Biology of Extinction: Alien species as a driver of recent extinctions

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Abstract

We assessed the prevalence of alien species as a driver of recent extinctions in five major taxa (plants, amphibians, reptiles, birds, mammals), using data from the IUCN Red List. Our results show that alien species are the second most common threat associated with species that have gone completely extinct from these taxa since 1500AD. Aliens are the most common threat associated with extinctions in three of the five taxa analysed, and for vertebrate extinctions overall.

Introduction

Biological diversity naturally varies substantially over space and time, but this variation is ultimately the product of just four key processes: speciation, immigration, emigration and extinction [1]. These processes are increasingly being perturbed, and subsequently shaped, by the actions of humans [2]. Human exploitation of species and appropriation of land and water have greatly increased extinction rates in recent centuries relative to the background levels in the fossil record [3,4]. Human activities have also greatly increased rates of immigration [5,6], by deliberately or accidentally transporting and introducing large numbers of species to areas beyond normal biogeographical barriers to their spread, where they may establish viable populations (here termed alien) [7]. Alien species have had a range of impacts documented in their new environments [8], and there are well-documented examples of native species that have been driven extinct by aliens [9,10]. Indeed, alien species are often cited as the second commonest cause of recent and ongoing extinctions (since 1500AD) after habitat destruction (i.e. for the U.S., see [11]).

Human activities are clearly elevating extinction rates, but it is contentious how much of that elevation is due to direct effects of exploitation and appropriation, and how much arises indirectly as a consequence of our elevation of species' immigration. As a consequence, the role of aliens as important drivers of past extinctions and/or current extinction risk has been disputed [12-14], the evidence underpinning the "second commonest cause" claim has been questioned [15], and indeed speciation by aliens has even been argued to lead to a net increase in diversity in some taxa in some regions [16]. These arguments form part of a narrative that the detrimental effects of alien species have been overemphasised [14-18].

Some of the arguments about the impacts of alien species [12,19] have been based on data on extinction, and extinction risk, from the IUCN Red List. This is a dynamic resource, for which regular updates add ever greater and more accurate information on the conservation status of increasing numbers of species. Here, we revisit this resource to assess the current state of knowledge on associated causes of extinction in five of the best-studied taxa worldwide. Specifically, we assess the frequency with which alien species are cited under the causes of loss of plant, amphibian, reptile, bird and mammal species considered to be extinct (category EX) and extinct in the wild (category EW).

Methods

The Red-listing process identifies and classifies 12 major threats to the persistence of species (IUCN threat classification scheme version 3.0) [20]. We compiled data on the total numbers of described, extinct and possibly extinct

71 (category EX), and extinct in the wild (category EW) plant, amphibian, reptile,
72 bird and mammal species from the 2013 IUCN Red List with threat information
73 (N = 247) [21]. We maintained the same classification scheme as IUCN except for
74 threat category number 8 ("Invasive and other problematic species, genes &
75 diseases"), which we subdivided into Alien Species (i.e., invasive non-native
76 [alien] species and diseases) and Other Problematic Species (i.e., native species
77 or species of unknown origin).
78
79 We ascribed threats to each EX and EW species according to the information in
80 the IUCN Red list. For instance, if a species is recorded as threatened by
81 Biological Resource use according to IUCN, it was given a '1' in the data matrix;
82 otherwise it received a value of '0'. We repeated this process for the 12 external
83 threats listed. This allows that species may have been affected by multiple
84 threats. For each taxonomic group, we calculated the number of EX + EW species
85 for which alien species are cited as a threat among species with known threats.
86 This allowed us to calculate the proportion of all threats that relate to alien
87 species. We classified EX and EW species either as an island endemic or
88 mainland species using the IUCN Red List database (www.iucnredlist.org;
89 accessed June 2015). Geographic range distributions were also used to assign
90 each EX and EW species to one of 12 biogeographic regions (see Figure 1).
91
92 All analyses were conducted in R version R 3.2.0 [22].
93

Results

A total of 215 species from the five taxa considered here are recorded as extinct on the IUCN Red List, and a further 32 are extinct in the wild (Table 1). Alien species are listed as a cause for 58% of all EX, and 31% of all EW species of the species for which a cause is given (see electronic supplementary material, Table S1, for the species list). These percentages vary across taxa (Table 1). Aliens are less important as an extinction (EX +EW) driver for plants (27%, 15/55 species) than for vertebrates (62%, 119/192), and indeed they are listed as a driver for more than half of the extinctions in each of the vertebrate taxa analysed (Table 1). Extinct species commonly have more than one threat identified (mean = 1.90), but aliens comprise from 14% (plants) to 45% (mammals) of all listed threats for a given taxon, and 28.51% of all threats listed (Table 1). For those species with just a single extinction (EX + EW) driver listed, this driver is alien species for 17% of plants, no amphibians, 25% of reptiles, 27% of birds and 47% of mammals.

For all four vertebrate taxa, the top three threats ranked by the percentage of extinct (EX) species impacted are Agriculture & aquaculture, Alien species and Biological resource use (overexploitation) (Table 2). Alien species is the top ranked threat for extinct amphibians, reptiles and mammals. For plants, Residential & commercial development is one of the top three threats, displacing alien species down to fourth (Table 2). In total, 58% of EX species (125/215) in the five taxa analysed were listed as impacted by Biological resource use, which is the highest ranked overall. Alien species comes in a close second, with 58% of

118 extinct species (124/215) impacted, while Agriculture & aquaculture ranks a
119 distant third (61/215; 28%).
120
121 Most recorded extinctions (EX + EW) in the taxa analysed for which alien species
122 are a listed driver have concerned island endemic species (86%, 115/134
123 species; electronic supplementary material, Figure S1). All EX + EW plants and
124 reptiles were island endemic species, while 27% of amphibians, 93% of birds
125 and 80% of mammals were island endemics. Nevertheless, there are 8
126 amphibian, 5 bird and 6 mammal species with continental mainland populations
127 for which alien species are listed as an extinction driver (electronic
128 supplementary material, Figure S1). Most of the species that aliens have helped
129 to drive extinct have been lost from Australia, New Zealand and other locations
130 in the Pacific (Figure 1). However, most amphibian losses have been from the
131 Americas (Figure 1).
132
133 **Discussion**
134 Our results confirm that, for the five major taxa analysed here, alien species are
135 the second most common threat associated with species that have gone
136 completely extinct since 1500AD. They are relegated into second place by
137 Biological resource use, by the smallest possible margin (125 vs 124 species
138 affected). In fact, alien species are the most common threat associated with
139 extinctions in three of the five taxa analysed, and for vertebrate extinctions
140 overall. Alien species are listed as having contributed to the extinction of more
141 than half of all the species in our analyses (EX + EW), and to almost two thirds of
142 the vertebrates. Around 30 alien taxa are implicated, including “bees”, rainbow

143 trout *Oncorhynchus mykiss,* “tortoises”, great horned owls *Bubo virginianus* and
144 guinea pigs *Cavia porcellus*, but especially rats *Rattus* spp. and cats *Felis catus* for
145 extinct birds and mammals, diseases (especially chytridiomycosis and avian
146 malaria) for extinct amphibians and birds, and herbivores (especially goats
147 *Capra hircus*, sheep *Ovis aries* and European rabbits *Oryctolagus cuniculus*), and
148 alien plants for extinct plant species [21]. Extinctions since 1500AD are only a
149 small proportion of the vertebrate species lost in the period following human
150 expansion out of Africa [23,24]. However, well-typified fossil assemblages, reveal
151 a number of extinctions that are most likely to have been caused by alien species
152 [25]. Thus, alien-driven extinctions are unlikely to be just a modern phenomenon.
153
154 The IUCN Red List represents probably the best available data on the factors
155 associated with recent extinctions, and of current extinction risk, and we have
156 taken the causes of extinction it records at face value. It remains possible that the
157 Red List may systematically over-estimate the impact of alien species, if these are
158 not the causal agents of extinction, but symptoms of the real causes (e.g. habitat
159 destruction) [13]. We doubt that any such overestimation is substantial. Alien
160 species may often act in synergy with other extinction drivers – and indeed most
161 extinctions are associated with more than one – but the impacts of alien species
162 have been well documented in multiple contexts [9 ; 26]. Further, habitat loss,
163 harvesting, and human disturbance, co-occur randomly with impact from aliens
164 as threats to vertebrates on the IUCN Red List [27]. One could argue equally
165 convincingly that the impacts of alien species may in many cases be
166 underestimated, as many interactions (especially between alien parasites and
167 native hosts) [28] are very hard to detect. Nevertheless, in many cases the true

168 contribution of alien species versus other extinction drivers will never be known,
169 given that the impacted species concerned are now extinct.
170
171 Aliens species are not just a problem for island species. While most of the recent
172 extinctions associated with alien species relate to island endemics (Figure 1),
173 14% of alien-related extinctions have concerned species with mainland
174 populations. Alien species are a significant concern for mainland species
175 currently threatened with extinction. In particular, the highest absolute number
176 of species threatened by alien species are located in South American countries
177 [29]. In summary, our results do not support arguments that the detrimental
178 effects of alien species have been overemphasised [14-18].
179
180 **Ethics**
181 The Authors have no ethical issues to report.
182
183 **Data Accessibility**
184 The data on which this paper is based are freely available on the IUCN Red List
185 website (www.redlist.org). A list of extinct species is given in the online
186 supplementary material.
187
188 **Competing Interests**
189 The Authors have no competing interests.
190
191 **Authors' contributions**
192 CB, PC and TMB conceived the study; CB compiled and analysed the data; CB, PC

and TMB wrote the paper. The authors agree to be accountable for all aspects of the work reported.

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References

1. Cracraft J. 1994 Species diversity, biogeography, and the evolution of biotas. *Am. Zool*. **34**, 33–47.

2. Vitousek PM, D'Antonio CM, Loope LL, Rejmánek M, Westbrooks R. 1997 Introduced species: a significant component of human-caused global change. *N. Z. J. Ecol.* **21**, 1–16.

3. Lawton JH., May RM. 1995 *Extinction rates*. Oxford: Oxford University Press.

4. Ceballos G, Ehrlich PR, Barnosky AD, García A, Pringle RM, Palmer TM. 2015 Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Sci. Adv.* **1(5)**, e1400253.abstract.

5. Gaston KJ, Jones AG, Hanel C, Chown SL. 2003 Rates of species introduction to a remote oceanic island. *Proc. R. Soc. Lond. B* **270**, 1091–1098.

6. Hulme PE. 2009 Trade, transport and trouble: managing invasive species pathways in an era of globalization. *J Appl. Ecol.* **46**,10–18.

7. Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM. 2011 A proposed unified framework for biological invasions. *Trends Ecol. Evol*. **26**, 333-339.

8. Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, San Y, Pyšek P. 2011 Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol. Lett.* **14**, 702-708.

9. Courchamp F, Chapuis J-L, Pascal M. 2003 Mammal invaders on islands: impact, control and control impact. *Biol. Rev*. **78**, 347-383.

10. Clavero M, Brotons L, Pons P, Sol D. 2009 Prominent role of invasive species in avian biodiversity loss. *Biol. Conserv*. **142**, 2043–2049.

11. Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E. 1998 Quantifying threats to imperiled species in the United States. *BioScience* **48**, 607-615.

12. Gurevitch J, Padilla DK. 2004 Are invasive species a major cause of extinctions? *Trends Ecol. Evol.* **19**, 470–474.

13. Didham RK, Tylianakis JM, Hutchison MA, Ewers RM, Gemmell NJ. 2005 Are invasive species the drivers of ecological change? *Trends Ecol. Evol.* **20**, 470–474.

14. Thomas CD, Palmer G. 2015 Non-native plants add to the British flora without negative consequences for native diversity. *Proc. Nat. Acad. Sci. USA* **2015**, 1–6.

15. Thompson K. 2014 *Where do camels belong? The story and science of invasive species*. UK: Profile Books.

16. Thomas CD. 2013 The Anthropocene could raise biological diversity. *Nature* **502**, 7.

17. Davis MA, Chew MK, Hobbs RJ, Lugo AE, Ewel JJ, Vermeij GJ, Brown JH, Rosenzweig ML, Gardener MR, Carroll SP, et al. 2011 Don't judge species on their origins. *Nature*, *474*, 153–154.

18. Brown JH, Sax D. 2004 An essay on some topics concerning invasive species. *Austral Ecol.* **29**, 530–536.

19. Clavero M, Garciá-Berthou E. 2005 Invasive species are a leading cause of animal extinctions. *Trends Ecol. Evol.* **20**, 110.

20. Salafsky N, Salzer D, Stattersfield, AJ, Hilton-Taylor C, Neogarten R, Butchart SHM, Collen B, Cox n, Master LL, O'Connor S, Wilkie D. 2008. A standard lexicon for biodiversity conservation: unified classifications of threats and actions. *Conserv*. *Biol*. **22**, 897–911.

21. IUCN. 2013 *The IUCN Red List Categories and Criteria: Version 3.1.* Gland, Switzerland.

256 22 R Core Team 2014 *R: A language and environment for statistical computing*. R
257 Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-
258 project.org/.

259 23. Martin PS, Klein R. 1984 *Quaternary extinctions: A prehistoric revolution*.
260 Tuscon: University of Arizona Press.

261 24. Turvey ST, ed. 2009 *Holocene extinctions.* Oxford: Oxford University Press.

262 25. Holdaway RN. 1999 Introduced predators and avifaunal extinction in New
263 Zealand. In MacPhee RDE, ed, *Extinctions in near time: Causes, contexts, and*
264 *consequences*, pp. 189–238. New York: Kluwer Academic/Plenum.

265 26. Pyšek P, Blackburn TM, Garcia-Berthou E, Perglová I, Rabitsch W. 2016
266 Displacement and local extinction of native and endemic species. In: Vila M,
267 Hulme PE, Ruiz G, editors. Impact of biological invasions on ecosystem services,
268 Springer.

269 27. Berglund H, Järemo J, Bengtsson G. 2013. Associations of invasive alien
270 species and other threats to IUCN Red List species (Chordata: vertebrates). *Biol.*
271 *Inv*. **15**, 1169–1180.

272 28. Blackburn TM, Ewen J. 2016 Parasites as drivers and passengers of human-
273 mediated biological invasions. *EcoHealth* in revision.

274 29. Bellard C, Genovesi P, Jeschke JM. (in prep.) Global patterns in vertebrates
275 threatened by biological invasions.

276

277 Table 1. The total number of species either extinct (EX) or extinct in the wild
278 (EW) according to the IUCN Red List (2014) in each of five major taxa, and the
279 total number (S_{Alien}) and percentage ($\%S_{Alien}$) for which alien species are listed as
280 a causal threat, the mean number of threats recorded per species (± standard
281 deviation), and the percentage of all listed threat categories that relate to aliens
282 (%T).
283

Taxon	**Status**	**Species**	**S_{Alien}**	**% S_{Alien}**	**Threats**	**%T**
Plants	EX	32	9	28	2 (±1)	14
	EW	23	6	26	2 (±1)	15
Amphibians	EX	15	10	67	4 (±2)	19
	EW	2	1	50	4 (±1)	13
Reptiles	EX	6	4	67	2 (±1)	29
	EW	1	0	0	1	0
Birds	EX	119	71	60	2 (±1)	35
	EW	4	3	75	3 (±2)	27
Mammals	EX	43	30	70	2 (±1)	45
	EW	2	0	0	3 (±1)	0
Total		**247**	**134**	**54**	**2** (±1)	**29**

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285
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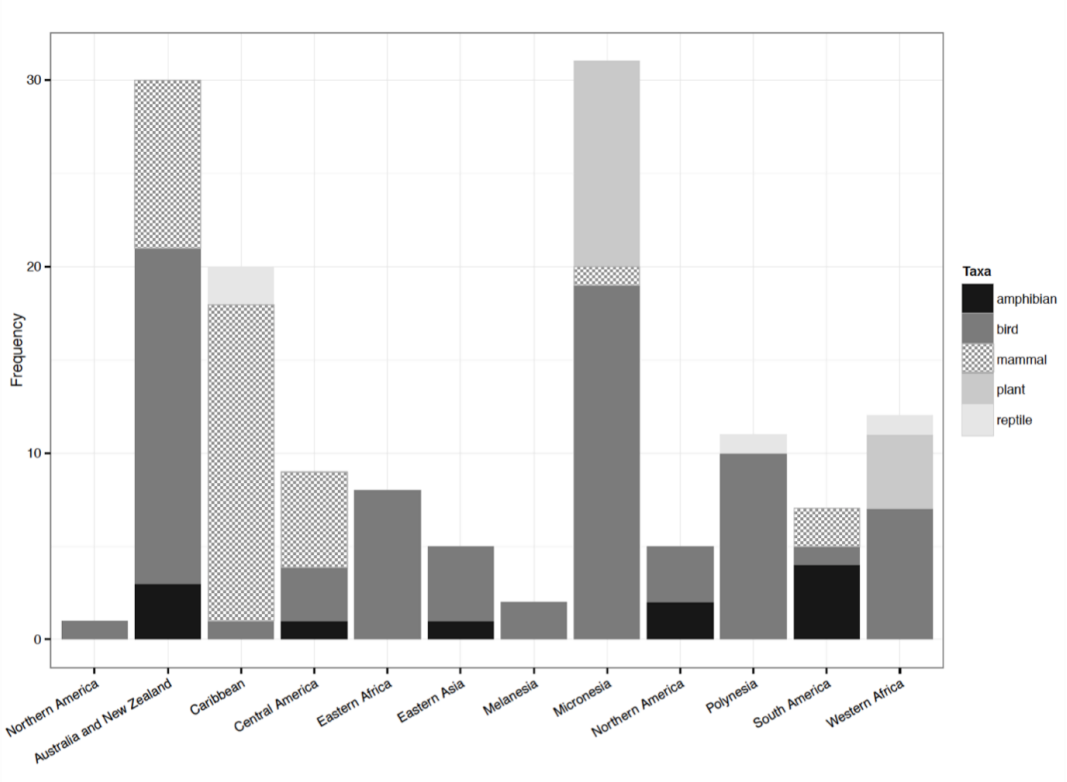
Table 2. The top four threats associated with extinct (EX) species in each taxon, and the percentage and (in parentheses) numbers of extinct species for which each threat was listed. Only three threats are listed for reptiles because the percentages for the fourth to seventh ranked threats were all equal (17%). Alien species (AS) is highlighted in bold. Other threats are: AG = Agriculture & aquaculture, CC = Climate change & severe weather, BR = Biological resource use (overexploitation), PO = Pollution, SM = Natural system modifications, UR = Residential & commercial development (urbanisation).

Taxon	**Status**	**Rank 1**	**Rank 2**	**Rank 3**	**Rank 4**
Plants	Threat	AG	BR	UR	**AS**
	% (number)	59 (19)	44 (14)	34 (11)	**28 (9)**
Amphibians	Threat	**AS**	AG	BR	PO
	% (number)	**67 (10)**	60 (9)	53 (8)	47 (7)
Reptiles	Threat	**AS**	BR	AG	
	% (number)	**67 (4)**	50 (3)	33 (2)	
Birds	Threat	BR	**AS**	AG	SM
	% (number)	70 (83)	**60 (71)**	17 (20)	8 (10)
Mammals	Threat	**AS**	BR	AG	SM
	% (number)	**70 (30)**	40 (17)	26 (11)	7 (3)

300 Figure 1. The locations of the (now lost) native ranges of the 134 extinct (EX +

301 EW) species for which alien species are listed as a driver.



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303

304 Electronic Supplementary Material.

305 Table S1. Table with the name of all of the extinct species (EX-EW), with the

306 particular alien species that are associated with each of their extinctions

307 according to the IUCN Red List. For some of the extinct species more than one

308 alien species are associated with the extinctions.

309

Extinct species	Alien species
Achyranthes atollensis	Unspecified species
Alectroenas rodericana	Rattus norvegicus
	Rattus rattus
Anaxyrus baxteri	Chytrid
Anthornis melanocephala	Felis catus
	Rattus spp
Aplonis corvina	Rattus spp
Aplonis fusca	Rattus rattus
Aplonis mavornata	Rattus norvegicus
Atelopus ignescens	Chytrid
Atelopus longirostris	Chytrid
Bowdleria rufescens	Capra hircus
	Felis catus
	Orytolagus cuniculus
Brotomys voratus	Rattus spp
Bulweria bifax	Introduced predators
Cabalus modestus	Capra hircus
	Felis catus
	Orytolagus cuniculus
	Ovis aries
	Rattus spp
Caloprymnus campestris	Felis catus
	Vulpes vulpes
Celestus occiduus	Introduced predators (e.g., mangooses)
Chaeropus ecaudatus	Felis catus
	Orytolagus cuniculus

	Ovis aries
	Vulpes vulpes
Chaunoproctus ferreorostris	Felis catus
Chioninia coctei	Canis familiaris
	Felis catus
	Rattus spp
Ciridops anna	Rattus spp
Clermontia peleana	Felis catus
	Sus scrofa
Columba duboisi	Felis catus
Columba jouyi	Felis catus
Columba versicolor	Felis catus
Commidendrum rotundifolium	Cryptotermes (ants)
Conuropsis carolinensis	Bees
Corvus hawaiiensis	West nile virus
Coturnix novaezelandiae	Canis lupus
	Felis catus
Coua delalandei	Rattus spp
Craugastor chrysozetetes	Chytrid
Craugastor escoces	Chytrid
Cyanea marksii	Invasive plants
	Rattus spp
	Sus scrofa
Cyanea pinnatifida	Invertebrates
	Rattus spp
	Sus scrofa
Cyanea superba	Invasive plants
	Rattus spp
	Molusc
	Sus scrofa
Cyanea truncata	Invasive plants
	Rattus spp
	Sus scrofa
Cyanoramphus ulietanus	Rattus norvegicus
Cyanoramphus zealandicus	Rattus norvegicus
Cyclura onchiopsis	Capra hircus

	Felis catus
Cynops wolterstorffi	Amphibian
	Fish
Cyrtandra waiolani	Sus scrofa
Drepanis funerea	Axis axis
	Bos taurus
Drepanis pacifica	Unspecified disease
Dryopteris ascensionis	Buddleja madagascariensis
Dysmorodrepanis munroi	Felis catus
Dysmoropelia dekarchiskos	Felis catus
Ectopistes migratorius	NVD
Fregilupus varius	Unspecified disease
Gallicolumba norfolciensis	Felis catus
Gallicolumba salamonis	Canis lupus
	Felis catus
	Sus scrofa
Gallirallus dieffenbachii	Canis lupus
	Felis catus
Gallirallus owstoni	Boiga irregularis
Gallirallus pacificus	Felis catus
Geocapromys thoracatus	Felis catus
Gerygone insularis	Rattus rattus
Haematopus meadewaldoi	Felis catus
	Rattus rattus
Hemignathus ellisianus	Introduced predators
	Unspecified disease
Hemignathus obscurus	Unspecified disease
Heteralocha acutirostris	Unspecified disease
Incilius periglenes	Chytrid
Isolobodon portoricensis	Introduced predators (e.g., mangooses)
	Rattus rattus
Lagorchestes asomatus	Felis catus
	Vulpes vulpes
Lithobates fisheri	Lithobates catesbeianus
Macropus greyi	Introduced predators
Macrotis leucura	Felis catus

	Orytolagus cuniculus
	Vulpes vulpes
Megalomys desmarestii	Mangoose
Megalomys luciae	Mangoose
Melicope haleakalae	Unspecified species
Melicope paniculata	unspecified species
Mergus australis	Canis lupus
	Felis catus
	Sus scrofa
Microgoura meeki	Canis lupus
	Felis catus
Moho apicalis	Unspecified disease
Moho bishopi	Axis axis
	Canis lupus
	Capra hircus
	Felis catus
	Miconia calvescens
	Rattus rattus
	Sus scrofa
Moho braccatus	Rattus rattus
	Sus scrofa
Moho nobilis	Unspecified disease
Mundia elpenor	Felis catus
	Rattus rattus
Myadestes myadestinus	Sus scrofa
Myiagra freycineti	Boiga irregularis
Neotoma anthonyi	Felis catus
Neotoma bunkeri	Felis catus
Neotoma martinensis	Felis catus
Nesillas aldabrana	Capra hircus
Nesoclopeus poecilopterus	Felis catus
Nesophontes edithae	Rattus spp
Nesophontes hypomicrus	Rattus spp
Nesophontes major	Rattus spp
Nesophontes micrus	Rattus spp
Nesophontes paramicrus	Rattus spp

Nesophontes zamicrus	Rattus spp
Nesoryzomys darwini	Rattus rattus
Nesoryzomys indefessus	Rattus rattus
Oldenlandia adscensionis	Capra hircus
	Leucaena leucocephala
	Ovis aries
Oligoryzomys victus	Rattus norvegicus
	Rattus rattus
Onychogalea lunata	Felis catus
	Orytolagus cuniculus
	Vulpes vulpes
Oryzomys antillarum	Mangoose
Oryzomys nelsoni	Rattus rattus
Paroreomyza flammea	Unspecified disease
Perameles eremiana	Felis catus
	Vulpes vulpes
Pezophaps solitaria	Felis catus
Podiceps andinus	Oncorhynchus mykiss
Podilymbus gigas	Micropterus salmoides
Pomarea fluxa	Felis catus
	Rattus exulans
	Rattus norvegicus
Pomarea nukuhivae	Capra hircus
Pomarea pomarea	Unspecified species
Porphyrio kukwiedei	Canis lupus
Porzana astrictocarpus	Felis catus
Porzana monasa	Rattus spp
Porzana palmeri	Cavia porcellus
	Orytolagus cuniculus
	Rattus rattus
Porzana sandwichensis	Canis lupus
	Felis catus
Prosobonia ellisi	Rattus spp
Prosobonia leucoptera	Rattus norvegicus
Psephotus pulcherrimus	Felis catus
	Opuntia stricta

Pterodroma rupinarum	Felis catus
Pteropus tokudae	Boiga irregularis
Ptilinopus mercierii	Bubo virginianus
	Felis catus
Raphus cucullatus	Unspecified species
Rattus macleari	Rattus rattus
Rattus nativitatis	Rattus rattus
Rheobatrachus silus	Ageratina riparia
	Sus scrofa
Rheobatrachus vitellinus	Chytrid
Sceloglaux albifacies	Rattus exulans
Solenodon marcanoi	Rattus spp
Sporobolus durus	Melinis minutiflora
Tachybaptus rufolavatus	Eichhornia crassipes
	Micropterus salmoides
Tachygyia microlepis	Canis familiaris
	Rattus spp
	Sus scrofa
Taudactylus diurnus	Ageratina riparia
	Chytrid
	Lantana camara
	Sus scrofa
Traversia lyalli	Felis catus
Turnagra capensis	Rattus rattus
Turnagra tanagra	Felis catus
	Felis catus
	Rattus rattus
	Rattus rattus
Upupa antaios	Felis catus
Wikstroemia skottsbergiana	Unspecified species
Wikstroemia villosa	Unspecified species
Zenaida graysoni	Felis catus
Zoothera terrestris	Felis catus
Zosterops strenuus	Rattus rattus

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311

312 Figure S1. The cumulative number of species extinct (EX) and extinct in the wild
313 (EW) according to the IUCN Red List (2013) in each of five major taxa for which
314 alien species are listed as a threat that are located in mainland and islands.
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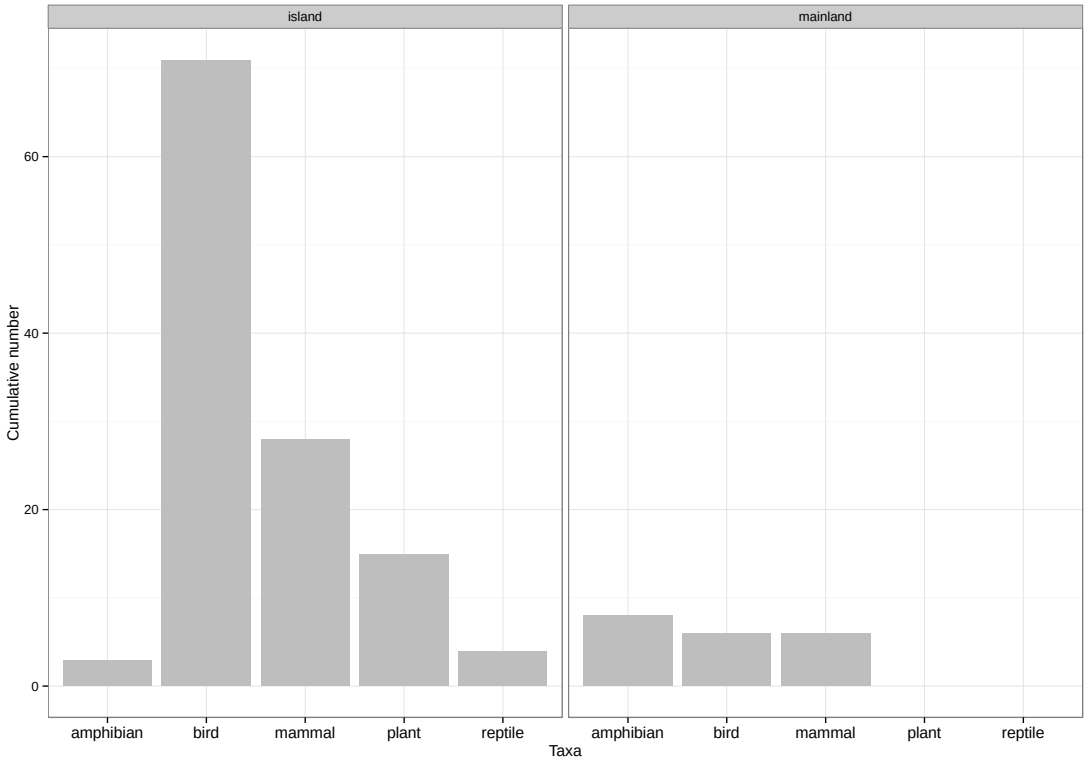

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