al., 2009), the present-day precarity of many Australian mammals is very likely to be irreversible if the landscape-scale processes that caused their initial, historical declines continue to operate. This is especially so if the processes driving past declines and extinctions have led to increased susceptibility to, or interact with, the recent and emerging threats of climate and environmental change, including catastrophic wildfires (Abram et al., 2021; Legge et al., 2022; Woinarski et al., 2015). One key case in point may be that of the greater glider *Petauroides volans*, whose decline was historically driven by forest clearing and fire, but which more recently is being exacerbated by changing climate (Wagner et al., 2020).

Applying process-explicit models to the ongoing collapse of the Australian mammal fauna could help to address longstanding questions in conservation biology. For example, it could help to establish how ecological characteristics of species interact dynamically with environmental threats to cause initial population declines, a central question in ecology that has never been resolved (Beissinger, 2000; Chichorro et al., 2019). Furthermore, output from these models is likely to provide additional practical biogeographic insights for conservation planning, including providing geographically explicit guidance for establishment and connection of reserves through landscape-scale restoration (Sweeney et al., 2019), along with more accurate assessment of the conservation value of remnant, peripheral populations (Fisher, 2011; Lesica & Allendorf, 1995). Our protocol for advancing conservation biogeography also holds potential for determining where and in what numbers species should be reintroduced (Armstrong & Seddon, 2008), and how these strategies may vary across predator inhabited (e.g. cat and fox) and predator-free safe havens.

4 | LOOKING FORWARD

Halting the ongoing declines of Australian mammals requires a better understanding of the biogeographic patterns and drivers of geographic range collapse since 1788. While reconstructing 230 years of range dynamics for all Australian mammals is not plausible, the pool of candidate species for which there are suitable data for model development is ecologically and evolutionarily diverse. This includes several species currently identified as threatened under Australian legislation: numbat (*Myrmecobius fasciatus*), mala (*Lagorchestes hirsutus*), woylie (*Bettongia penicillata*), western quoll (*Dasyurus geoffroii*), eastern quoll (*Dasyurus viverrinus*), brush-tailed rabbit-rat (*Conilurus penicillatus*), greater bilby (*Macrotis lagotis*), eastern barred bandicoot (*Perameles gunnii*) and golden bandicoot (*Isoodon auratus*). Emerging and rapidly expanding databases on the historical dynamics of Australia's mammalian assemblages (Peters et al., 2019) will facilitate geographically- and process-explicit simulation analyses, particularly if they are made open source (Fordham & Nogues-Bravo, 2018). This will enable a more comprehensive understanding of the dynamics of geographic range collapse, which may guide more effective strategies for conserving remnant populations of even the most threatened species.

Improved integration of palaeo- and modern ecological data is key to such future development and collaboration. The current incompleteness and poor resolution of the Australian fossil record is being addressed using new geochronological techniques (Bravenec et al., 2018), better systematic excavation, and the development and harmonization of palaeo-environmental proxies at finer spatiotemporal resolution (Kaufman et al., 2020). Museums hold substantial volumes of information that remain difficult to access in non-digital formats, and digitizing these data will vastly enhance ecological inferences about the past (Marshall et al., 2018). High-resolution dating of the wealth of Australian Holocene fossil sites and digitizing the field notes of naturalists and explorers (Figure 1; Horner & Johnson, 2021) is of particular relevance to mitigating Australian mammal extinctions. Data mining algorithms trained to efficiently extract information on past mammal occurrences from these field notes could prove to be particulary powerful tools for conservation biogeography (Gallant et al., 2016; Nunez-Mir et al., 2016).

While continuous climate projections are now available from the Last Glacial Maximum into the future (Brown et al., 2020), reconstructing regional changes to fire regimes presents a major research challenge because of the relative invisibility of fire regimes in the historical record, especially in sparsely populated parts of Australia. Nevertheless, descriptions of changes in fire regimes in explorers' journals (Fensham, 1997; Vigilante, 2001), and mid-20th century aerial photographs (Burrows et al., 2006) can be integrated into DGVMs with detailed fire sub-models (Rabin et al., 2017) to explore different scenarios of change in fire regimes.

5 | CONCLUSION

The rapid and ongoing rate of range collapse and extinction of mammals in Australia since European colonization, and the wealth of spatiotemporal information on the potential drivers of these extinctions, makes the last 230 years of Australia's natural history a very tractable, large-scale unplanned experiment that can be leveraged for prescriptive conservation biogeography. Where similar information is available on past occurrence records and extinction threats for other taxonomic groups in Australia, and biota on other continents, the approach we describe here can be adapted to conserve other threatened wildlife across the globe.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Figshare at: https://doi.org/10.6084/m9.figshare.16713874.v3.

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REFERENCES

Abbott, I. (2001). The bilby *Macrotis lagotis* (Marsupialia: Peramelidae) in South-Western Australia: Original range limits, subsequent decline, and presumed regional extinction. *Records of the Western Australian Museum*, *20*, 271–306.

Abbott, I. (2008a). Historical perspectives of the ecology of some conspicuous vertebrate species in south-West Western Australia. *Conservation Science Western Australia*, *6*, 1–214.

Abbott, I. (2008b). The spread of the cat, *Felis catus*, in Australia: Re-examination of the current conceptual model with additional information. *Conservation Science Western Australia*, *7*, 1–17.

Abram, N. J., Henley, B. J., Gupta, A. S., Lippmann, T. J. R., Clarke, H., Dowdy, A. J., Sharples, J. J., Nolan, R. H., Zhang, T., Wooster, M. J., Wurtzel, J. B., Meissner, K. J., Pitman, A. J., Ukkola, A. M., Murphy, B. P., Tapper, N. J., & Boer, M. M. (2021). Connections of climate change and variability to large and extreme forest fires in Southeast Australia. *Communications Earth & Environment*, *2*, 8.

Archer, M., Bates, H., Hand, S. J., Evans, T., Broome, L., McAllan, B., Geiser, F., Jackson, S., Myers, T., Gillespie, A., & Palmer, C. (2019). The Burramys project: A conservationist's reach should exceed history's grasp, or what is the fossil record for? *Philosophical Transactions of the Royal Society B*, *374*, 20190221.

Armstrong, D. P., & Seddon, P. J. (2008). Directions in reintroduction biology. *Trends in Ecology and Evolution*, *23*, 20–25.

Australia, G. O. (2021). *Environment protection and biodiversity conservation act, 1999*. Commonwealth of Australia.

Barnosky, A. D., Hadly, E. A., Gonzalez, P., Head, J., Polly, P. D., Lawing, A. M., Eronen, J. T., Ackerly, D. D., Alex, K., Biber, E., & Blois, J. (2017). Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. *Science*, *355*, 6325.

Beissinger, S. R. (2000). Ecological mechanisms of extinction. *Proceedings of the National Academy of Sciences of the United States of America*, *97*, 11688–11689.

Bradshaw, C. J. (2012). Little left to lose: Deforestation and forest degradation in Australia since European colonization. *Journal of Plant Ecology*, *5*, 109–120.

Bravenec, A. D., Ward, K. D., & Ward, T. J. (2018). Amino acid racemization and its relation to geochronology and archaeometry. *Journal of Separation Science*, *41*, 1489–1506.

Broome, L., Archer, M., Bates, H., Shi, H., Geiser, F., McAllan, B., Heinze, D., Hand, S., Evans, T., & Jackson, S. (2012). A brief review of the life history of, and threats to, *Burramys parvus* with a pre-history based proposal for ensuring that it has a future. In D. Lunney & P. Hutchins (Eds.), *Wildlife and climate change: Towards robust conservation strategies for Australian fauna* (pp. 114–126). Royal Zoological Society of NSW.

Brown, S. C., Wigley, T. M., Otto-Bliesner, B. L., & Fordham, D. A. (2020). StableClim, continuous projections of climate stability from 21000 BP to 2100 CE at multiple spatial scales. *Scientific Data*, *7*, 1–13.

Bulte, E. H., Horan, R. D., & Shogren, J. F. (2003). Is the Tasmanian tiger extinct? A biological–economic re-evaluation. *Ecological Economics*, *45*, 271–279.

Burbidge, A., Johnson, K., Fuller, P., & Southgate, R. (1988). Aboriginal knowledge of the mammals of the central deserts of Australia. *Australian Wildlife Research*, *15*, 9–39.

Burbidge, A. A., & McKenzie, N. L. (1989). Patterns in the modern decline of Western Australia's vertebrate fauna; causes and conservation implications. *Biological Conservation*, *50*, 143–198.

Burrows, N. D., Burbidge, A. A., Fuller, P. J., & Behn, G. (2006). Evidence of altered fire regimes in the Western Desert region of Australia. *Conservation Science Western Australia*, *5*, 272–284.

Canteri, E., Brown, S. C., Schmidt, N. M., Heller, R., Nogués-Bravo, D., & Fordham, D. A. (2022). Spatiotemporal influences of climate and humans on muskox range dynamics over multiple millennia. *Global Change Biology*, *28*, 6602–6617. https://doi.org/10.1111/gcb.16375

Caughley, G. (1994). Directions in conservation biology. *Journal of Animal Ecology*, *63*, 215–244.

Channell, R., & Lomolino, M. V. (2000). Dynamic biogeography and conservation of endangered species. *Nature*, *403*, 84–86.

Chapman, T. F. (2015). Reintroduced burrowing bettongs (*Bettongia lesueur*) scatter hoard sandalwood (*Santalum spicatum*) seed. *Australian Journal of Zoology*, *63*, 76–79.

Chichorro, F., Juslén, A., & Cardoso, P. (2019). A review of the relation between species traits and extinction risk. *Biological Conservation*, *237*, 220–229.

Colwell, R. K., & Rangel, T. F. (2010). A stochastic, evolutionary model for range shifts and richness on tropical elevational gradients under quaternary glacial cycles. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 3695–3707.

Connolly, S. R., Keith, S. A., Colwell, R. K., & Rahbek, C. (2017). Process, mechanism, and modeling in macroecology. *Trends in Ecology and Evolution*, *32*, 835–844.

Dahl, K. (1926). *In savage Australia: An account of a hunting and collecting expedition to Arnhem land and Dampier land*. Philip Allan.

Davidson, A. D., Hamilton, M. J., Boyer, A. G., Brown, J. H., & Ceballos, G. (2009). Multiple ecological pathways to extinction in mammals. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 10702–10705.

Dennis, A. J. (2003). Scatter-hoarding by musky rat-kangaroos, *Hypsiprymnodon moschatus*, a tropical rain-forest marsupial from Australia: Implications for seed dispersal. *Journal of Tropical Ecology*, *19*, 619–627.

Elith, J., & Leathwick, J. R. (2009). Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, *40*, 677–697.

Elliott, T. F., Townley, S., Johnstone, C., Meek, P., Gynther, I., & Vernes, K. (2020). The endangered Hastings River mouse (*Pseudomys oralis*) as a disperser of ectomycorrhizal fungi in eastern Australia. *Mycologia*, *112*, 1–11.

Evans, M. C., Watson, J. E., Fuller, R. A., Venter, O., Bennett, S. C., Marsack, P. R., & Possingham, H. P. (2011). The spatial distribution of threats to species in Australia. *Bioscience*, *61*, 281–289.

Fairfax, R. J. (2019). Dispersal of the introduced red fox (*Vulpes vulpes*) across Australia. *Biological Invasions*, *21*, 1259–1268.

Fensham, R. J. (1997). Aboriginal fire regimes in Queensland, Australia: Analysis of the explorers' record. *Journal of Biogeography*, *24*, 11–22.

Finlayson, H. H. (1961). *On central Australian mammals: The distribution and status of central Australian species*. South Australian Museum.

Fisher, D. O. (2011). Trajectories from extinction: Where are missing mammals rediscovered? *Global Ecology and Biogeography*, *20*, 415–425.

Fisher, D. O., Johnson, C. N., Lawes, M. J., Fritz, S. A., McCallum, H., Blomberg, S. P., VanDerWal, J., Abbott, B., Frank, A., Legge, S., & Letnic, M. (2014). The current decline of tropical marsupials in Australia: Is history repeating? *Global Ecology and Biogeography*, *23*, 181–190.

Fisher, D. O., & Owens, I. P. (2004). The comparative method in conservation biology. *Trends in Ecology and Evolution*, *19*, 391–398.

Flannery, T. (1994). *The future eaters*. New Holland Publishers.

Fordham, D. A., Akçakaya, H. R., Alroy, J., Saltré, F., Wigley, T. M., & Brook, B. W. (2016). Predicting and mitigating future biodiversity loss using long-term ecological proxies. *Nature Climate Change*, *6*, 909–916.

Fordham, D. A., Akçakaya, H. R., Araújo, M. B., Keith, D. A., & Brook, B. W. (2013). Tools for integrating range change, extinction risk and climate change information into conservation management. *Ecography*, *36*, 956–964.

Fordham, D. A., Brown, S. C., Akçakaya, H. R., Brook, B. W., Haythorne, S., Manica, A., Shoemaker, K. T., Austin, J. J., Blonder, B., Pilowsky, J., & Rahbek, C. (2022). Process-explicit models reveal pathway to extinction for woolly mammoth using pattern-oriented validation. *Ecology Letters*, *25*, 125–137.

Fordham, D. A., Haythorne, S., Brown, S. C., Buettel, J. C., & Brook, B. W. (2021). Poems: R package for simulating species' range dynamics using pattern-oriented validation. *Methods in Ecology and Evolution*, *12*, 2364–2371.

Fordham, D. A., Jackson, S. T., Brown, S. C., Huntley, B., Brook, B. W., Dahl-Jensen, D., Gilbert, M. T. P., Otto-Bliesner, B. L., Svensson, A., Theodoridis, S., & Wilmshurst, J. M. (2020). Using paleo-archives to safeguard biodiversity under climate change. *Science*, *369*, eabc5654.

Fordham, D. A., & Nogues-Bravo, D. (2018). Open-access data is uncovering past responses of biodiversity to global environmental change. *Pages*, *26*, 77.

Friend, J. A. (1990). The numbat *Myrmecobius fasciatus* (Myrmecobiidae): History of decline and potential for recovery. *Proceedings of the Ecological Society of Australia*, *16*, 369–377.

Friend, J. A. (1994). *Recovery plan for the numbat (Myrmecobius fasciatus), 1995–2004*. Department of Conservation and Land Management (Western Australia).

Friend, J. A., & Page, M. J. (2017). *Numbat (Myrmecobius fasciatus) recovery plan*. Wildlife Management Program No. 60. Department of Parks and Wildlife.

Gallagher, R. V., Falster, D. S., Maitner, B. S., Salguero-Gómez, R., Vandvik, V., Pearse, W. D., Schneider, F. D., Kattge, J., Poelen, J. H., Madin, J. S., Ankenbrand, M. J., Penone, C., Feng, X., Adams, V. M., Alroy, J., Andrew, S. C., Balk, M. A., Bland, L. M., Boyle, B. L., … Enquist, B. J. (2020). Open Science principles for accelerating trait-based science across the tree of life. *Nature Ecology & Evolution*, *4*, 294–303.

Gallant, D., Gauvin, L. Y., Berteaux, D., & Lecomte, N. (2016). The importance of data mining for conservation science: A case study on the wolverine. *Biodiversity and Conservation*, *25*, 2629–2639.

Geyle, H. M., Woinarski, J. C., Baker, G. B., Dickman, C. R., Dutson, G., Fisher, D. O., Ford, H., Holdsworth, M., Jones, M. E., Kutt, A., & Legge, S. (2018). Quantifying extinction risk and forecasting the number of impending Australian bird and mammal extinctions. *Pacific Conservation Biology*, *24*, 157–167.

Goldberg, A., Mychajliw, A. M., & Hadly, E. A. (2016). Post-invasion demography of prehistoric humans in South America. *Nature*, *532*, 232–235.

Goldingay, R. L., Carthew, S. M., & Whelan, R. J. (1991). The importance of non-flying mammals in pollination. *Oikos*, *61*, 79–87.

Goring, S. J., & Williams, J. W. (2017). Effect of historical land-use and climate change on tree-climate relationships in the upper Midwestern United States. *Ecology Letters*, *20*, 461–470.

Grace, M., Akcakaya, H. R., Bennett, E., Hilton-Taylor, C., Long, B., Milner-Gulland, E. J., Young, R., & Hoffmann, M. (2019). Using historical and palaeoecological data to inform ambitious species recovery targets. *Philosophical Transactions of the Royal Society of London B*, *374*, 20190297.

Grimm, V., & Railsback, S. F. (2012). Pattern-oriented modelling: A 'multi-scope' for predictive systems ecology. *Philosophical Transactions of the Royal Society B*, *367*, 298–310.

Hanna, E., & Cardillo, M. (2013). A comparison of current and reconstructed historic geographic range sizes as predictors of extinction risk in Australian mammals. *Biological Conservation*, *158*, 196–204.

Hanski, I. (1998). Metapopulation dynamics. *Nature*, *396*, 41–49.

Hawke, T., Bates, H., Hand, S., Archer, M., & Broome, L. (2019). Dietary analysis of an uncharacteristic population of the mountain pygmy-possum (*Burramys parvus*) in the Kosciuszko National Park, New South Wales, Australia. *PeerJ*, *7*, e6307.

Haythorne, S., Fordham, D. A., Brown, S. C., Buettel, J. C., & Brook, B. W. (2021). *poems: Pattern-oriented ensemble modeling system*. The Comprehensive R Archive Network.

Haythorne, S., Pilowsky, J., Brown, S. C., & Fordham, D. A. (2021). *paleopop: Pattern-oriented modeling framework for coupled niche-population paleo-climatic models*. The Comprehensive R Archive Network.

Heinze, D., Broome, L., & Mansergh, I. (2004). A review of the ecology and conservation of the mountain pygmy-possum *Burramys parvus*. In R. L. Goldingay & S. M. Jackson (Eds.), *Biology of Australian possums and gliders* (pp. 254–267). Surrey Beatty and Sons.

Helgen, K. M., Portela Miguez, R., Kohen, J., & Helgen, L. (2012). Twentieth century occurrence of the Long-beaked echidna *Zaglossus bruijnii* in the Kimberley region of Australia. *ZooKeys*, *255*, 103–132.

Holt, B. G., Lessard, J.-P., Borregaard, M. K., Fritz, S. A., Araújo, M. B., Dimitrov, D., Fabre, P.-H., Graham, C. H., Graves, G. R., Jønsson, K. A., Nogués-Bravo, D., Wang, Z., Whittaker, R. J., Fjeldså, J., & Rahbek, C. (2013). An update of Wallace's zoogeographic regions of the world. *Science*, *339*, 74–78.

Horner, P., & Johnson, K. (2021). The HH Finlayson mammal collection. *Australian Mammalogy*, *44*, 1–15.

James, A. I., Eldridge, D. J., Koen, T. B., & Moseby, K. E. (2011). Can the invasive European rabbit (*Oryctolagus cuniculus*) assume the soil engineering role of locally-extinct natives? *Biological Invasions*, *13*, 3027–3038.

Jetz, W., McPherson, J. M., & Guralnick, R. P. (2012). Integrating biodiversity distribution knowledge: Toward a global map of life. *Trends in Ecology and Evolution*, *27*, 151–159.

Johnson, C. (2006). *Australia's mammal extinctions: A 50,000 year history*. Cambridge University Press.

Johnson, C. N., Alroy, J., Beeton, N. J., Bird, M. I., Brook, B. W., Cooper, A., Gillespie, R., Herrando-Pérez, S., Jacobs, Z., Miller, G. H., Prideaux, G. J., Roberts, R. G., Rodríguez-Rey, M., Saltré, F., Turney, C. S. M., & Bradshaw, C. J. A. (2016). What caused extinction of the Pleistocene megafauna of Sahul? *Proceedings of the Royal Society B*, *283*, 20152399.

Johnson, C. N., Dortch, J., & Worthy, T. H. (2023). Interactions with megafauna. In I. J. McNiven & B. David (Eds.), *The Oxford handbook of the archaeology of indigenous Australia and New Guinea*. Oxford University Press.

Kaufman, D., McKay, N., Routson, C., Erb, M., Davis, B., Heiri, O., Jaccard, S., Tierney, J., Dätwyler, C., Axford, Y., Brussel, T., Cartapanis, O., Chase, B., Dawson, A., de Vernal, A., Engels, S., Jonkers, L., Marsicek, J., Moffa-Sánchez, P., … Zhilich, S. (2020). A global database of Holocene paleotemperature records. *Scientific Data*, *7*, 115.

Knowles, L. L., Carstens, B. C., & Keat, M. L. (2007). Coupling genetic and ecological-niche models to examine how past population distributions contribute to divergence. *Current Biology*, *17*, 940–946.

Knowles, L. L., & Massatti, R. (2017). Distributional shifts—Not geographic isolation—As a probable driver of montane species divergence. *Ecography*, *40*, 1475–1485.

Kuussaari, M., Bommarco, R., Heikkinen, R. K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M., & Steffan-Dewenter, I. (2009). Extinction debt: A challenge for biodiversity conservation. *Trends in Ecology and Evolution*, *24*, 564–571.

Legge, S., Rumpff, L., Woinarski, J. C., Whiterod, N. S., Ward, M., Southwell, D. G., Scheele, B. C., Nimmo, D. G., Lintermans, M., Geyle, H. M., & Garnett, S. T. (2022). The conservation impacts of ecological disturbance: time-bound estimates of population loss and recovery for fauna affected by the 2019–20 Australian megafires. *Global Ecology Biogeography*, *31*, 2085–2104.

Lesica, P., & Allendorf, F. W. (1995). When are peripheral populations valuable for conservation? *Conservation Biology*, *9*, 753–760.

Lindenmayer, D. B., Wood, J. T., McBurney, L., MacGregor, C., Youngentob, K., & Banks, S. C. (2011). How to make a common species rare: A case against conservation complacency. *Biological Conservation*, *144*, 1663–1672.

Lomolino, M. V., & Channell, R. (1995). Splendid isolation: Patterns of geographic range collapse in endangered mammals. *Journal of Mammalogy*, *76*, 335–347.

Lomolino, M. V., & Channell, R. (1998). Range collapse, re-introductions, and biogeographic guidelines for conservation. *Conservation Biology*, *12*, 481–484.

Lomolino, M. V., & Heaney, L. R. (2004). In M. V. Lomlino & L. R. Heaney (Eds.), *Reticulations and reintegration of modern biogeography*. Sinauer and Associates.

Lomolino, M. V., Riddle, B. R., & Whittaker, R. J. (2017). *Biogeography* (5th ed.). Oxford University Press.

Maiorano, L., Cheddadi, R., Zimmermann, N. E., Pellissier, L., Petitpierre, B., Pottier, J., Laborde, H., Hurdu, B. I., Pearman, P. B., Psomas, A., & Singarayer, J. S. (2013). Building the niche through time: Using 13,000 years of data to predict the effects of climate change on three tree species in Europe. *Global Ecology and Biogeography*, *22*, 302–317.

Marshall, C. R., Finnegan, S., Clites, E. C., Holroyd, P. A., Bonuso, N., Cortez, C., Davis, E., Dietl, G. P., Druckenmiller, P. S., Eng, R. C., Garcia, C., Estes-Smargiassi, K., Hendy, A., Hollis, K. A., Little, H., Nesbitt, E. A., Roopnarine, P., Skibinski, L., Vendetti, J., & White, L. D. (2018). Quantifying the dark data in museum fossil collections as palaeontology undergoes a second digital revolution. *Biology Letters*, *14*, 20180431.

McDowell, M. C., Haouchar, D., Aplin, K. P., Bunce, M., Baynes, A., & Prideaux, G. J. (2015). Morphological and molecular evidence supports specific recognition of the recently extinct *Bettongia anhydra* (Marsupialia: Macropodidae). *Journal of Mammalogy*, *96*, 287–296.

McKenzie, N. L. (1981). Mammals of the Phanerozoic south-West Kimberley, Western Australia: Biogeography and recent changes. *Journal of Biogeography*, *8*, 263–280.

Menkhorst, P. W. (2009). Blandowski's mammals: Clues to a lost world. *Proceedings of the Royal Society of Victoria*, *121*, 61–89.

Murphy, B. P., Woolley, L. A., Geyle, H. M., Legge, S. M., Palmer, R., Dickman, C. R., Augusteyn, J., Brown, S. C., Comer, S., Doherty, T. S., & Eager, C. (2019). Introduced cats (*Felis catus*) eating a continental fauna: The number of mammals killed in Australia. *Biological Conservation*, *237*, 28–40.

Nevill, P. G., Bradbury, D., Williams, A., Tomlinson, S., & Krauss, S. L. (2014). Genetic and palaeo-climatic evidence for widespread persistence of the coastal tree species *Eucalyptus gomphocephala* (Myrtaceae) during the last glacial maximum. *Annals of Botany*, *113*, 55–67.

Nogués-Bravo, D. (2009). Predicting the past distribution of species climatic niches. *Global Ecology and Biogeography*, *5*, 521–531.

Nogués-Bravo, D., Rodríguez-Sánchez, F., Orsini, L., De Boer, E., Jansson, R., Morlon, H., Fordham, D. A., & Jackson, S. T. (2018). Cracking the code of biodiversity responses to past climate change. *Trends in Ecology and Evolution*, *33*, 765–776.

Nunez-Mir, G. C., Iannone, B. V., III, Pijanowski, B. C., Kong, N., & Fei, S. (2016). Automated content analysis: Addressing the big literature challenge in ecology and evolution. *Methods in Ecology and Evolution*, *7*, 1262–1272.

Peacock, D., & Abbott, I. (2014). When the 'native cat'would 'plague': historical hyperabundance in the quoll (Marsupialia: Dasyuridae) and an assessment of the role of disease, cats and foxes in its curtailment. *Australian Journal of Zoology*, *62*, 294–344.

Perry, G. L., Wainwright, J., Etherington, T. R., & Wilmshurst, J. M. (2016). Experimental simulation: Using generative modeling and palaeoecological data to understand human-environment interactions. *Frontiers in Ecology and Evolution*, *4*, 109.

Peters, K. J., Saltré, F., Friedrich, T., Jacobs, Z., Wood, R., McDowell, M., Ulm, S., & Bradshaw, C. J. (2019). FosSahul 2.0, an updated database for the late quaternary fossil records of Sahul. *Scientific Data*, *6*, 1–7.

Pilowsky, J. A., Colwell, R. K., Rahbek, C., & Fordham, D. A. (2022). Process-explicit models reveal the structure and dynamics of biodiversity. *Science Advances*, *8*, eabj2271.

Pilowsky, J. A., Haythorne, S., Brown, S. C., Krapp, M., Armstrong, E., Brook, B. W., Rahbek, C., & Fordham, D. A. (2022). Range and extinction dynamics of the steppe bison in Siberia: A pattern-oriented modelling approach. *Global Ecology and Biogeograph*, *31*, 2483–2497.

Power, M. J., Marlon, J., Ortiz, N., Bartlein, P. J., Harrison, S. P., Mayle, F. E., Ballouche, A., Bradshaw, R. H., Carcaillet, C., Cordova, C., & Mooney, S. (2008). Changes in fire regimes since the last glacial maximum: An assessment based on a global synthesis and analysis of charcoal data. *Climate Dynamics*, *30*, 887–907.

Prowse, T. A. A., Johnson, C. N., Lacy, R. C., Bradshaw, C. J. A., Pollak, J. P., Watts, M. J., & Brook, B. W. (2013). No need for disease: Testing extinction hypotheses for the thylacine using multi-species metamodels. *Journal of Animal Ecology*, *82*, 355–364.

Rabin, S. S., Melton, J. R., Lasslop, G., Bachelet, D., Forrest, M., Hantson, S., Kaplan, J. O., Li, F., Mangeon, S., Ward, D. S., Yue, C., Arora, V. K., Hickler, T., Kloster, S., Knorr, W., Nieradzik, L., Spessa, A., Folberth, G. A., Sheehan, T., … Arneth, A. (2017). The fire modeling Intercomparison project (FireMIP), phase 1: Experimental and analytical protocols with detailed model descriptions. *Geoscientific Model Development*, *10*, 1175–1197.

Rangel, T. F., Edwards, N. R., Holden, P. B., Diniz-Filho, J. A. F., Gosling, W. D., Coelho, M. T. P., Cassemiro, F. A., Rahbek, C., & Colwell, R. K. (2018). Modeling the ecology and evolution of biodiversity: Biogeographical cradles, museums, and graves. *Science*, *361*, 6399.

Ringma, J., Legge, S., Woinarski, J. C., Radford, J. Q., Wintle, B., Bentley, J., Burbidge, A. A., Copley, P., Dexter, N., Dickman, C. R., & Gillespie, G. R. (2019). Systematic planning can rapidly close the protection gap in Australian mammal havens. *Conservation Letters*, *12*, e12611.

Ryeland, J., Derham, T. T., & Spencer, R. J. (2021). Past and future potential range changes in one of the last large vertebrates of the Australian continent, the emu *Dromaius novaehollandiae*. *Scientific Reports*, *11*, 1–13.

Saltré, F., Chadoeuf, J., Peters, K. J., McDowell, M. C., Friedrich, T., Timmermann, A., Ulm, S., & Bradshaw, C. J. (2019). Climate-human interaction associated with southeast Australian megafauna extinction patterns. *Nature Communications*, *10*, 1–9.

Saltré, F., Rodríguez-Rey, M., Brook, B. W., Johnson, C. N., Turney, C. S. M., Alroy, J., Cooper, A., Beeton, N., Bird, M. I., Fordham, D. A., Gillespie, R., Herrando-Pérez, S., Jacobs, Z., Miller, G. H., Nogués-Bravo, D., Prideaux, G. J., Roberts, R. G., & Bradshaw, A. D. (2016). Climate change not to blame for late quaternary megafauna extinctions in Australia. *Nature Climate Change*, *7*, 10511.

Short, J., & Calaby, J. (2001). The status of Australian mammals in 1922—Collections and field notes of museum collector Charles Hoy. *Australian Zoologist*, *31*, 533–562.

Smith, A. P., & Quin, D. G. (1996). Patterns and causes of extinction and decline in Australian conilurine rodents. *Biological Conservation*, *77*, 243–267.

Soule, M. E. (1983). What do we really know about extinction? In C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, & W. L. Thomas (Eds.), *Genetics and conservation: A reference for managing wild animals and plant populations*. Benjamin/Cummings.

Staniczenko, P. P., Sivasubramaniam, P., Suttle, K. B., & Pearson, R. G. (2017). Linking macroecology and community ecology: Refining predictions of species distributions using biotic interaction networks. *Ecology Letters*, *20*, 693–707.

Stobo-Wilson, A. M., Murphy, B. P., Legge, S. M., Caceres-Escobar, H., Chapple, D. G., Crawford, H. M., Dawson, S. J., Dickman, C. R., Doherty, T. S., Fleming, P. A., & Garnett, S. T. (2022). Counting the bodies: Estimating the numbers and spatial variation of Australian reptiles, birds and mammals killed by two invasive mesopredators. *Diversity and Distributions*, *28*, 976–991. https://doi.org/10.1111/ddi.13497

Stobo-Wilson, A. M., Stokeld, D., Einoder, L. D., Davies, H. F., Fisher, A., Hill, B. M., Mahney, T., Murphy, B. P., Scroggie, M. P., Stevens, A., Woinarski, J. C. Z., Rangers, B., Rangers, W., & Gillespie, G. R. (2020). Bottom-up and top-down processes influence contemporary patterns of mammal species richness in Australia's monsoonal tropics. *Biological Conservation*, *247*, 108638.

Stodart, E., & Parer, I. (1988). *Colonisation of Australia by the rabbit, Oryctolagus cuniculus*. CSIRO.

Sweeney, O. F., Turnbull, J., Jones, M., Letnic, M., Newsome, T. M., & Sharp, A. (2019). An Australian perspective on rewilding. *Conservation Biology*, *33*, 812–820.

Teresa, C. M., Antoine, G., Carmen, C., Tiziana, S., Anna, L., & Laura, C. M. (2014). A multi-temporal approach to model endangered species distribution in Europe. The case of the Eurasian otter in Italy. *Ecological Modelling*, *274*, 21–28.

Tilman, D., May, R. M., Lehman, C. L., & Nowak, M. A. (1994). Habitat destruction and the extinction debt. *Nature*, *371*, 65–66.

Travouillon, K. J., & Phillips, M. J. (2018). Total evidence analysis of the phylogenetic relationships of bandicoots and bilbies (Marsupialia: Peramelemorphia): Reassessment of two species and description of a new species. *Zootaxa*, *4378*, 224–256.

Valentine, L. E., Ruthrof, K. X., Fisher, R., Hardy, G. E. S. J., Hobbs, R. J., & Fleming, P. A. (2018). Bioturbation by bandicoots facilitates seedling growth by altering soil properties. *Functional Ecology*, *32*, 2138–2148.

Vieira, E. M., Finlayson, G. R., & Dickman, C. R. (2007). Habitat use and density of numbats (*Myrmecobius fasciatus*) reintroduced in an area of mallee vegetation, New South Wales. *Australian Mammalogy*, *29*, 17–24.

Vigilante, T. (2001). Analysis of explorers' records of aboriginal landscape burning in the Kimberley region of Western Australia. *Australian Geographical Studies*, *39*, 135–155.

Wagner, B., Baker, P. J., Stewart, S. B., Lumsden, L. F., Nelson, J. L., Cripps, J. K., Durkin, L. K., Scroggie, M. P., & Nitschke, C. R. (2020). Climate change drives habitat contraction of a nocturnal arboreal marsupial at its physiological limits. *Ecosphere*, *11*, e03262.

Waller, N. L., Gynther, I. C., Freeman, A. B., Lavery, T. H., & Leung, L. K.-P. (2017). The bramble cay melomys *Melomys rubicola* (Rodentia: Muridae): A first mammalian extinction caused by human-induced climate change? *Wildlife Research*, *44*, 9–21.

Watson, J. E., Fuller, R. A., Watson, A. W., Mackey, B. G., Wilson, K. A., Grantham, H. S., Turner, M., Klein, C. J., Carwardine, J., Joseph, L. N., & Possingham, H. P. (2009). Wilderness and future conservation priorities in Australia. *Diversity and Distributions*, *15*, 1028–1036.

Wayne, A. F., Maxwell, M. A., Ward, C. G., Vellios, C. V., Wilson, I., Wayne, J. C., & Williams, M. R. (2015). Sudden and rapid decline of the abundant marsupial *Bettongia penicillata* in Australia. *Oryx*, *49*, 175–185.

Westaway, M. C., Price, G., Miscamble, T., McDonald, J., Cramb, J., Ringma, J., Grün, R., Jones, D., & Collard, M. (2019). A palaeontological perspective on the proposal to reintroduce Tasmanian devils to mainland Australia to suppress invasive predators. *Biological Conservation*, *232*, 187–193.

Wilson, E. O. (1999). Prologue. In G. Daws & M. Fujita (Eds.), *Archipelago: The Islands of Indonesia* (pp. xi–xii).

Woinarski, J. C., Braby, M. F., Burbidge, A. A., Coates, D., Garnett, S. T., Fensham, R. J., Legge, S. M., McKenzie, N. L., Silcock, J. L., & Murphy, B. P. (2019). Reading the black book: The number, timing, distribution and causes of listed extinctions in Australia. *Biological Conservation*, *239*, 108261.

Woinarski, J. C., Burbidge, A. A., & Harrison, P. L. (2015). Ongoing unraveling of a continental fauna: Decline and extinction of Australian mammals since European settlement. *Proceedings of the National Academy of Sciences of the United States of America*, *112*, 4531–4540.

Woinarski, J. C. Z., Legge, S., Fitzsimons, J. A., Traill, B. J., Burbidge, A. A., Fisher, A., Firth, R. S. C., Gordon, I. J., Griffiths, A. D., Johnson, C. N., McKenzie, N. L., Palmer, C., Radford, I., Rankmore, B., Ritchie, E. G., Ward, S., & Ziembicki, M. (2011). The disappearing mammal fauna of northern Australia: Context, cause, and response. *Conservation Letters*, *4*, 192–201.

Zamberletti, P., Papaïx, J., Gabriel, E., & Opitz, T. (2022). Understanding complex spatial dynamics from mechanistic models through spatiotemporal point processes. *Ecography*, *2022*, e05956.

Ziembicki, M. R., Woinarski, J. C. Z., & Mackey, B. (2013). Evaluating the status of species using indigenous knowledge: Novel evidence for major native mammal declines in northern Australia. *Biological Conservation*, *157*, 78–92.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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