Alien versus native species as drivers of recent extinctions

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Native plants and animals can rapidly become superabundant and dominate ecosystems, leading to claims that native species are no less likely than alien species to cause environmental damage, including biodiversity loss. We compared how frequently alien and native species have been implicated as drivers of recent extinctions in a comprehensive global database, the 2017 International Union for Conservation of Nature (IUCN) Red List of Threatened Species. Alien species were considered to be a contributing cause of 25% of plant extinctions and 33% of animal extinctions, whereas native species were implicated in less than 5% and 3% of plant and animal extinctions, respectively. When listed as a putative driver of recent extinctions, native species were more often associated with other extinction drivers than were alien species. Our results offer additional evidence that the biogeographic origin, and hence evolutionary history, of a species are determining factors of its potential to cause disruptive environmental impacts.

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A defining feature of the Anthropocene is the human-mediated translocation of species to areas beyond their natural biogeographic boundaries (Ricciardi 2007; Kueffer 2017). Although the ecological impacts of most introduced species are unknown or appear to be negligible, others have been found to cause substantial changes to food webs, ecosystem function, and biodiversity (Gandhi and Herms 2010; Simberloff *et al*. 2013), including extinctions on local to global scales (Clavero and García-Berthou 2005; Bellard *et al*. 2016a; Doherty *et al*. 2016; Downey and Richardson 2016). Nevertheless, some researchers have argued that the impacts of alien species are exaggerated and contend that they are no more likely than native species to cause environmental damage, such as extinctions (Sagoff 2005; Davis *et al*. 2011; Pearce 2015), and that the biogeographic origin of a species is irrelevant to its ecological impact (Davis *et al*. 2011; Valéry *et al*. 2013). It follows therefore that efforts to control or eradicate alien species in general are unnecessary and only serve to drain resources from more constructive conservation projects (Marris 2011; Pearce 2015). This view is being fueled in part by the emerging concept of "native invasions" – that is, native plants and animals that spread, attain extremely high abundances within their historical range (Nackley *et al*. 2017), and, according to some (Carey *et al*. 2012), cause impacts that rival those of invasive alien species. However, as far as we are aware, no one has yet formally tested whether alien species are more or less likely than natives to cause extinctions. We investigate that question by analyzing recent global extinctions in the IUCN Red List database (IUCN 2017).

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Methods

We compiled data from the 2017 IUCN Red List database (IUCN 2017) on the total numbers of species that are extinct (including those that are possibly extinct) and extinct in the wild (categories EX and EW; plants [n = 153] and animals [n = 782]). These are species that have gone globally extinct since 1500 CE (Common Era), or would have done so had the last few individuals not been taken into captivity. The IUCN Red List is widely recognized as the most comprehensive, objective, global source for evaluating the conservation status of plants and animals. It is based on an explicit, scientifically rigorous framework for the classification of species according to their extinction risk, and is the result of the work of hundreds of experts in the status and conservation of the taxa listed (IUCN 2017). The IUCN Red List identifies 12 broad categories of extinction drivers (Threats Classification Scheme v3.2; IUCN 2017); we maintained this classification scheme for our analysis, with the exception that we subdivided threat category 8 ("Invasive and other problematic species, genes & diseases") into two subcategories, *alien species* and *other problematic species*, to give a total of 13 threat categories. The origin (native or alien) of some species in threat category 8 is unknown, and we therefore assumed that these are native, which adds three species to the list of those threatened by natives. For two of these additional three species, aliens are also listed as a threat. Six of the 935 total extinct species (ie both plants and animals) had threats listed under categories 100.37 and 110.43. These refer to old threat listings relating to pollution, and we therefore added these six species to the pollution threat category (category

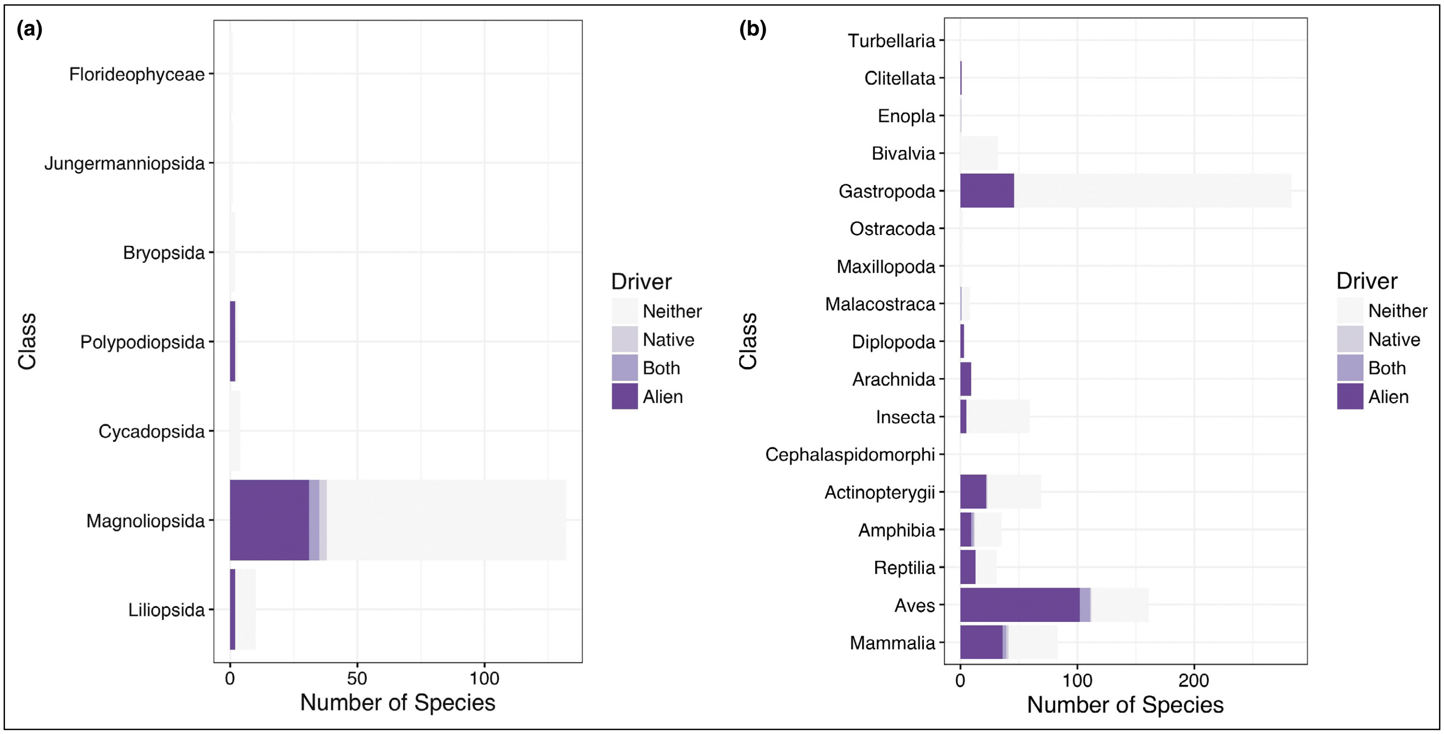

Figure 1. The number of recently extinct (International Union for Conservation of Nature [IUCN] categories "extinct" [EX] and "extinct in the wild" [EW]) species in each (a) plant and (b) animal class, along with recorded extinctions for which alien species, native species, both alien and native species, or neither are listed as associated extinction drivers (from data in WebTable 1).

9 in Threats Classification Scheme v3.2). The resulting data frame is listed in WebTable 1.

We used a chi-squared test to assess the distribution of IUCN category 8 threats between alien and native species, and nonparametric Kruskal-Wallis tests to compare the number of other drivers associated with alien- and native-influenced extinctions, conducted in R (v3.5.0; R Core Team 2018). No extinction driver was listed for almost half of the EX or EW animal and plant species (461 of 935). Excluding these species from our analysis would approximately double the overall proportions of EX and EW species for which aliens or natives are listed as a driver (63% and 6% for aliens and natives, respectively), but would not change our conclusions.

Results

Of the 935 total recent extinctions in our dataset, 261 of 782 animal species (33.4%) and 39 of 153 plant species (25.5%) had aliens listed as one of the extinction drivers (Figure 1). Alien species ranked first as a driver of animal extinctions, well ahead of the second-ranked driver, biological resource use (ie hunting and harvesting), with 18.8% of species affected. Aliens also ranked first for plant extinctions, slightly ahead of biological resource use (a driver in 23.5% of plant extinctions) and agriculture (19.6%). In contrast, only 2.7% of animal extinctions (21 species; rank 8th) and 4.6% of plant extinctions (seven species; rank 7th) had native species listed as one of the extinction drivers. In total, 261 animal extinctions since 1500 CE have been associated with the impacts of alien taxa, more than 12 times as many as native taxa (21 extinctions). Alien species also outnumber native species as a driver of plant extinctions, accounting for 5.6 times as many extinctions (n = 39) as do natives (n = 7). Overall, IUCN category 8 impacts were significantly more likely to relate to alien than to native species (χ^2 = 225, degrees of freedom [df] = 1, P < 0.001). Fourteen classes of plants and animals have suffered recent extinctions for which aliens are listed as a contributory driver versus only seven classes for which natives are listed as a driver (Figure 1).

Extinct species for which one or more alien species were listed as an extinction driver were also associated with 1.00 ± 1.24 (average ± standard deviation) other extinction drivers (ie IUCN threat categories). The most common drivers co-occurring with alien-influenced extinctions were biological resource use and agriculture (occurred in 29% and 21.7% of alien-influenced extinctions, respectively). Species driven extinct in part by alien species had significantly more additional recognized extinction drivers than those unaffected by alien species (1.00 additional drivers on average versus 0.42 additional drivers; Kruskal-Wallis chi-squared = 78.1, df = 1, P < 0.0001). Nevertheless, aliens were the sole driver for 126 extinct species, or 42% of the 300 species with aliens as a named driver.

Native species were the sole driver for none of the extinct animals or plants. Species with natives listed as an extinction driver were associated with an average of 2.57 ± 1.50 other extinction drivers, with alien species (67.9% of cases) and agriculture (57.1%) the most common associated drivers; in other words, 19 of the 28 species for which natives were listed as an extinction driver also had aliens listed as a driver. Species driven extinct in part by native species were associated with significantly more additional extinction drivers than species unaffected by native species (2.57 versus 0.84; Kruskal-Wallis chi-squared = 41.7, df = 1, $P < 0.0001$), and were associated with more additional threat types than were species with aliens as an extinction driver (2.57 versus 1.00; Kruskal-Wallis chi-squared = 33.1, df = 1, $P < 0.0001$). Therefore, native species are more likely to be acting in synergy with (eg be triggered by) other extinction drivers than are aliens. Species with both natives and aliens as extinction drivers were double counted in this analysis (ie they contribute to the totals of the number of species driven extinct by natives, and the number driven extinct by aliens), but the result was more or less the same when these extinctions were excluded (1.67 additional extinction drivers associated with natives versus 0.86 for aliens; Kruskal-Wallis chi-squared = 10.3, df = 1, $P = 0.001$). As noted above, most recently extinct species with natives listed as a driver also had aliens listed, and so the sample size was reduced in the latter analysis.

Classes of organisms in which aliens were implicated in the majority of extinctions (Figure 1) include Arachnida (100%), Diplopoda (100%), Aves (68.9%), Polypodiopsida (66.7%), and Clitellata (50%), although the number of extinct species in some of these classes is small. Alien species were also implicated in 42% and 47% of reptile and mammal extinctions, respectively. In contrast, aside from Enopla ($n = 1$), native species are associated with at most 12.5% of extinctions in any class (Malacostraca). Examples of alien and native species implicated in recent extinctions are shown in Figures 2 and 3, respectively.

Discussion

The impacts of native species in driving extinctions are much less widespread and prevalent as compared with those of alien species, according to data derived from the assessments of the hundreds of experts who compiled the IUCN Red List (Figure 1). Alien species are implicated in the recent extinction of more than ten times as many species, of a much broader phylogenetic diversity of taxa, than natives. Our results are conservative in this regard, as we consider all extinction-driving species of unknown origin to be natives, and do not question the origins of the native species listed as causing impacts (although in several cases these seem more likely to be alien). Moreover, most species do not establish alien populations (Seebens *et al.* 2018). As such, we provide a new line of evidence that the biogeographic origin of a species is relevant to its ecological impact, contrary to assertions that the distinction between native and alien species has no theoretical or practical importance to conservation (Davis *et al.* 2011; Valéry *et al.* 2013).

Previous analyses have shown that alien species contribute substantially to recent terrestrial vertebrate and plant extinctions, being the second most frequent extinction driver (after

Figure 2. Alien species cited as contributing to the extinction of species on the IUCN Red List (categories EX or EW). (a) Rosy wolfsnail (*Euglandina rosea*), which was widely introduced across the South Pacific as a biocontrol agent of the giant African land snail (*Achatina fulica*) but has instead predated on other island endemic snails, and is thought to have been directly responsible for the extinction of at least 134 snail species. (b) Brown tree snake (*Boiga irregularis*), which caused the local extinction of more than half of Guam's native bird and lizard species, two of Guam's three native bat species, and several global extinctions. (c) Black rat (*Rattus rattus*), which has directly contributed to the extinction of many species of birds, mammals, reptiles, invertebrates, and plants, especially on islands.

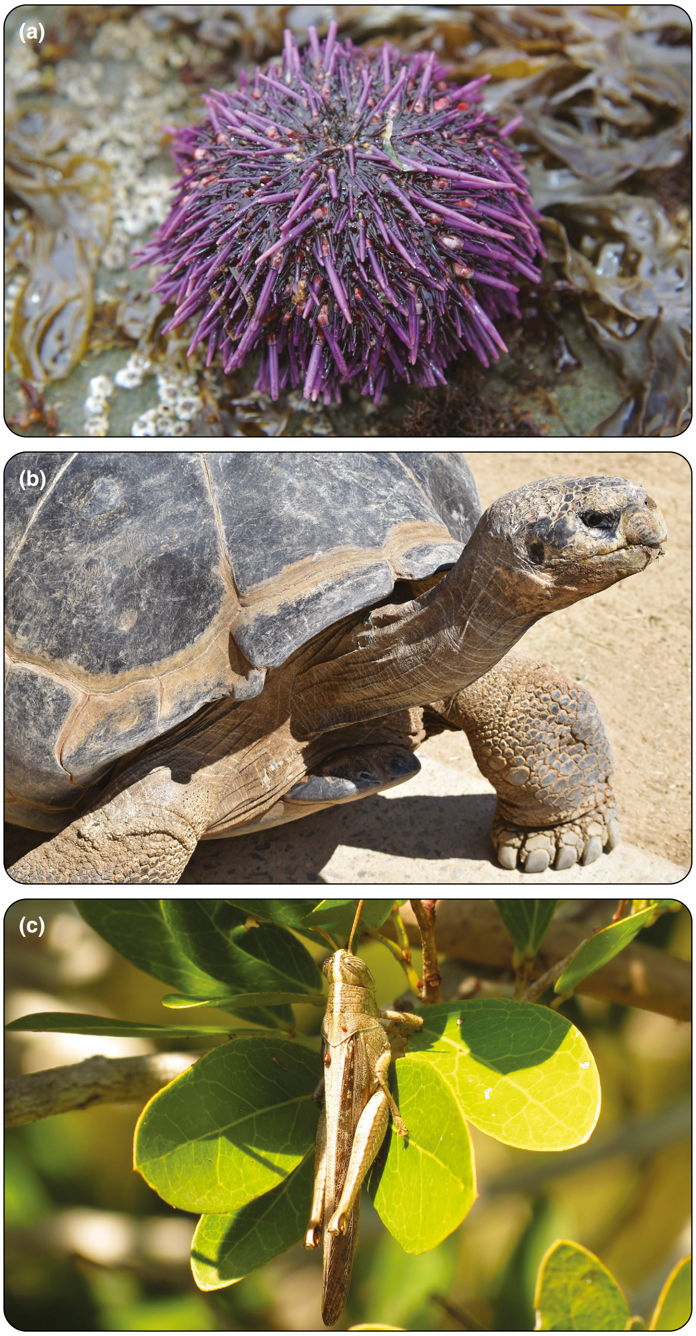

Figure 3. Native species cited as contributing to the extinction of species on the IUCN Red List (categories EX or EW). (a) Purple sea urchin (*Strongylocentrotus purpuratus*), which has been implicated in the extinction of Steller's sea cow (*Hydrodamalis gigas*). Human hunting of sea otters (*Enhydra lutris*) led to a population explosion of sea urchins, including *S purpuratus*, which in turn largely eliminated the kelp on which Steller's sea cows fed (IUCN 2017). (b) Aldabra tortoise (*Geochelone gigantea*), which has been implicated in the extinction of the Aldabra brush-warbler (*Nesillas aldabrana*). (c) Outbreaks of the locust *Schistocerca piceifrons* (shown here in the Celestún Biosphere Reserve, Yucatán, México) have reduced the extent of prime habitat for the Socorro dove (*Zenaida graysoni*), which is now extinct in the wild (IUCN 2017).

biological resource use) across all species assessed by the IUCN, and the driver most frequently associated with vertebrate extinctions (Bellard *et al.* 2016a). The present analysis uses updated IUCN data from a broader range of taxa and reveals that alien species are now the primary extinction driver of both animal and plant extinctions, pushing biological resource use into second place. This may be due in part to the inclusion of extinctions in a range of taxa not analyzed by Bellard *et al.* (2016a) for which alien species have been the primary extinction driver (eg Arachnida, Diplopoda). Aside from birds, the proportion of extinctions ascribed to alien impacts in the taxa analyzed by Bellard *et al.* is lower in the updated IUCN data (compare Figure 1 with Table 1 in Bellard *et al.* 2016a).

Alien taxa are not random samples of species; anthropogenic mechanisms tend to select species whose attributes are conducive to invasion success, and such taxa are often introduced to areas lacking the co-evolved enemies that limit their abundance in their native range (Buckley and Catford 2015; Rejmánek and Simberloff 2017). These are among the reasons why species often generate greater ecological impacts outside their native range (Rejmánek and Simberloff 2017). Although native species can form spreading or superabundant populations, alien plants are 40 times more likely to spread rapidly and dominate communities than native plants (Simberloff *et al.* 2012), and they are several times more likely than natives to achieve a maximum cover of at least 80% (Seabloom *et al.* 2015). When native plants do undergo damaging outbreaks, such events are almost invariably triggered by anthropogenic disturbances (Simberloff *et al.* 2012), which is consistent with our results showing that when native species are listed as a putative driver of recent extinctions, they are associated with more co-occurring extinction drivers than are recent extinctions in which native species are not implicated, or in which alien species are implicated. Indeed, no extinction in the current data was ascribed to the effects of native species alone, in contrast with 126 extinctions ascribed solely to the effects of alien species. Although the impacts of alien species have been argued to be a consequence of other environmental changes ("passengers"), as opposed to causative drivers (Didham *et al.* 2005), our data suggest that passenger status is more likely for native species when it comes to recent extinctions.

Ongoing anthropogenic disturbance, such as land transformation and climate change, can release native species from biotic constraints, perhaps causing them to dominate their communities to the detriment of biodiversity. Anthropogenic disturbances can also interact with alien species to exacerbate their impacts on natives (van der Wal *et al.* 2008; Schweiger *et al.* 2010; Blaustein *et al.* 2011). Native species undergoing outbreaks – even those expanding their range into adjacent territory – are less likely than alien species to encounter resident natives that lack evolutionary experience with them. This is in contrast to long-distance species translocations associated with human transportation systems, which have introduced functionally novel alien taxa at unprecedented rates worldwide (Ricciardi 2007). These aliens can cause declines and extinctions in native species through a range of mechanisms, including competition (Gilbert and Levine 2013), disease transmission (Lips 2016), and predation (Doherty *et al.* 2016). This is particularly true for islands, where most recent extinctions have occurred and where, in the future, alien species are still more likely to harm biodiversity than native ones (Bellard *et al.* 2016b). Alien consumers introduced to a community where functionally similar species are absent are more likely to disrupt native species populations (eg Ricciardi and Atkinson 2004; Russell *et al.* 2017). Across different biomes and habitat types, alien predators and herbivores cause more damage to native populations than do native consumers (Salo *et al.* 2007; Paolucci *et al.* 2013). We suspect that most of the alien species introductions linked to extinctions in the IUCN database are cases of evolutionary mismatches involving naïve native populations. The accelerating rate of establishment by alien species worldwide (Seebens *et al.* 2017, 2018) is of particular concern in this respect.

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Supporting Information

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