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Reading the black book: The number, timing, distribution and causes of listed extinctions in Australia

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ABSTRACT

Through collation of global, national and state/territory threatened species lists, we conclude that 100 Australian endemic species (one protist, 38 vascular plants, ten invertebrates, one fish, four frogs, three reptiles, nine birds and 34 mammals) are validly listed as extinct (or extinct in the wild) since the nation's colonisation by Europeans in 1788. This tally represents about 6–10% of the world's post-1500 recognised extinctions. The actual number of extinctions is likely to be far more than those recognised in formal lists. Mammals have suffered the highest proportional rate of extinction (ca. 10% of the endemic mammal fauna). There are four main distributional features of these extinctions: (i) consistent with global patterns, island endemic species are disproportionately represented; (ii) many non-island extinct species had highly restricted mainland ranges; but conversely (iii) many extinct mammals had extensive ranges; and (iv) there have been no recognised extinctions of species confined to Australia's mainland monsoonal tropics. Extinctions have occurred largely continuously since Australia's European settlement, with at least three extinctions in the last decade. Mammal extinctions were caused mainly by introduced predators; plant extinctions by habitat loss; frog extinctions by disease; reptile extinctions by an introduced snake; and invertebrate extinctions by a range of anthropogenic processes. Causality has changed over time, with recent extinctions more likely to be associated with disease, introduced reptiles and introduced fish and less likely to be associated with hunting and introduced mammalian predators. The most recent extinction is the sole case for which climate change was a major factor.

1. Introduction

'The past is a foreign country; they do things differently there' (L.P. Hartley The Go-Between, 1953)
'Those who don't know history are destined to repeat it' (Edmund Burke Reflections on the Revolution in France, 1790)

The colonisation of Australia by Europeans in 1788 has led to substantial environmental transformation of the isolated continent. Many plant, animal and pathogen species have been (and continue to be) introduced; many vegetation types have been (and continue to be) extensively cleared (Bradshaw, 2012); fire regimes have been (and continue to be) modified; some native plant and animal species have been intensively harvested and hunted; and freshwater and coastal environments have been (and continue to be) exploited and transformed. In response to such changes, many species have declined and some have become extinct. Here, we review the record of extinctions. We ask the following: (1) how many extinctions have occurred; (2) whether particular taxonomic groupings have been most affected; (3) when did they occur; (4) where did they occur; and (5) what factors caused or contributed to them?

This accounting and autopsy is not straightforward, for many reasons. First, it is likely that there have been many more extinctions than those currently recognised in official lists. Many species, particularly of less charismatic groups, disappeared with little or no documentation or collection. Second, it is often challenging enough to identify what factor

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or combination of factors are causing the decline of extant threatened species or of recently extinct species (Woinarski, 2018): it is typically harder to ascribe causality to historic extinctions. Third, extinctions can be difficult to prove (Lee et al., 2017; Thompson et al., 2017; Butchart et al., 2018) and there are happily some examples of rediscovery of Australian species that had been considered extinct (Keith and Burgman, 2004; Silcock et al., 2019 in press). Fourth, sparse, fragmentary and imprecise evidence about many extinct species means that the year of the death of the last individual may be very hard to determine. Fifth, the former distributions of many now-extinct species are poorly documented because in many cases few specimens were collected and the collection site was often very imprecisely described.

Although there have been some notable reviews of extinctions in some components of the Australian biota (Johnson, 2006; Woinarski et al., 2015; Silcock et al., 2019 in press), there has been no previous comprehensive review of the extent of extinctions on this continent, and such a doomsday account (a 'black book') is worth compiling for its own sake. However, we also wish to assess the extent to which we can learn from these losses such that future losses may be averted or less likely to occur. Hence, as context to this review, we consider which of the quotes above better fits the pattern of extinctions, as either a relic of the past (and due to factors now no longer operating or now effectively controlled) or as a seamless fabric (and hence likely to continue to recur).

We also note the caveat that biodiversity loss is more nuanced and extensive than species extinctions alone. Many extant Australian species, particularly mammals, have current distributions and population sizes that comprise only a minute proportion of their former range and abundance (Woinarski et al., 2015).

2. Methods

2.1. Compilation of listed extinct species

Our assessment relates to the set of Australian endemic species that are currently listed as extinct (or extinct in the wild) under at least one of three possible sources, as at April 2019: (1) Australian national legislation (the *Environment Protection and Biodiversity Conservation Act 1999*: EPBC Act); (2) the legislation of Australian states and territories (after excluding species listed as extinct in one state or territory but known to be extant in another), noting that the external territories of Norfolk Island and Christmas Island do not have their own threatened species listings; and (3) globally (by the IUCN), based on downloading records of all extinct species present in the geographic regions of Australia and its island territories from the IUCN Red List of Threatened Species (www.iucnredlist.org). Note that there are some inconsistencies among these sources in the manner in which extinction is defined (see Appendix B), and in the extent of documentation of extinction for individual species.

After initial collation across these sources, we excluded species for which records subsequent to listing demonstrate that the species is extant, for which subsequent taxonomic assessment has led to the taxon no longer being recognised as a species (see Appendix A for our justification of such deletions and inclusions), or that are extant beyond Australia (*i.e.* our listing relates only to Australian endemic species). The EPBC Act includes some extinct subspecies, but we exclude these in order to allow more ready comparability among the three sources of listed extinctions, and because there are marked taxonomic biases in the extent of recognition of subspecies and the documentation of their conservation status.

We also sought to exclude listed extinct species for which the extinction most likely happened prior to European settlement (1788). This disqualification criterion is challenging for some species, particularly mammals and land snails known only from relatively recent (but not necessarily precisely dated) subfossil material. For example, many invertebrate species are likely to have become extinct on Norfolk Island prior to its European settlement but after an earlier (but subsequently abandoned) colonisation by Polynesians, and their commensal Polynesian rat *Rattus exulans*, from about 800 CE (Anderson and White, 2001; Neuweger et al., 2001).

We compared, across main taxonomic groups, the relative proportion of extinct species to the estimated number of Australian species, using the species richness (and endemic species richness) tallies given in Chapman (2009).

2.2. Timing of extinctions

The dating of extinctions is challenging for many species. Some species are known only from subfossils thought to post-date the arrival of Europeans (Cramb and Hocknull, 2010). Many are known only from a single collection or small number of early collections, in some cases without precise dates. Furthermore, the date of the last known collection is not necessarily a reliable measure of the date of extinction. For example, Indigenous reports indicate that many now-extinct mammal species persisted many decades after the last known museum specimens were collected (Burbidge et al., 1988). While recognising these caveats, we report the date of the last known record (based on collections or other account, including information from Indigenous sources) of a species in the wild. We then tally the estimated number of extinctions per decade and cumulative number of extinctions across decades.

2.3. Former distribution of extinct species

There are marked challenges in trying to circumscribe the distributions for now extinct species at the cusp of European settlement. Perhaps exceptionally in a global context, many now extinct Australian mammal species had near continental ranges 200 years ago (Hanna and Cardillo, 2013), but scattered collection effort across this range means that it is now difficult to delineate those distributions precisely. Many other now extinct species are known from only a single collection or few collections, with many early collections having no, or imprecise, locational data. To deal with this distributional imprecision, we follow the approach used by McKenzie et al. (2007) and Woinarski et al. (2014) in describing distribution by presence/absence across the set of 89 Australian bioregions (Thackway and Cresswell, 1995).

We tally and map the absolute number of extinct species that formerly occurred in each bioregion, and a *range weighted extinction* metric – an index weighted inversely by the number of bioregions in which individual species are thought to have occurred in 1788:

$$\textit{range weighted extinction metric} = \sum_{i=1}^{n} \frac{1}{r_i}$$

Where n is the number of extinct species formerly in the bioregion and r_i is the number of bioregions in which species i formerly occurred. For example, if a bioregion formerly contained three now-extinct species, which formerly occurred in 1, 3 and 5 bioregions, the range weighted extinction metric for the bioregion would be $^1/_1 + {^1/_3} + {^1/_5} = 1.53$.

To further explore the spatial patterning of extinction, we modelled the bioregional extinctions with a set of environmental and other factors of each bioregion. We identified seven variables that we considered might plausibly affect the number of extinct species in each bioregion. Four of these were static environmental variables: mean annual rainfall, mean annual temperature, topographic complexity (ruggedness), and the extent to which the bioregion is dominated by islands. The other three variables related to anthropogenic disturbance: the proportion of the bioregion cleared, proportion in conservation reserves, and human population density.

To describe topographic complexity, we used a ruggedness index, defined as the standard deviation of elevation within a 5 km radius, based on a 30-m digital elevation model. Mean annual rainfall (Australian Bureau of Meteorology, 2016b), mean annual temperature

(Australian Bureau of Meteorology, 2016a), the ruggedness index and human population density (Center for International Earth Science Information Network, 2016) were averaged across each bioregion. Mean annual rainfall and mean annual temperature were primarily from the Australian Bureau of Meteorology (2016a,b), except for offshore islands. In these cases WorldClim data were used (Fick and Hijmans, 2017). The extent of cleared vegetation was obtained from National Vegetation Information System (2018), and extent of conservation reserves from the Collaborative Australian Protected Area Database (Department of the Environment and Energy, 2016). We recognise some interpretational caveats with these variables, notably that the values for some variables (*e.g.* current human population density) may post-date at least some extinctions.

We examined the extent to which the loss of species varied among bioregions, relative to the total number of species present in the bioregion in 1788. Such original species richness tallies are available for mammals and plants, with estimates of native species richness for each bioregion given in McKenzie et al. (2007) (and an updated, unpublished version of that dataset) and Haque (2014), respectively. However, for other taxonomic groups, there is no readily available information on species richness of each bioregion. We analysed three response variables: (1) the number of extinct species (including all taxonomic groups) in each bioregion; (2) the proportion of plant species extinct in each bioregion; and (3) the proportion of mammal species extinct in each bioregion. The taxonomic groups other than plants and mammals were not analysed separately because they had relatively few extinct species (10 or fewer species, cf. 38 plant species and 34 mammal species).

To explain variation in the three response variables, we developed a set of 128 candidate models, representing all combinations of the seven explanatory variables (without interactions). To account for varying species richness of bioregions when analysing the number of extinct species (including all taxonomic groups), we included an index of species richness as a predictor variable in all 128 models. The index was based on the species richness of plants and mammals (which we assume are correlated with total species richness):

$$Species\ richness\ index = 0.5 \times \left(\frac{S_{plants}}{\max(S_{plants})} + \frac{S_{mammals}}{\max(S_{mammals})} \right)$$

Where S_{plants} and $S_{mammals}$ are the species richness of plants and mammals in each bioregion. The models of the number of extinct species (including all taxonomic groups) were fitted as zero-inflated poisson models (Zuur and Ieno, 2016). The models of the proportion of plant and mammal species extinct in each bioregion were initially fitted as generalized linear models with binomial error family, suitable for proportion data (*i.e.* proportion of species extinct).

Some of the explanatory variables were correlated, which can lead to issues of collinearity. Following Zuur et al. (2010), we used the variance inflation factor (VIF) to identify variables which led to excessive collinearity, and these variables were excluded from the analysis. We used a conservative VIF threshold of 3. As a result of this process, ruggedness was excluded from the analysis of all groups combined and plants.

For each of the 128 candidate models, we calculated Akaike's Information Criterion (AIC) and used this to rank the models. We present the best-supported models (ΔAIC ≤ 2; Burnham and Andersen 2003) in Table 3. In the case of all groups combined and mammals, there was evidence of overdispersion, so model selection was based on quasi-AIC (QAIC) (Burnham and Anderson, 2003). We report D^2, the proportion of the null deviance explained by each model, as an expression of model fit. D^2 cannot be readily calculated for zero-inflated Poisson models (used for the analysis of the number of extinct species including all taxonomic groups), so in this instance we report the D^2 of a poisson GLM.

2.4. Causes of extinction

For a few species, the primary cause of extinction is well documented and unarguable – an example is the recent extinction of at least four Australian frog species due to the disease chytridiomycosis (Skerratt et al., 2007). However, for most species, causality is less well established; and for some species there is unresolved dispute about the cause(s) of extinction (Paddle, 2002; Abbott, 2006; Prowse et al., 2013). In some cases, several potential threats affected the species more or less synchronously: for example, with the plant *Streblorrhiza speciosa*, the only known location – Phillip Island in the Norfolk Island group – was rapidly and severely degraded very soon after its discovery by Europeans by the introduction of pigs *Sus scrofa*, goats *Capra hircus* and rabbits *Oryctolagus cuniculus* (Coyne, 2009). In some cases, there may have been a temporal succession of contributing threat factors. Furthermore, it is highly likely that some species were driven to extinction by several threat factors operating interactively and synergistically (Brook et al., 2008), with the impact of such interactions among threats also recently demonstrated for some extant but declining Australian mammal species (Legge et al., 2019). Indeed, some previous reviews of extinctions of Australian mammals have noted that decline and extinction involved the compounding impacts of habitat degradation (due mainly to unsustainable livestock grazing and/or the spread of the rabbit) and introduced predators (Morton, 1990; Lunney, 2001). However, we did not specifically evaluate interactions among threat factors in attributing causality, given the unwieldy number of potential 2-, 3- and higher-order interactions possible among our ca. 20 threat factors. In other cases, the extinction appears quixotic, and no cause is obvious: for example, *Wendlandia psychotrioides*, listed as extinct under Queensland legislation, is known from only one collection, in 1887, from Mt Bellenden Ker in the Wet Tropics bioregion, but that location and habitat is largely unmodified and no other threats to the plant species are known.

We chose to use the best available information – typically including Red List accounts, listing advices under national and state/territory legislation, and reviews of the conservation status of large components of Australian biodiversity (Briggs and Leigh, 1996; Garnett et al., 2011; Woinarski et al., 2014; Taylor et al., 2018; Chapple et al., 2019 in press) – to make an assessment of the likely relative contribution of factors to each extinction. The causal factors used were based on the IUCN threat classification system (Salafsky et al., 2008), but for some analyses we pooled similar categories (*e.g.* land clearance for housing and urban areas, land clearance for commercial and industrial areas, land clearance for tourism and recreational areas, land clearance for non-timber crops, *etc.*) and further subdivided other categories (*e.g.* the threat factor 'invasive non-native species' was subdivided into invasive non-native invertebrates, fish, reptiles, birds and several categories of mammals). For every extinct species, at least three of the co-authors each independently assigned their assessments of the relative likelihood of individual threat factors contributing to that extinction, with these likelihoods summing to 100 for each species. This scoring was then averaged across co-authors. We recognise some subjectivity in this assessment, but it is likely that the definitive cause of many of these extinctions will never be proven. To illustrate geographic patterns in causes of extinction, we summed these relative contributions to extinctions across all species formerly occurring in each bioregion.

We used Kruskal-Wallis analysis of variation to compare the percentage contribution to extinction of main causal factors (i) among taxonomic groups, (ii) between island-endemic species and those occurring on the mainland (with the large island of Tasmania (64,519 km^2) being treated as 'mainland'), and (iii) across three time periods of extinction: 1788–1900, 1901–1960 and 1961–2018. This segmentation was based in part on the date of the federation of the Australian nation (1901), broadly comparable tallies of extinctions, and with the most recent of these periods largely encompassing the major expansion of the conservation reserve system, the introduction of

Table 1
Australian endemic species listed as Extinct, and considered here to be valid species with no records since listing as Extinct. Date of current listing is given for EPBC Act listed species; for IUCN listed species, dates are given for earliest and most recent listing for the status given.

Species	Common name	EPBCA	IUCN	State listing
Protists				
Vanvoorstia bennettiana	Bennett's seaweed	EX (2001)	EX (2003)	NSW
Plants				
Acacia kingiana		EX (2000)		WA
Amphibromus whitei		EX (2000)		QLD
Caladenia magnifica	magnificent spider-orchid			VIC
Caladenia thysanochila	fringed spider-orchid	EN (2000)		VIC
Calotis glabrescens				QLD
Coleanthera virgata	hidden coleanthera	EX (2000)		WA
Corchorus thozetii				QLD
Deyeuxia lawrencei		EX (2000)		TAS
Embelia flueckigeri				QLD
Euphrasia ruptura		EX (2000)		NSW
Frankenia decurrens	decurrent-leaved frankenia	EX (2000)		WA
Goodenia arenicola				QLD
Lepidium drummondii	Drummond's lepidium	EX (2000)		WA
Leptomeria dielsiana				WA
Leucopogon cryptanthus	small-flowered leucopogon	EX (2000)		WA
Marsdenia araujacea		EX (2000)		QLD
Musa fitzalanii	Daintree River banana	EX (2000)		QLD
Myriocephalus nudus				WA
Olearia oliganthema		EX (2000)		NSW
Ozothamnus selaginoides	clubmoss everlasting, Table Mountain daisy bush	EX (2000)		TAS
Paspalum batianoffii		EX (2000)		QLD
Persoonia laxa		EX (2000)		NSW
Persoonia prostrata		EX (2000)		QLD
Picris compacta				WA
Prasophyllum colemaniae	lilac leek-orchid	VU (2000)		VIC
Prasophyllum morganii	mignonette leek-orchid	VU (2000)		VIC
Ptilotus caespitulosus				WA
Ptilotus senarius				QLD
Pultenaea maidenii	Maiden's bush-pea	EX (2000)		VIC
Scholtzia sp. Bickley (W.H. Loaring s.n. PERTH 06165184*)*				WA
Senecio georgianus	grey groundsel	EX (2000)		VIC, TAS, NSW
Senecio helichrysoides	woolly fireweed			VIC (one SA record in 1850s)
Solanum bauerianum	bridal flower	EX (2018)		NSW
Streblorrhiza speciosa	Phillip Island glory pea		EX (1998)	
Tetratheca fasciculata	Cronin's tetratheca	EX (2000)		WA
Thomasia gardneri	Mt Holland thomasia	EX (2000)		WA
Trianthema cypseleoides		EX (2000)		NSW
Wendlandia psychotrioides				QLD
Invertebrates				
Bothriembryon praecelsus			EN (1996) [* as *B. praecelcus*]	WA
Bothriembryon whitleyi			VU (1996)	WA
Costora iena	Great Lakes caddis fly			TAS
Crenoicus mixtus				VIC
Hadronyche pulvinator	Cascade funnel-web spider			TAS
Helicarion castanea				WA
Hybomorphus melanosomus	Lord Howe Island ground weevil			NSW
Hypolimnus pedderensis	Lake Pedder earthworm	EX (2009)	EX (2003)	TAS
Occirhenea georgiana			EN (1996)	WA
Posticobia norfolkensis			EX (1996)	
Fish				
Galaxias pedderensis	Pedder galaxias	EX(W) (2005)	CR (1996)	
Frogs				
Rheobatrachus silus	southern gastric-brooding frog	EX (2000)	EX (2004)	QLD
Rheobatrachus vitellinus	northern gastric-brooding frog	EX (2000)	EX (2004)	
Taudactylus acutirostris	sharp-snouted day frog	EX (2000)	CR (2004)	QLD
Taudactylus diurnus	southern day frog	EX (2000)	EX (2004)	QLD
Reptiles				
Cryptoblepharus egeriae	Christmas Island blue-tailed skink	CR (2014)	EX(W) (2017)	
Emoia nativitatis	Christmas Island forest skink	CR (2014)	EX (2017)	
Lepidodactylus listeri	Lister's gecko	CR (2014)	EX(W) (2017)	
Birds				
Aplonis fusca	Tasman starling	EX (2000)	EX (1988-2012)	
Dromaius ater	King Island emu	EX (2000)	EX (1988-2012)	TAS
Dromaius baudinianus	Kangaroo Island emu	EX (2000)	EX (1988-2012)	
Gerygone insularis	Lord Howe gerygone	EX (2000)	EX (1988-2012)	NSW
Nestor productus	Norfolk Island kaka	EX (2000)	EX (1988-2012)	
Porphyrio albus	white gallinule	EX (2000)	EX (1988-2012)	NSW
Psephotellus pulcherrimus	paradise parrot	EX (2000)	EX (1994-2014)	QLD, NSW

(*continued on next page*)

Table 1 (*continued*)

Species	Common name	EPBCA	IUCN	State listing
Zosterops albogularis	white-chested white-eye	EX (2000)	CR (1994-2016)	
Zosterops strenuus	robust white-eye	EX (2000)	EX (1988-2012)	NSW
Mammals				
Bettongia anhydra	desert bettong		EX (2016)	WA
Bettongia pusilla	Nullarbor dwarf bettong		EX (2008-2016)	WA
Caloprymnus campestris	desert rat-kangaroo	EX (2000)	EX (1994-2016)	
Chaeropus ecaudatus	pig-footed bandicoot (southern pig-footed bandicoot)	EX (2000)	EX (1982-2016)	WA, Vic, NT, NSW [although NT listing refers now to the subsequently described *C. yirratji*]
Chaeropus yirratji	yirratji (northern pig-footed bandicoot)	EX (2000) [included in *C. ecaudatus*]	EX (1982-2016) [included in *C. ecaudatus*]	WA, NT [included in *C. ecaudatus*]
Conilurus albipes	white-footed rabbit-rat	EX (2000)	EX (1982-2016)	Vic, QLD, NSW
Conilurus capricornensis	Capricorn rabbit-rat		EX (2016)	
Lagorchestes asomatus	central hare-wallaby	EX (2000)	EX (1982-2016)	WA, NT
Lagorchestes leporides	eastern hare-wallaby	EX (2000)	EX (1982-2016)	Vic, NSW
Leporillus apicalis	lesser stick-nest rat	EX (2000)	EX (1982-2016)	WA, Vic, NT, NSW
Macrotis leucura	yallara, lesser bilby	EX (2000)	EX (1982-2016)	WA, NT
Melomys rubicola	Bramble Cay melomys	EX (2019)	EX (2016)	QLD
Notomacropus greyi	toolache wallaby	EX (2000)	EX (1982-2016)	
Notomys amplus	short-tailed hopping-mouse	EX (2000)	EX (1982-2016)	WA, NT
Notomys longicaudatus	long-tailed hopping-mouse	EX (2000)	EX (1982-2016)	WA, NT. NSW
Notomys macrotis	large-eared hopping-mouse	EX (2000)	EX (1982-2016)	WA
Notomys mordax	Darling Downs hopping-mouse	EX (2000)	EX (1982-2016)	QLD
Notomys robustus	broad-cheeked hopping-mouse		EX (2016)	
Nyctophilus howensis	Lord Howe long-eared bat	EX (2001)	CR(PE) (2008; EX-1996)	NSW
Onychogalea lunata	crescent nail-tailed wallaby	EX (2000)	EX (1982-2016)	WA, NSW
Perameles eremiana	desert bandicoot	EX (2000)	EX (1982-2016)	WA
Perameles fasciata	Liverpool Plains striped bandicoot			NSW (as *P. bougainville*)
Perameles myosuros	marl			WA
Perameles notina	south-eastern striped bandicoot			VIC (as *P. bougainville fasciata*)
Perameles papillon	Nullarbor barred bandicoot			WA
Pipistrellus murrayi	Christmas Island pipistrelle	CR (2016)	EX (2017)	
Potorous platyops	broad-faced potoroo	EX (2000)	EX (1982-2016)	WA
Pseudomys auritus	long-eared mouse		EX (2016)	Vic
Pseudomys glaucus	blue-grey mouse		EX (2008-2016)	NSW
Pseudomys gouldii	Gould's mouse	EX (2000)	EX (1990-2016)	NSW
Pteropus brunneus	dusky flying-fox		EX (1996-2008)	QLD
Rattus macleari	Maclear's rat	EX (2000)	EX (1994-2016)	
Rattus nativitatis	bulldog rat	EX (2000)	EX (1994-2016)	
Thylacinus cynocephalus	thylacine	EX (2000)	EX (1982-2016)	TAS

threatened species legislation, and a marked increase in conservation management efforts.

We also illustrated patterns of variation among extinct species in the causes of extinction, using MDS ordination (of species by the relative contribution of threat factors to their extinction). We then assessed the fit of the three species-group factors (taxonomic group, island cf. mainland, and time period of extinction) to the resemblance matrix (based on relative contribution to extinction of individual threats) of pairs of species, using ANOSIM (Clarke and Gorley, 2001).

3. Results

3.1. Number of valid listed extinct species and their taxonomic composition

Collation across our three source lists indicates that 100 Australian endemic species are validly listed as extinct (Table 1). There is marked variation among taxonomic groups in the number and proportion of listed extinctions ($\chi^2 = 4252$, df = 6, $p < 0.001$), with the tally of extinctions comprising one protist, 38 vascular plant species (0.18% of the estimated Australian flora, and 0.21% of endemic Australian vascular plant species), ten invertebrate species (0.01%, with endemic proportion unknown because there has been no estimate of the number of endemic Australian invertebrates), one fish species (0.02%, 0.08%), four frog species (1.8%, 1.9%), three reptile species (0.33%, 0.35%), nine bird species (1.1%, 2.4%) and 34 mammal species (8.7%, 10.0%) (Table 2). This tally includes three species that are extinct in the wild, but persist as captive populations (two reptiles) or as populations introduced beyond their original range (one fish).

Table 2
Taxonomic summary of numbers of Australian endemic species listed as extinct under Australian national legislation, Australian state/territory lists, and by the IUCN. Note that row totals don't necessarily equal the sum of the three constituent columns because the same species may be listed under more than one source.

Taxonomic group	Australian	State/Territory	IUCN	Total
Protists	1	1	1	1
Plants	24	37	1	38
Invertebrates	1	9	2	10
Fish	1	0	0	1
Frogs	4	3	3	4
Reptiles	0	3	0	3
Birds	9	5	9	9
Mammals	22	29	29	34
Total	62	87	45	100

Only one of the listed extinct species was marine (the seaweed *Vanvoorstia bennettiana*), although two other marine species (*Hadrachaeta aspeta* and *Metaprotella haswelliana*) are listed as extinct in New South Wales and arguably may be so across their broader Australian range (Appendix A). Seven listed extinct species were primarily associated with freshwater habitats, comprising four frog species, one fish and two invertebrates (*Costora iena* and *Crenoicus mixtus*); the extinct herb *Myriocephalus nudus* mostly occurred in swamp habitats.

There is marked variation in the complement of species listed as extinct across the three sources, with far more Australian plant species listed as extinct under national legislation (24 species) than by the

IUCN (one species), but few invertebrates listed by the former (one species listed under the EPBC Act cf. nine listed under state/territory legislation and two by the IUCN). Notably, the national listing (EPBC Act) includes only 62 of the 100 extinctions recognised here across the three sources. Note that 37 plant taxa and 54 animal taxa are listed as extinct under the EPBC Act, and another animal as extinct in the wild, but this listing includes several species that are not Australian endemics (*e.g.*, *Didymoglossum exiguum*, *Hymenophyllum lobbii*, *Lycopodium volubile*, *Monogramma dareicarpa* and *Tmesipteris lanceolata*), some species recently rediscovered (*e.g.*, *Acacia prismifolia* and *Opercularia acolytantha*), and many subspecies; these taxa are not included here. The state/territory listing is the most comprehensive (Table 1), with most of the extinct species missing from these jurisdictional lists being those from Christmas and Norfolk Islands, not covered by any jurisdictional listings.

3.2. Timing of extinctions

The first extinction of an Australian species subsequent to European settlement probably occurred within a decade of that settlement, with no records of the white gallinule *Porphyrio albus* from its sole known location on Lord Howe Island after 1788 (Garnett et al., 2011). Fig. 1 indicates that extinctions have occurred more or less continuously since, with every decade since 1830 including the last record of at least one extinct species. Three reported extinctions, and two extinctions in the wild, have occurred in the last decade (Woinarski et al., 2017). Note that the date of last record marks a very conservative estimate of the date of actual extinction: many species may have persisted unreported long after this date. There are some fluctuations indicated in Fig. 1.

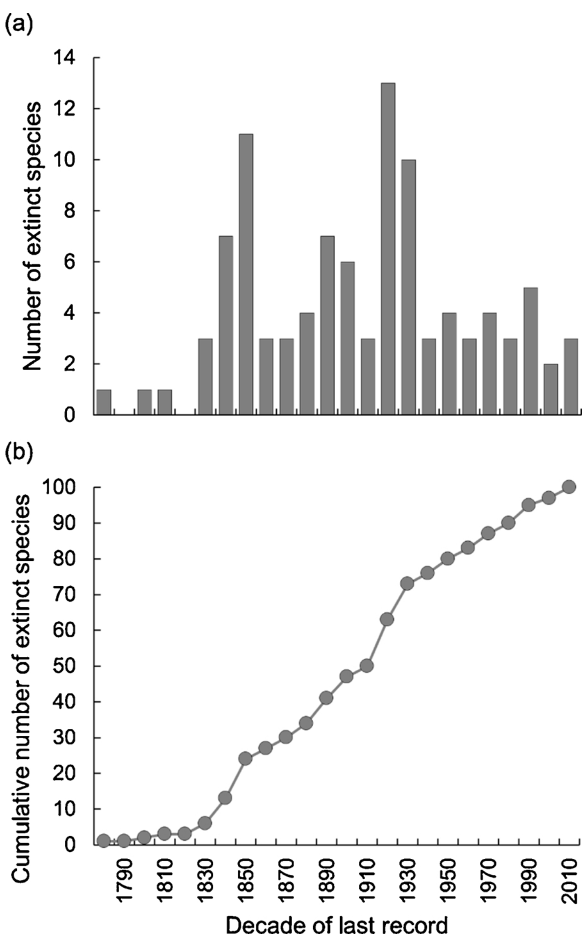

Fig. 1. Dates of last known records for Australian extinct species: (a) number of last records of species by decade; (b) expressed as a cumulative tally.

Peaks may reflect collection effort and/or the synchronous extirpation of many species due to the entry of a novel threat (*e.g.* red fox *Vulpes vulpes* in central Australia around the 1930s, chytrid fungus in the 1970s, introduction of the wolf snake *Lycodon capucinus* to Christmas Island in about 1982). Extinctions of plants, invertebrates, birds and mammals occurred across all three time periods. In contrast, all extinctions of Australian fish, frogs and reptiles post European settlement were in the most recent (1961–2018) time period.

3.3. Geographic distribution of extinct species

Of the 100 extinct species, 21 were restricted to islands smaller than Tasmania, yet islands smaller than this threshold comprise only 0.5% of the Australian land mass (Woinarski et al., 2018). This tally of extinct island species comprises three plant species, two invertebrate species, three reptile species (100% of the Australian extinct reptile species), seven bird species (78%) and six mammal species (18%), *i.e.* there have been no extinctions of mainland reptile species and extinction of only one mainland bird species, but all extinctions of frogs were of mainland species (although there is only one island-endemic Australian frog species).

There is marked and highly significant variation among taxonomic groups (Kruskal-Wallis ANOVA $H = 33.3$, $p < 0.0001$ for the taxonomic groups with > 2 extinct species) in the pre-extinction distributional extent of individual species, with extinct plant (mean no. bioregions 1.47, s.e. 0.22), invertebrate (mean 1.40, s.e. 0.12), fish (1 bioregion), frog (mean of 1 bioregion), reptile (mean of 1 bioregion) and bird (mean 1.22, s.e. 0.22) species having highly restricted former distributions, whereas most of the extinct mammal species formerly had relatively extensive distributions (mean 6.74 bioregions, s.e. 1.27) – although even amongst the mammals, several extinct species were restricted to single islands (*e.g.*, Maclear's rat *Rattus macleari*, bulldog rat *Rattus nativitatis*, Christmas Island pipistrelle *Pipistrellus murrayi*, Lord Howe long-eared bat *Nyctophilus howensis*, Bramble Cay melomys *Melomys rubicola*). Of the 79 extinct species that occurred on the mainland, we estimate that 41 (comprising one protist, 27 plants, six invertebrates, one fish, one frog, no birds or reptiles, and four mammals) had areas of occupancy that were less than 100 km^2 (Appendix C), although we reiterate that estimation of range is challenging for extinct species with few records and imprecise collection details.

Extinctions have occurred across most of Australia, with 78 of the 89 bioregions having at least one extinct species (Fig. 2a and b). The number of extinct species (including all taxonomic groups) in each bioregion was correlated with two static environmental variables (mean annual rainfall, proportion of bioregion on islands) and one variable reflecting anthropogenic disturbance (proportion of bioregion in conservation reserves). These three variables were in all of the well-supported models (*i.e.* $\Delta AIC \leq 2$; Table 3a). There tended to be more extinctions in arid areas and in bioregions dominated by islands (Appendix D). Somewhat counter-intuitively, there tended to be more extinctions in those bioregions with a greater proportional area within conservation reserves (Appendix D). The best models of the extinction index (for all taxonomic groups combined) had relatively poor explanatory power ($D^2 \leq 0.21$; Table 3a).

The proportion of plant species extinct in each bioregion was not clearly correlated with any static environmental variable, although it was correlated with two variables reflecting anthropogenic disturbance (proportion of bioregion cleared, human population density). These two variables were in all of the well-supported models (*i.e.* $\Delta AIC \leq 2$; Table 3b). There tended to be more extinctions in bioregions that have been cleared to a greater extent (Appendix D) and in bioregions with greater human populations (Appendix D). The best models of the number of extinct species in each bioregion had moderate explanatory power ($D^2 \leq 0.38$; Table 3b).

The proportion of extinct mammal species in each bioregion was correlated with three static environmental variables (mean annual

Table 3
Model ranking table for the three response variables examined: (a) the number of extinct species in each bioregion, including all taxonomic groups; (b) proportion of plant species extinct in each bioregion; and (c) proportion of mammal species extinct in each bioregion. Models were ranked according to AIC (b and c) or QAIC (a). ΔAIC represents the difference between a model's AIC or QAIC value and the minimum AIC or QAIC value in the set of candidate models. The set of candidate models included all combinations of the explanatory variables, but only the models with ΔAIC ≤2 are shown. D^2 is the proportion of deviance explained by the model. NA indicates variables which were excluded from the analysis due to excessive collinearity. The shading indicates variables for which there is clear evidence of a relationship (*i.e.* the variable appears in all models with ΔAIC ≤2).

	Static environmental variables				Human disturbance variables				
Response	Mean annual rainfall (mm)	Mean annual temperature (°C)	Proportion island	Ruggedness index	Proportion cleared	Human population density (km^{-2})	Proportion in reserves	ΔAIC	D^2
(a) All species	*		*	NA	*		*	0.0	0.20
	*	*	*	NA			*	0.3	0.19
	*	*	*	NA	*		*	0.4	0.21
	*	*	*	NA		*	*	0.4	0.20
	*		*	NA	*	*	*	0.9	0.21
	*	*	*	NA	*	*	*	1.0	0.21
(b) Plants	*				*	*		0.0	0.37
	*	*			*	*		1.0	0.38
				*	*	*		1.2	0.36
	*		*		*	*		1.5	0.38
	*			*	*	*		1.6	0.38
	*				*	*	*	1.8	0.37
(c) Mammals	*	*	*	NA			*	0.0	0.41
	*	*	*	NA	*		*	1.7	0.41
	*	*	*	NA		*	*	2.0	0.41

rainfall, mean annual temperature, proportion of bioregion on islands) and one variable reflecting anthropogenic disturbance (proportion of bioregion in conservation reserves). These four variables were in all of the well-supported models (*i.e.* ΔAIC ≤2; Table 3c). There was a very strong tendency for more extinctions in arid areas (Appendix D) and in bioregions dominated by islands (Appendix D). To a much lesser extent, there was a tendency for more extinctions in cooler climates (Appendix D), most likely reflecting the absence of mammal extinctions in most of the north of the continent. There tended to be more extinctions in bioregions with a greater proportional area within conservation reserves (Appendix D). The best models of the number of extinct species in each bioregion had relatively high explanatory power ($D^2 \leq 0.41$; Table 3c).

3.4. Causes of extinction

Our assessment of the relative contribution of threat factors to every extinction is given in Appendix E, and summarised across taxonomic groups, island-endemic species *vs* mainland species, and period of extinction in Table 4. Introduced animals and habitat loss (clearing) were the two factors that contributed most to extinctions, here considered to have contributed to 64 and 62 extinctions, respectively. There was marked variation among taxonomic groups in the relative contribution of different causal factors. Clearing was the major causal factor for extinctions of plants and invertebrates, disease for frogs, and introduced animals was the major causal factor for all other vertebrate groups, with hunting also a major factor in bird extinctions (being the primary cause of three [all island-endemic species] of the nine bird extinctions).

There was also marked variation in the contribution of factors causing extinction of island-endemic species relative to mainland species, with introduced animals and hunting contributing more to extinctions of island endemic species, and clearing contributing less. Within the set of introduced animals, mammalian predators (cats *Felis catus* and foxes) contributed far more to extinctions of mainland species, whereas introduced rodents (primarily the black rat *Rattus rattus*) and reptiles (the wolf snake) contributed more to extinctions of island endemic species (Table 4). Introductions of plant, invertebrate, fish, reptile, bird and mammal species have contributed to Australian extinctions. Although the sole established introduced amphibian, the cane toad *Rhinella marina*, has caused severe declines for many Australian species (Shine, 2010), it has not been implicated in any listed Australian extinctions.

The relative contribution of causal factors varied among time periods, with disease, introduced fish, introduced invertebrates and introduced reptiles contributing relatively more substantially to extinctions in the most recent time period (1961–2018). Hunting contributed to six of the 41 extinctions in the 1788–1900 period, but to no extinctions in the 1961–2018 period. Introduced mammalian predators were major contributors to extinctions in the periods 1788–1900 and 1901-60, but contributed relatively little to extinctions since 1960.

The sole extinction due at least in part to climate change was the most recent extinction (*Melomys rubicola*), occurring between 2009 and 2014. The only species for which pollution was a primary cause of extinction was the only marine species (and sole protist), *Vanvoorstia bennettiana*. An initial ordination of all species based on the relative contribution of threats to extinction was overwhelmingly dominated by these two idiosyncratic extinctions, so ordination was repeated with these two species omitted (Fig. 3). This ordination showed a tight cluster of most extinct mammal species (presenting a syndrome with the primary causal factor being introduced mammalian predators). Seven mammal species were distinct from this cluster: the thylacine *Thylacinus cynocephalus* and six island-endemic mammal species, with these latter species mostly falling within a suite of other island-endemic species whose extinction was caused mainly by introductions of animal species other than cats and foxes. All three reptile species were tightly clustered (*i.e.* their extinctions had similar causal factors), as were the four frog species; most plant species were also clustered. There was a loose grouping of three species whose extinctions were largely due to hydrological modification (the fish *Galaxias pedderensis* and two invertebrates *Hypolimnus pedderensis* and *Costora iena*), a loose grouping of three island-endemic bird species whose extinctions were mostly due to hunting (*Dromaius ater*, *Dromaius baudinianus* and *Porphyrio albus*). The resemblance matrix underlying this ordination was strongly associated with taxonomic group ($R = 0.62$, $p < 0.001$), island-endemic cf. mainland species ($R = 0.46$, $p < 0.001$) and, less so, time period of extinction ($R = 0.12$, $p < 0.001$).

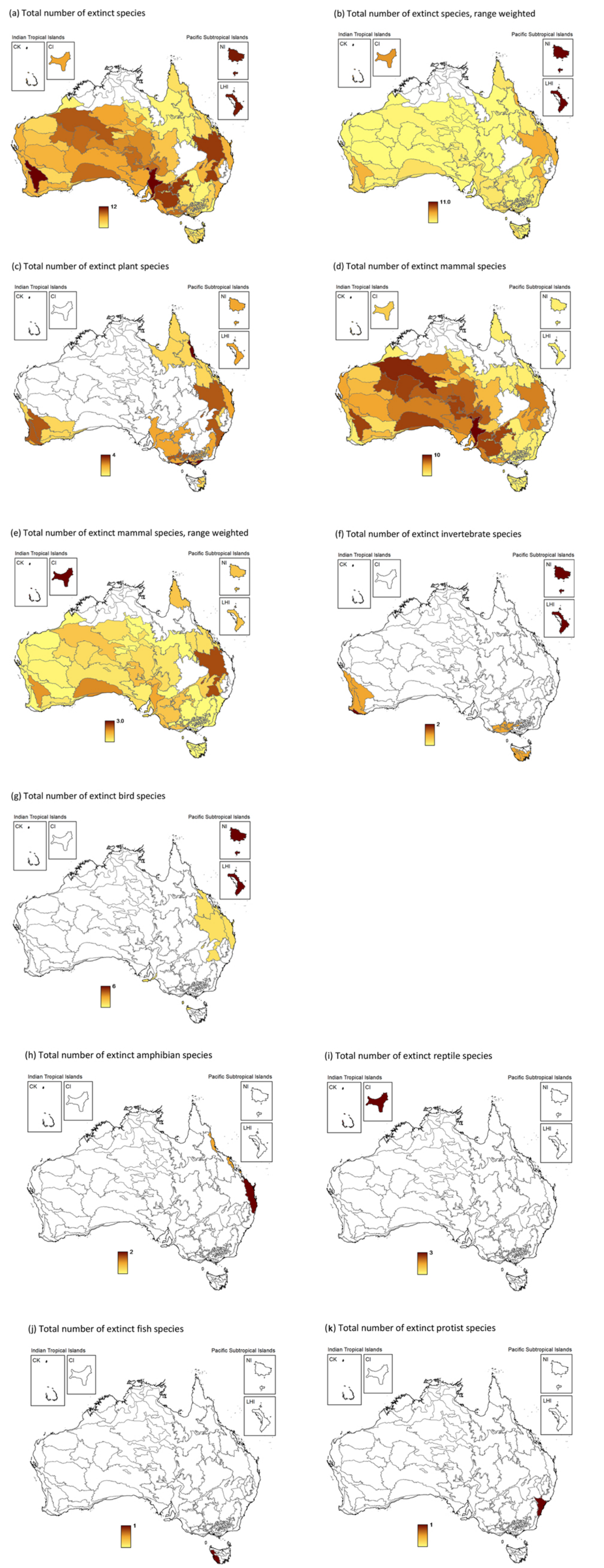

Fig. 2. The number of extinct species formerly occurring in each bioregion, for all species and for taxonomic groups. For total species and for mammals, maps are given for absolute values and range weighted value (see text). For all other taxonomic groups, most species occurred in only one bioregion, so only the total number of extinctions per bioregion is mapped. The taxonomic groups are shown in decreasing order of the total number of extinctions in each. Two of the remote island bioregions (Indian Tropical Islands and Pacific Subtropical Islands) are shown inset (not to scale).

There is clear geographic variation in the factors contributing most to extinctions (Fig. 4a). Across most of Australia, introduced mammalian predators (foxes and cats) have been the primary drivers of extinction (a pattern due largely to the relatively large number of species, and extensive former distributions, of extinct mammals), especially in the central Australian arid zone (Fig. 4a and g). Habitat loss (clearing) has been a much more restricted causal factor, with its contributions to extinctions mainly in temperate south-western and eastern Australia (Fig. 4b).

4. Discussion

Our collation across three sources of threatened species' listing (IUCN, Commonwealth, State/Territory) allowed us to provide the first comprehensive assessment of recognised extinctions in the Australian biota. We conclude that 100 Australian endemic species are validly recognised as extinct since 1788: a rate of loss of about 4.3 species per decade since European colonisation of the continent. This rate is not diminishing and we interpret this more-or-less constant but continuing rate of loss as indicating that current conservation investments and policy (*e.g.* a substantial conservation reserve system, environmental laws, policy commitments to attempt to prevent extinctions and many management actions for threatened species based on generally robust evidence) developed over recent decades have not abated the rate of loss. However, they may be working to reduce what would otherwise be an accelerating rate of loss due to: the increasing impacts of some threats (*e.g.* climate change); the persistence and variably effective control of many long-established pervasive threats; new threats such as the recent introduction to Australia of myrtle rust and the increasingly widespread application of synthetic pesticides in agricultural landscapes (Sánchez-Bayo and Wyckhuys, 2019); and an extinction debt legacy (Kuussaari et al., 2009) arising from much historic loss, fragmentation and degradation of ecosystems. Conversely, some relatively recent management actions (notably translocations to islands or exclosures from which introduced mammalian predators are excluded) have undoubtedly prevented otherwise likely extinctions of threatened Australian mammals (Legge et al., 2018).

The global context for the Australian tally of extinctions is difficult to evaluate. As at March 2019, the IUCN Red List includes 872 species as extinct globally and a further 69 species as extinct in the wild (= 941 species) (https://www.iucnredlist.org/), but the IUCN list includes only 45 of the 100 Australian endemic species recognised here as extinct, and nine of the Australian species recognised as extinct by the IUCN are not considered to be extinct here (Appendix A). Hence, the Australian proportion of global extinctions cannot readily be determined, but these tallies suggest that Australian species may comprise about 5–10% of the world's extinctions over the last ca. 500 years, roughly consistent with Australia's contribution to global land area (5.2%).

In part to make our task tractable, our assessment includes only those species that are recognised as extinct in 'official' lists. Our compilation highlights marked variation among, and deficiencies in each of, the three sources. The IUCN listing is notably deficient for recognising known extinctions in Australian plants, an under-representation that is also apparent globally (Gray, 2019). The formal national list (*i.e.* under the EPBC Act) of extinct species is also substantially incomplete, including only 62% of the tally of extinct species collated across the three sources, with this deficiency especially evident for invertebrates. This under-estimate may not have any practical consequences for present

Table 4

Main causes of extinctions for Australian species: (a) for mainland species compared with island endemic species; (b) across three time periods of last known records; (c) for major taxonomic groups. Figures in body of table are means and, in brackets, standard error and number of species with that threat implicated in extinction. H values are from Kruskal-Wallis ANOVA. The main category of introduced animals is also subdivided by types of introduced animal, with these latter categories italicised. Main categories are ordered from those with largest to least contribution to extinctions.

(a) Mainland species (including species occurring on both mainland and islands) cf. island endemic species

Causal factor	Mainland (N = 79)	Island (N = 21)	Total (N = 100)	H
Introduced animals	29.5 (4.1, 48)	55.7 (9.3, 17)	35.0 (3.9, 65)	9.0 (p = 0.003)
Introduced invertebrates	*1.1 (0.6, 4)*	*3.6 (1.6, 5)*	*1.6 (0.6, 9)*	*6.4 (p = 0.012)*
Introduced fish	*1.3 (1.0, 6)*	*0*	*1.1 (0.8, 6)*	*1.7 (p = 0.19)*
Introduced reptiles	*0*	*14.3 (6.7, 4)*	*3.0 (1.5, 4)*	*15.3 (p = 0.0001)*
Introduced birds	*0*	*1.8 (1.3, 3)*	*0.4 (0.3, 3)*	*11.4 (p = 0.0007)*
Introduced mammalian predators (cat, fox)	*25.3 (4.0, 29)*	*0.7 (0.3, 4)*	*20.2 (3.3, 33)*	*3.9 (p = 0.05)*
Introduced rodents	*0.02 (0.02, 1)*	*29.4 (8.0, 13)*	*6.2 (2.1, 14)*	*50.5 (p < 0.0001)*
Introduced mammalian herbivores	*1.8 (0.3, 23)*	*4.7 (3.4, 4)*	*2.4 (0.8, 27)*	*0.2 (p = 0.63)*
Introduced pig	*0*	*1.2 (0.8, 3)*	*0.3 (0.2, 3)*	*11.4 (p = 0.0007)*
Clearing	37.5 (4.3, 54)	8.6 (3.2, 8)	31.4 (3.7, 62)	9.7 (p = 0.002)
Livestock grazing	10. 0 (1.6, 56)	1.8 (1.0, 3)	8.3 (1.3, 59)	15.8 (p = 0.0001)
Disease	5.2 (2.5, 9)	7.7 (4.9, 4)	5.7 (2.2, 13)	0.8 (p = 0.36)
Hunting	2.3 (1.5, 5)	14.0 (6.7, 4)	4.8 (1.9, 9)	3.5 (p = 0.06)
Fire	5.1 (0.8, 45)	2.9 (2.4, 2)	4.6 (0.8, 47)	111.2 (p = 0.0008)
Water modification	4.1 (1.9, 8)	0.4 (0.4, 1)	3.3 (1.5, 9)	0.6 (p = 0.43)
Introduced plants	3.0 (0.7, 21)	0	2.4 (0.5, 21)	6.9 (p = 0.009)
Other modification	1.8 (1.2, 4)	3.2 (2.4, 3)	2.1 (1.1, 7)	2.1 (p = 0.14)
Pollution	1.4 (1.3, 2)	0	1.1 (1.0, 2)	0.5 (p = 0.46)
Climate change	0	3.6 (3.6, 1)	0.8 (0.8, 1)	3.7 (p = 0.054)
Logging	0.1 (0.1, 1)	0.7 (0.5, 3)	0.2 (0.1, 4)	7.3 (p = 0.007)

(b) Timing of extinction

Causal factor	EX 1788-1900 (N = 41)	EX 1901-1960 (N = 42)	EX 1961-2018 (N = 17)	H
Introduced animals	28.7 (5.6, 22)	42.2 (6.1, 31)	32.4 (10.7, 12)	5.0 (p = 0.08)
Introduced invertebrates	*0*	*2.4 (1.1, 5)*	*3.8 (2.0, 4)*	*8.6 (=p = 0.01)*
Introduced fish	*0*	*0.6 (0.6, 1)*	*4.7 (4.5, 5)*	*19.4 (p = 0.0001)*
Introduced reptiles	*0*	*0*	*17.7 (8.1, 4)*	*19.9 (p < 0.0001)*
Introduced birds	*0.6 (0.6, 1)*	*0.2 (0.2, 1)*	*0.2 (0.2, 1)*	*0.5 (p = 0.77)*
Introduced mammalian predators (cat, fox)	*22.3 (5.2, 13)*	*25.9 (5.8, 16)*	*0.9 (0.4, 4)*	*2.8 (p = 0.68)*
Introduced rodents	*2.4 (1.9, 2)*	*10.8 (4.2, 8)*	*4.6 (4.0, 4)*	*4.8 (p = 0.09)*
Introduced herbivores	*2.9 (1.8, 8)*	*2.6 (0.6, 17)*	*0.6 (0.4, 2)*	*5.6 (p = 0.06)*
Introduced pig	*0.5 (0.4, 2)*	*0.1 (0.1, 1)*	*0*	*1.1 (p = 0.59)*
Clearing	36.8 (6.1, 30)	31.7 (5.5, 27)	17.7 (7.2, 7)	4.7 (p = 0.09)
Livestock grazing	8.2 (1.4, 27)	9.6 (2.4, 26)	5.3 (3.5, 5)	5.9 (p = 0.052)
Disease	2.2 (1.8, 4)	2.3 (1.8, 4)	23.2 (10.5, 4)	2.9 (p = 0.24)
Hunting	9.6 (4.1, 6)	2.0 (1.7, 3)	0	3.5 (p = 0.17)
Fire	5.8 (1.6, 20)	4.4 (0.8, 24)	2.6 (1.8, 3)	5.3 (p = 0.07)
Water modification	0.2 (0.2, 2)	4.9 (2.6, 5)	7.1 (5.9, 2)	1.7 (p = 0.43)
Introduced plants	2.4 (0.8, 9)	2.5 (0.9, 7)	1.9 (1.1, 5)	0.6 (p = 0.75)
Other modification	3.2 (2.3, 2)	0.3 (0.2, 2)	3.7 (3.0, 3)	3.3 (p = 0.19)
Pollution	2.4 (2.4, 1)	0.2 (0.2, 1)	0	0.4 (p = 0.81)
Climate change	0	0	4.4 (4.4, 1)	4.8 (p = 0.09)
Logging	0.3 (0.2, 2)	0.2 (0.1, 2)	0	0.9 (p = 0.65)

(c) Taxonomic groups. Note that Kruskal-Wallis ANOVA excluded the two groups with only one species

Causal factor	Protists (N = 1)	Plants (N = 38)	Invertebrates (N = 10)	Fish (N = 1)	Frogs (N = 4)	Reptiles (N = 3)	Birds (N = 9)	Mammals (N = 34)	H
Introduced animals	0	5.4 (2.7, 12)	24.8 (9.2, 7)	76.7	0.8 (-, 4)	100 (-, 3)	41.7 (14.9, 6)	67.5 (4.8, 32)	54.1 (p < 0.0001)

(*continued on next page*)

Table 4 (*continued*)

(c) Taxonomic groups. Note that Kruskal-Wallis ANOVA excluded the two groups with only one species

Causal factor	Protists (N = 1)	Plants (N = 38)	Invertebrates (N = 10)	Fish (N = 1)	Frogs (N = 4)	Reptiles (N = 3)	Birds (N = 9)	Mammals (N = 34)	H
Introduced invertebrates	0	*1.1 (1.1, 1)*	*8.8 (3.8, 4)*	0	0	*11.7 (-, 3)*	0	*0.9 (0.9, 1)*	*44.2 (p < 0.0001)*
Introduced fish	0	0	*2.5 (2.5, 1)*	76.7	*0.8 (-, 4)*	0	0	0	*81.4 (p < 0.0001)*
Introduced reptiles	0	0	0	0	0	*81.7 (-, 3)*	0	*1.7 (1.7, 1)*	*74.7 (p < 0.0001)*
Introduced birds	0	0	*2.5 (2.5, 1)*	0	0	0	*0.4 (0.4, 1)*	*0.3 (0.3, 1)*	*5.1 (p = 0.65)*
Introduced mammalian predators (cat, fox)	0	0	*0.1 (0.1, 1)*	0	0	*3.3 (-, 3)*	*2.6 (2.0, 2)*	*58.2 (5.7, 27)*	*64.1 (p < 0.0001)*
Introduced rodents	0	0	*10.1 (7.6, 3)*	0	0	*3.3 (-, 3)*	*38.1 (15.3, 4)*	*3.7 (2.5, 3)*	*30.4 (p = 0.0001)*
Introduced mammalian herbivores	0	*3.9 (1.9, 12)*	*0.8 (0.4, 3)*	0	0	0	0	*2.6 (0.7, 12)*	*8.0 (p = 0.33)*
Introduced pig	0	*0.4 (0.4, 1)*	0	0	0	0	*0.6 (0.6, 1)*	*0.2 (0.2, 1)*	*2.5 (p = 0.93)*
Clearing	0	63.9 (5.1, 34)	42.8 (11.1, 8)	0	0	0	10.6 (4.2, 6)	5.7 (2.3, 14)	52.8 (p < 0.0001)
Livestock grazing	0	11.1 (2.7, 28)	2.8 (0.9, 6)	0	0	0	5.4 (5.4, 1)	9.9 (1.5, 24)	21.9 (p = 0.0026)
Disease	0	0	0	0	98.7 (0.2, 4)	0	0.9 (0.7, 2)	5.3 (3.1, 7)	41.7 (p < 0.0001)
Hunting	0	0	0	0	0	0	37.8 (14.9, 5)	4.1 (2.7, 4)	30.7 (p = 0.0001)
Fire	0	7.2 (1.8, 20)	2.3 (0.9, 4)	0	0	0	2.8 (1.9, 2)	4.2 (0.8, 21)	11.0 (p = 0.14)
Water modification	0	1.7 (1.3, 4)	24.6 (12.3, 4)	20.0	0	0	0	0	27.5 (p = 0.0003)
Other modification	0	4.7 (2.7, 3)	1.3 (0.8, 2)	3.3	0	0	0	0.3 (0.3, 1)	15.8 (p = 0.027)
Introduced plants	0	5.9 (1.2, 18)	1.0 (1.0, 1)	0	0.4 (0.2, 2)	0	0	0	30.3 (p = 0.0001)
Pollution	100	0	0.6 (0.6, 1)	0	0	0	0	0	53.9 (p < 0.0001)
Climate change	0	0	0	0	0	0	0	2.3 (2.3, 1)	2.0 (p = 0.96)
Logging	0	0	0	0	0	0	0.9 (0.5, 3)	0.3 (0.3, 1)	21.7 (p = 0.0029)

and future conservation outcomes, but it does misrepresent the extent of loss experienced by Australia's biodiversity; and this deficiency should be remedied.

The three lists may be reasonably comprehensive and accurate for terrestrial vertebrate groups, for which the assemblage of Australian species has generally been well inventoried, and for which typically there has been enough recent survey effort to be reasonably confident in ascribing extinction. However, even amongst some terrestrial vertebrate groups, the tallies of extinct Australian species have not yet settled. For example, on the basis of a recent taxonomic review, what was considered to be a single extant bandicoot species (*Perameles bougainville*) is now recognised to comprise four extinct species (*P. fasciata, P. myosorus*, *P. notina* and *P. papillon*) and one extant species (Travouillon and Phillips, 2018), and the previously considered monotypic pig-footed bandicoot *Chaeropus ecaudatus* has also recently been redefined as two species, both now extinct (Travouillon et al., 2019). Likewise, subfossil discoveries continue to reveal previously unknown Australian mammal species that may have been present at the time of European settlement, notably including three undescribed rodent species in northern Australian bioregions that have otherwise not experienced reported extinctions (Start et al., 2012). Furthermore, an additional Australian endemic mammal species, the Christmas Island shrew *Crocidura trichura*, may be extinct, with the most recent IUCN assessment recognising it as Critically Endangered (Possibly Extinct), with only two records in the last 60 years, and the most recent record in 1985 (Eldridge et al., 2014; Woinarski et al., 2016).

For taxonomic groups less well-known than terrestrial vertebrates, the formal listing of extinct species is likely to be a substantial underestimate of the actual number of extinctions because many known extinctions of Australian species have not yet been recognised in official lists and, for many other (described and undescribed) species, extinctions may have occurred without being noticed. For example, while 12 plant species endemic to Western Australia are recognised formally (and here) as extinct, a further 23 endemic Western Australian plant species have not been collected for at least 50 years, and most of these are presumed extinct, although are not formally listed as extinct (Gibson, 2016).

Evidence for undocumented extinctions is especially compelling for invertebrates. For example, one isopod (*Crenoicus mixtus*) is listed as extinct (under Victorian legislation), but a recent review of that genus informed by patterns of endemicity concluded that 'land clearing in the last 200 years along the Great Dividing Range in New South Wales is likely to have been responsible for the extinction of many *Crenoicus* species, by causing the disappearance of the highland springs and Sphagnum bogs where they occur' (Wilson, 2008). Less speculatively, whereas one beetle species (*Hybomorphus melanosomus*) endemic to Lord Howe Island is listed as extinct, another nine species are presumed extinct but not yet listed: *Melobasis empyria* (not collected since the 1880s), *Lacordairea fugax* (pre-1900), *Elasmotena insulana* (1880s), *Somatidia pulchella* (1910s), *Cormodes darwini* (1910s), *Howeotranes insularis* (1920s), *Leptopius etheridgei* (1910s), *Tomoxia howensis* (1880s) and *Cafius gigas* (1910s) (Cassis et al., 2003; Department of Environment and Climate Change (NSW), 2007). Taxonomic bias (against poorly known groups, such as most invertebrates) is well established in threatened species listings in Australia (Walsh et al., 2012) and globally (Régnier et al., 2009), and is likely to also be the case for listing of extinct species. As an example, of the 16 terrestrial vertebrate species endemic to Christmas Island, six are formally listed as extinct and six as threatened; whereas of ca. 200 endemic invertebrate species, none are listed as extinct – even though about 50 of these invertebrate species have not been reported for > 100 years – and only one is listed as threatened (James et al., 2019 in press). Furthermore, an endemic tick (*Ixodes nitens*) and flea (*Xenopsylla nesiotes*), both hosted only by the two endemic Christmas Island *Rattus* species that became extinct about 1904, are also recognised by relevant experts as following their obligate hosts to extinction (Mihalca et al., 2011; Colwell et al., 2012; Kwak,

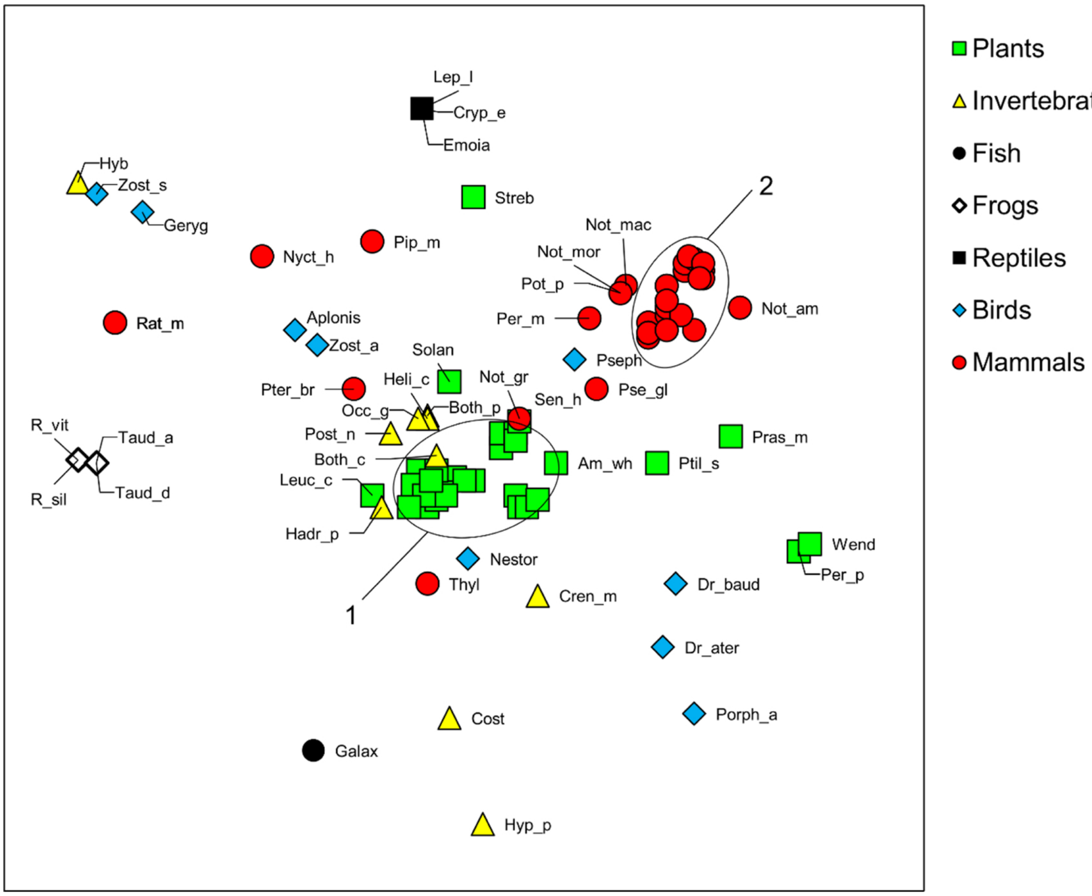

Fig. 3. Ordination of extinct species by the relative contribution of the factors causing those extinctions. Note that this ordination excludes two species with idiosyncratic causal factors, *Melomys rubicola* and *Vanvoorstia bennettiana* (the sole protist species). Stress level for the ordination is 0.12. Acronyms for species mentioned in text: Galax = *Galaxias pedderensis*, Hyp_ped = *Hypolimnus pedderensis*, Cost = *Costora iena*, Dr_ater = *Dromaius ater*, Dr_baud = *Dromaius baudinianus* and Porph_a = *Porphyrio albus*. Acronyms are not given for species in two tight clusters, 1 (plants) and 2 (mammals).

2018), but are not yet formally listed as such. Such co-extinction of host-specific species may be a widespread feature, but in all such cases in Australia, only the vertebrate host species has been formally recognised as extinct (Edwards et al., 2007; Taylor et al., 2018).

Given the likely extent of this under-reporting of extinction in invertebrates (and probably other poorly known groups), the actual number of extinct Australian species is likely to be far higher than that reported here from official lists. How much the tally is under-estimated is not readily calculable. The Western Australian plant example (Gibson, 2016) suggests that the number of formally recognised plant extinctions may be only 30–50% of the actual number of plant species extinctions. The Lord Howe and Christmas Islands examples suggest that only about 10% or less of Australia's invertebrate extinctions are officially recognised, but extrapolating from these two island examples to the mainland may be unjustifiable. Several factors contribute to this under-representation: relative to vertebrates, there is typically far less knowledge of the distribution, ecology, threats, population size and status of most invertebrates, so their loss may go unnoticed (Sands, 2018). Given the limited evidence base for most invertebrates, the standards of proof needed to demonstrate extinction in most official listing processes may be unobtainable. Furthermore, there is typically more public awareness of, and advocacy for, most vertebrate groups than for most invertebrate groups, so there is a greater likelihood that vertebrates will be nominated for listing as threatened or extinct in those listing processes that involve public input. As indicated by the Lord Howe Island beetles and the Christmas Island invertebrates, but also evident from many miscellaneous sources, many Australian species considered by experts as likely to be extinct or highly imperilled are not included yet on any formal lists. The status of such species is largely in an unrecognised limbo: there would be merit in trying to collate information on such species (and any others not recorded for many decades), and prioritising them for survey and/or listing, an approach taken by Gibson (2016) for Western Australian plants. Although formal listing as extinct on the basis of limited evidence is suboptimal and may risk the Romeo error – that listing as extinct results in the withdrawal of any conservation action directed at the species (Collar, 1998) – a systematic attempt to expedite the process for formally listing as extinct all those species reasonably considered as such by relevant experts would do much to redress the existing taxonomic bias and provide a more realistic indicator of the magnitude of species loss in Australia.

As discussed above, the complement of extinct Australian species reported here is likely to be taxonomically biased and a substantial under-estimate. But even accounting for those biases, it is likely that there are real differences among taxonomic groups in their extent of extinction, with the proportional loss of mammals being exceptional (Woinarski et al., 2015). Far more so than for Australian birds and reptiles, or for mammals on any other continent, the Australian mammal fauna has been remarkably susceptible to introduced predators, specifically the red fox and cat. In this feature, the loss of Australian mammals is consistent with the main driver of extinction on islands globally: introduced species (Sax and Gaines, 2008; Loehle and Eschenbach, 2012). Habitat loss is associated with extinctions of Australian species in most other taxonomic groups, a pattern more typical of other continents (Pimm and Raven, 2000). However, in contrast to its contribution to many extinctions in other continents (Maxwell et al., 2016), there is now relatively little hunting or harvesting of native

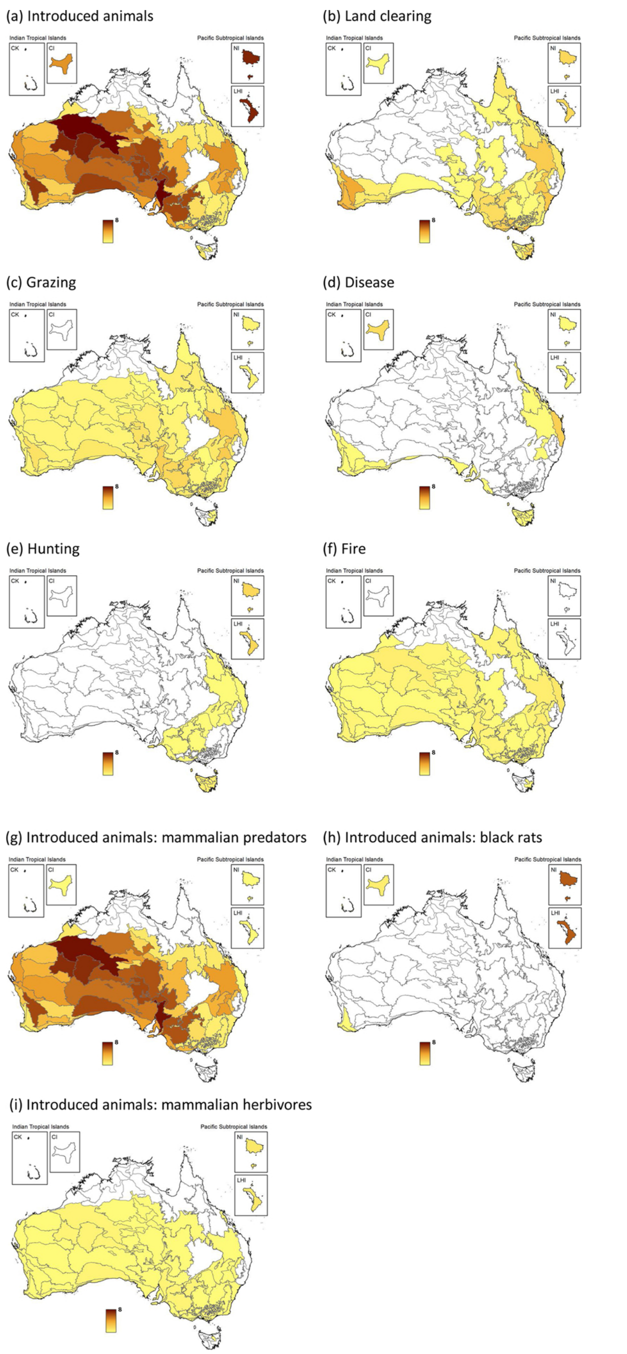

Fig. 4. Geographic variation in the factors that contributed to extinctions in each bioregion. The maps show the sum of extinctions in each bioregion attributed to each threatening process. The threatening processes are shown in decreasing order of the total number of extinctions attributed to each, with only the first seven shown (a–f). Introduced animals are also subdivided into mammalian predators, black rats and mammalian herbivores (g–i).

species in Australia and this factor accordingly is largely inconsequential as a cause of recent Australian extinction, or as a threat to extant but threatened Australian species (Kearney et al., 2019). The counter-intuitive result reported here of a greater number of extinctions in regions with a higher proportion of conservation reserves is, at least in part, due to the loss of mammals caused by predation by foxes and cats, which in Australia are as abundant and effective as predators in reserves as they are elsewhere (Legge et al., 2017).

Largely because of the high proportion (34%) of mammals in the tally of recognised Australian extinctions, and the formerly extensive distribution of many of these mammal species (notably in many bioregions that are relatively little modified), extinctions have occurred over most of the continent (Fig. 2a, 2d, 2e). The most obvious exception to this pervasiveness is the absence of listed extinctions in much of northern Australia. However, there is current severe decline of many mammal species in this area (Woinarski et al., 2010; Ziembicki et al., 2013, 2015; Davies et al., 2018), suggesting this unblemished record may not be maintained for long.

There are some other notable features in the geography of Australian extinctions. Concordant with global patterns (Loehle and Eschenbach, 2012; Szabo et al., 2012; Tershy et al., 2015; Gray, 2019), there is also a high rate of extinctions of Australia's island-endemic species (Woinarski et al., 2018). The reasons for such preponderance of extinctions in island species are well-established: island species typically have small population sizes, often have lost their anti-predator defence mechanisms (for example, in birds, by becoming flightless), often have low reproductive rates and may have little or no resistance to newly introduced diseases; and because many invasive species introduced to islands may escape some limitations (*e.g.* more crowded competition or predation contexts) that in their source areas constrained their population density. Most of the extinctions of island-endemic species in Australia have been from Christmas Island (137 km^2: six species recognised as extinct), Norfolk Island (and its satellite islands) (37 km^2: six species, with two of these shared with Lord Howe Island) and Lord Howe Island (and its satellite islands) (15 km^2: seven species, including the two species shared with Norfolk). There is also a more muted feature in the spatial patterning of Australian extinctions with about 40 species lost that formerly had highly restricted mainland ranges, mostly in bioregions subjected to intensive development or extensive habitat loss (*e.g.* Figs. 2c and 7b).

What does this review tell us about Australia's current conservation priorities and future conservation effort? To some extent, both scenarios in the quotes introducing this article apply: there is both continuity and change in the causes and patterning of Australia's extinctions. In general, within taxonomic groups, the main factors that caused extinctions for Australian species are largely the same as the main factors that are now causing decline in Australia's threatened species (Burgman et al., 2007; Kearney et al., 2019). However, although the rate of Australian extinctions since European settlement has been largely constant, and some threats remain undiminished, the results reported here indicate some change over time in the relative contribution of different causal factors to extinctions. Conservation efforts have largely curtailed hunting as a major cause of extinction, and have reduced the risk of extinction posed by introduced mammalian predators (Legge et al., 2018). However, the most recent time period considered here (1961–2018) has witnessed episodes of extinctions due to new factors, including disease (for frog species), an invasive snake species, invasive invertebrates, invasive fish and climate change. At least four (Christmas Island pipistrelle, Christmas Island forest skink *Emoia nativitatis*, blue-tailed skink *Cryptoblepharus egeriae*, Lister's gecko *Lepidodactylus listeri*) of the Australian extinctions experienced in the last ten or so years occurred very rapidly, with these island species collapsing from abundant to extinct (or extinct in the wild) within the space of two to three decades (Andrew et al., 2018; Woinarski, 2018): due to their small population sizes and constrained range, such island species may be particularly susceptible to rapid loss. However, many species in many parts of Australia are now exhibiting rapid and severe rates of decline (Woinarski et al., 2001; Wayne et al., 2017), and the rate of loss is predicted to increase (Geyle et al., 2018).

The arrival of these new threats, and the rapid detrimental impact of some of them, further amplifies the need for tighter biosecurity, but also illustrates that the isolation that long cossetted Australia's biodiversity will be increasingly likely to be breached in a more interconnected world. However, enhanced biosecurity is but part of a much more comprehensive set of responses needed to staunch the losses of Australian biodiversity and meet the objective of its national environmental legislation 'in particular prevent the extinction, and promote the recovery of, threatened species …' [EPBC Act s 3(2)(e)(i)] and global commitments to the Aichi target that 'By 2020 the extinction of known threatened species has been prevented'. Other measures include substantially increasing funding for threatened species management (including for more substantial monitoring and threat management), more effective constraints on natural resource use, and more decisive action to curb climate change and to develop effective adaptation responses.

Declaration of Competing Interest

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2019.108261.

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