BIOLOGY LETTERS

rsbl.royalsocietypublishing.org

Research

Cite this article: Bellard C, Cassey P, Blackburn TM. 2016 Alien species as a driver of recent extinctions. *Biol. Lett.* **12**: 20150623. http://dx.doi.org/10.1098/rsbl.2015.0623

Received: 16 July 2015
Accepted: 18 December 2015

Subject Areas:
ecology

Keywords:
non-native species, amphibian, bird, mammal, plant, reptile

Author for correspondence:
Tim M. Blackburn
e-mail: t.blackburn@ucl.ac.uk

An invited contribution to the special feature 'Biology of extinction: inferring events, patterns and processes' edited by Barry Brook and John Alroy.

Electronic supplementary material is available at http://dx.doi.org/10.1098/rsbl.2015.0623 or via http://rsbl.royalsocietypublishing.org.

THE ROYAL SOCIETY PUBLISHING

Conservation biology

Alien species as a driver of recent extinctions

Céline Bellard[1], Phillip Cassey[2] and Tim M. Blackburn[1,2,3,4]

[1]Department of Genetics, Evolution and Environment, Centre for Biodiversity and Environment Research, Darwin Building, UCL, Gower Street, London WC1E 6BT, UK
[2]School of Biological Sciences and the Environment Institute, The University of Adelaide, Adelaide, South Australia 5005, Australia
[3]Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK
[4]Distinguished Scientist Fellowship Program, King Saud University, Riyadh 1145, Saudi Arabia

TMB, 0000-0003-0152-2663

We assessed the prevalence of alien species as a driver of recent extinctions in five major taxa (plants, amphibians, reptiles, birds and 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 AD 1500. Aliens are the most common threat associated with extinctions in three of the five taxa analysed, and for vertebrate extinctions overall.

1. 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 the rates of immigration [5,6], by deliberately or accidentally transporting and introducing large numbers of species to areas beyond normal biogeographic 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 most common cause of recent and ongoing extinctions (since AD 1500) after habitat destruction (i.e. for the USA, 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 overemphasized [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 (International Union for Conservation of Nature) 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

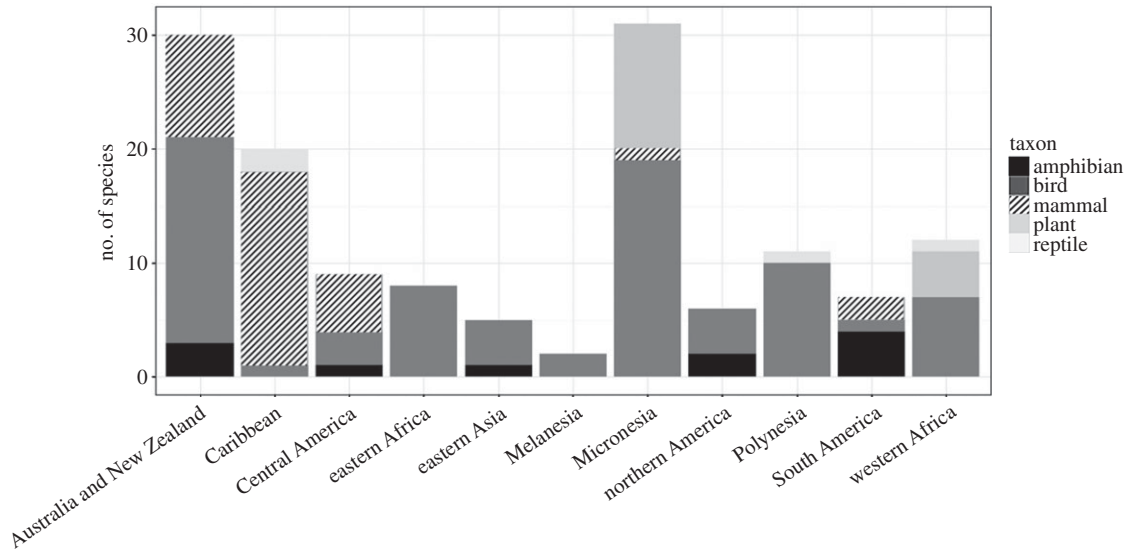

Figure 1. The locations of the (now lost) native ranges of the 134 extinct (EX + EW) species for which alien species are listed as a driver.

mammal species considered to be extinct (category EX) and extinct in the wild (category EW).

2. Methods

The Red-Listing process identifies and classifies 12 major threats to the persistence of species (IUCN threat classification scheme v. 3.0) [20]. We compiled data on the total numbers of described, extinct and possibly extinct (category EX), and extinct in the wild (category EW) plant, amphibian, reptile, bird and mammal species from the 2015 IUCN Red List with threat information ($n = 247$) [21]. We maintained the same classification scheme as IUCN except for threat category number 8 ('Invasive and other problematic species, genes & diseases'), which we subdivided into alien species (i.e. invasive non-native (alien) species and diseases) and other problematic species (i.e. native species or species of unknown origin).

We ascribed threats to each EX and EW species according to the information in the IUCN Red list. For instance, if a species is recorded as threatened by biological resource use according to IUCN, it was given a '1' in the data matrix; otherwise, it received a value of '0'. We repeated this process for the 12 external threats listed. This allows that species may have been affected by multiple threats. For each taxonomic group, we calculated the number of EX + EW species for which alien species are cited as a threat among species with known threats. This allowed us to calculate the proportion of all threats that relate to alien species. We classified EX and EW species either as an island endemic or mainland species using the IUCN Red List database (www.iucnredlist.org; accessed June 2015). Geographical range distributions were also used to assign each EX and EW species to one of 12 biogeographic regions (figure 1).

All analyses were conducted in R v. R 3.2.0 [22].

3. Results

A total of 215 species from the five taxa considered here are recorded as extinct in 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 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 compose 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 and 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 and 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 extinct species (124/215) impacted, whereas agriculture and aquaculture ranks a distant third (61/215; 28%).

Most recorded extinctions (EX + EW) in the taxa analysed for which alien species are a listed driver have concerned island endemic species (86%, 115/134 species; electronic supplementary material, figure S1). All EX + EW plants and reptiles were island endemic species, whereas 27% of amphibians, 93% of birds and 80% of mammals were island endemics. Nevertheless, there are eight amphibian, five bird and six mammal species with continental mainland populations for which alien species are listed as an extinction driver (electronic supplementary material, figure S1). Most of the species that aliens have helped to drive extinct have been lost from Australia, New Zealand and other locations in the Pacific (figure 1). However, most amphibian losses have been from the Americas (figure 1).

4. Discussion

Our results confirm that, for the five major taxa analysed here, alien species are the second most common threat

Table 1. The total number of species either extinct (EX) or extinct in the wild (EW) according to the IUCN Red List (2015) in each of five major taxa, and the total number (S_{alien}) and percentage ($\%S_{alien}$) for which alien species are listed as a causal threat, the mean number of threats recorded per species ($\pm$ s.d.), and the percentage of all listed threat categories that relate to aliens ($\%T$).

taxon	status	species	S_{alien}	$\%S_{alien}$	threats	$\%T$
plants	EX	32	9	28	2 ($\pm$1)	14
	EW	23	6	26	2 ($\pm$1)	15
amphibians	EX	15	10	67	4 ($\pm$2)	19
	EW	2	1	50	4 ($\pm$1)	13
reptiles	EX	6	4	67	2 ($\pm$1)	29
	EW	1	0	0	1	0
birds	EX	119	71	60	2 ($\pm$1)	35
	EW	4	3	75	3 ($\pm$2)	27
mammals	EX	43	30	70	2 ($\pm$1)	45
	EW	2	0	0	3 ($\pm$1)	0
total		247	134	54	2 ($\pm$1)	29

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 italics. Other threats are: AG, agriculture and aquaculture; CC, climate change and severe weather; BR, biological resource use (overexploitation); PO, pollution; SM, natural system modifications; UR, residential and commercial development (urbanization).

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)

associated with species that have gone completely extinct since AD 1500. They are relegated into second place by biological resource use, by the smallest possible margin (125 versus 124 species affected). In fact, alien species are the most common threat associated with extinctions in three of the five taxa analysed, and for vertebrate extinctions overall. Alien species are listed as having contributed to the extinction of more than half of all the species in our analyses (EX + EW), and to almost two-thirds of the vertebrates. Around 30 alien taxa are implicated, including 'bees', rainbow trout *Oncorhynchus mykiss*, 'tortoises', great horned owls *Bubo virginianus* and guinea pigs *Cavia porcellus*, but especially rats *Rattus* spp. and cats *Felis catus* for extinct birds and mammals, diseases (especially chytridiomycosis and avian malaria) for extinct amphibians and birds, and herbivores (especially goats *Capra hircus*, sheep *Ovis aries* and European rabbits *Oryctolagus cuniculus*) and alien plants for extinct plant species [21]. Extinctions since AD 1500 are only a small proportion of the vertebrate species lost in the period following human expansion out of Africa [23,24]. However, well-typified fossil assemblages reveal a number of extinctions that are most likely to have been caused by alien species [25]. Thus, alien-driven extinctions are unlikely to be just a modern phenomenon.

The IUCN Red List represents probably the best available data on the factors associated with recent extinctions, and on current extinction risk, and we have taken the causes of extinction it records at face value. It remains possible that the Red List may systematically overestimate the impact of alien species, if these are not the causal agents of extinction, but symptoms of the real causes (e.g. habitat destruction) [13]. We doubt that any such overestimation is substantial. Alien species may often act in synergy with other extinction drivers—and indeed, most extinctions are associated with more than one—but the impacts of alien species have been well documented in multiple contexts [9,26]. Further, habitat loss, harvesting and human disturbance co-occur randomly with impact from aliens as threats to vertebrates on the IUCN Red List [27]. One could argue equally convincingly that the impacts of alien species may in many cases be

underestimated, as many interactions (especially between alien parasites and native hosts) [28] are very hard to detect. Nevertheless, in many cases, the true contribution of alien species versus other extinction drivers will never be known, given that the impacted species concerned are now extinct.

Alien species are not just a problem for island species. While most of the recent extinctions associated with alien species relate to island endemics (figure 1), 14% of alien-related extinctions have concerned species with mainland populations. Alien species are a significant concern for mainland species currently threatened with extinction. In particular, the highest absolute number of species threatened by alien species are located in South American countries [29]. In summary, our results do not support arguments that the detrimental effects of alien species have been overemphasized [14–18].

Data accessibility. The data on which this paper is based are freely available on the IUCN Red List website (www.redlist.org). A list of extinct species is given in the electronic supplementary material.

Authors' contributions. C.B., P.C. and T.M.B. conceived the study; C.B. compiled and analysed the data; C.B., P.C. and T.M.B. wrote the paper. The authors agree to be accountable for all aspects of the work reported.

Competing interests. The authors have no competing interests.

Funding. C.B. was supported by an AXA Fellowship. P.C. was supported by an ARC Future Fellowship (FT0914420) and by an ARC Discovery grant (DP140102319). T.M.B. had no funding for this work.

Acknowledgements. We thank Barry Brook and John Alroy for inviting us to write this paper, and three anonymous referees for helpful comments.

References

1. Cracraft J. 1994 Species diversity, biogeography, and the evolution of biotas. *Am. Zool*. **34**, 33–47. (doi:10.1093/icb/34.1.33)
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, UK: 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**, e1400253.abstract. (doi:10.1126/sciadv.1400253)
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. (doi:10.1098/rspb.2003.2332)
6. Hulme PE. 2009 Trade, transport and trouble: managing invasive species pathways in an era of globalization. *J. Appl. Ecol*. **46**, 10–18. (doi:10.1111/j.1365-2664.2008.01600.x)
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. (doi:10.1016/j.tree.2011.03.023)
8. Vilà M *et al*. 2011 Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol. Lett*. **14**, 702–708. (doi:10.1111/j.1461-0248.2011.01628.x)
9. Courchamp F, Chapuis J-L, Pascal M. 2003 Mammal invaders on islands: impact, control and control impact. *Biol. Rev*. **78**, 347–383. (doi:10.1017/S1464793102006061)
10. Clavero M, Brotons L, Pons P, Sol D. 2009 Prominent role of invasive species in avian biodiversity loss. *Biol. Conserv*. **142**, 2043–2049. (doi:10.1016/j.biocon.2009.03.034)
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. (doi:10.2307/1313420)
12. Gurevitch J, Padilla DK. 2004 Are invasive species a major cause of extinctions? *Trends Ecol. Evol*. **19**, 470–474. (doi:10.1016/j.tree.2004.07.005)
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. (doi:10.1016/j.tree.2005.07.006)
14. Thomas CD, Palmer G. 2015 Non-native plants add to the British flora without negative consequences for native diversity. *Proc. Natl Acad. Sci. USA* **112**, 4387–4392. (doi:10.1073/pnas.1423995112)
15. Thompson K. 2014 *Where do camels belong? The story and science of invasive species*. London, UK: Profile Books.
16. Thomas CD. 2013 The Anthropocene could raise biological diversity. *Nature* **502**, 7. (doi:10.1038/502007a)
17. Davis MA *et al.* 2011 Don't judge species on their origins. *Nature* **474**, 153–154. (doi:10.1038/474153a)
18. Brown JH, Sax D. 2004 An essay on some topics concerning invasive species. *Austral. Ecol*. **29**, 530–536. (doi:10.1111/j.1442-9993.2004.01340.x)
19. Clavero M, Garciá-Berthou E. 2005 Invasive species are a leading cause of animal extinctions. *Trends Ecol. Evol*. **20**, 110. (doi:10.1016/j.tree.2005.01.003)
20. Salafsky N *et al.* 2008 A standard lexicon for biodiversity conservation: unified classifications of threats and actions. *Conserv. Biol*. **22**, 897–911. (doi:10.1111/j.1523-1739.2008.00937.x)
21. IUCN. 2015 *The IUCN red list categories and criteria: version 3.1*. Gland, Switzerland: International Union for Conservation of Nature.
22. R Core Team. 2014 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See http://www.R-project.org/.
23. Martin PS, Klein R. 1984 *Quaternary extinctions: a prehistoric revolution*. Tucson, AZ: University of Arizona Press.
24. Turvey ST (ed.). 2009 *Holocene extinctions*. Oxford, UK: Oxford University Press.
25. Holdaway RN. 1999 Introduced predators and avifaunal extinction in New Zealand. In *Extinctions in near time: causes, contexts, and consequences* (ed. RDE MacPhee), pp. 189–238. New York, NY: Kluwer Academic/Plenum.
26. Pyšek P, Blackburn TM, Garcia-Berthou E, Perglová I, Rabitsch W. 2016 Displacement and local extinction of native and endemic species. In *Impact of biological invasions on ecosystem services* (eds M Vila, PE Hulme, G Ruiz). Berlin, Germany: Springer.
27. Berglund H, Järemo J, Bengtsson G. 2013 Associations of invasive alien species and other threats to IUCN Red List species (Chordata: vertebrates). *Biol. Inv*. **15**, 1169–1180. (doi:10.1007/s10530-012-0359-x)
28. Blackburn TM, Ewen J. 2016 Parasites as drivers and passengers of human-mediated biological invasions. *EcoHealth*. (doi:10.1007/s10393-015-1092-6)
29. Bellard C, Genovesi P, Jeschke JM. 2016 Global patterns in threats to vertebrates by biological invasions. *Proc. R. Soc. B* **283**, 20152454. (doi:10.1098/rspb.2015.2454)