

Species invasions and extinction: The future of native biodiversity on islands

Dov F. Sax*[†] and Steven D. Gaines*[§]

*Brown University, Department of Ecology and Evolutionary Biology, Box G-W, Providence, RI 02912; [†]Department of Ecology, Evolution and Marine Biology and [§]Marine Science Institute, University of California, Santa Barbara, CA 93106

Predation by exotic species has caused the extinction of many native animal species on islands, whereas competition from exotic plants has caused few native plant extinctions. Exotic plant addition to islands is highly nonrandom, with an almost perfect 1 to 1 match between the number of naturalized and native plant species on oceanic islands. Here, we evaluate several alternative implications of these findings. Does the consistency of increase in plant richness across islands imply that a saturation point in species richness has been reached? If not, should we expect total plant richness to continue to increase as new species are added? Finally, is the rarity of native plant extinctions to date a misleading measure of the impact of past invasions, one that hides an extinction debt that will be paid in the future? By analyzing historical records, we show that the number of naturalized plant species has increased linearly over time on many individual islands. Further, the mean ratio of naturalized to native plant species across islands has changed steadily for nearly two centuries. These patterns suggest that many more species will become naturalized on islands in the future. We also discuss how dynamics of invasion bear upon alternative saturation scenarios and the implications these scenarios have for the future retention or extinction of native plant species. Finally, we identify invasion-motivated research gaps (propagule pressure, time-lags to extinction, abundance shifts, and loss of area) that can aid in forecasting extinction and in developing a more comprehensive theory of species extinctions.

birds | plants | species saturation

Species invasions have contributed to the extinction of many species world-wide (1), particularly on islands (2, 3). These extinctions have occurred disproportionately among taxonomic groups. For example, birds have lost many species, both in absolute terms and relative to their total number of species, whereas plants have lost few species (2, 4, 5). The lack of recorded extinctions in plants does not appear to be due to a lack of knowledge, particularly on well studied islands like New Zealand, where both historic and fossil records suggest that few native plant species have been lost (2). Why so few plant species have been lost is somewhat of a mystery, particularly considering the thousands of exotic plant species that have been introduced to islands (2). This near-lack of plant extinctions to date raises the obvious question of whether this trend will continue. In particular, should we expect few additional plant species to go extinct—even on individual islands where hundreds or thousands of exotic plant species have invaded? Should ongoing and future invasions eventually lead to mass extinction events among island plant taxa?

Our ability to accurately forecast future extinction events is limited by shortcomings in current ecological and evolutionary theory. In particular, we have a relatively poor understanding of the processes that ultimately limit how many species can inhabit any given place or area. One important concept, however, that arises from several prominent theories of species diversity is that for any given set of environmental conditions there is a “saturation point” that bounds the number of species a place or region can support (6–9). There are two basic ways that a saturation point for species richness could operate. First, the total number of species present in an area could be maintained as a balance

between extinction and colonization. At the saturation point, the addition of new colonizing species results in the local extinction of a like number of previously established species. We refer to this as “extinction-based saturation,” which is consistent with Island Biogeography Theory (IBT) (6, 7). Second, the total number of species in a place could be maintained by suppression of colonization. A saturation point is reached if the invasion of new species is inhibited by species already present. We refer to this as “colonization-based saturation,” which is consistent with the resistance to invasion in niche-based models of species diversity, such as Stochastic Niche Theory (SNT), where the total number of species in a place is determined by how finely resources can be partitioned among species (9).

These alternative pathways for species saturation have very different implications for the impact of invading species on native plant extinctions. Extinction-based saturation (like IBT) explicitly predicts species turnover, i.e., change in species composition, with the addition of species to islands (6, 7). Therefore, once a saturation point has been reached, the continued addition of exotic species should result in the extinction of native species, and the rate of extinction increases as the rate of colonization increases. If this holds true for islands, then we may eventually have dramatic increases in the number of native plant extinctions—particularly if exotics continue to be added in large numbers. In contrast, colonization-based saturation (like SNT) explicitly predicts that the addition of exotic species will become progressively less likely to occur as species richness increases (10). Colonization-based saturation (like SNT) also predicts that existing species should benefit from a priority effect that makes them unlikely to be displaced by incoming species—as long as invading species are more or less equivalent to native species in their efficiency in using resources (10). If this holds true on islands, then we should expect the rate of naturalization of exotic species to diminish dramatically and few currently established species (both native and exotic) to be at risk of extinction in the future. These are two very distinct views of the future, and distinguishing among these and other alternatives is important. Doing so will help us to advance our basic understanding of ecological and evolutionary theory while simultaneously advancing our understanding of a pressing applied issue, namely the future of plant diversity on islands worldwide.

Here, we evaluate the role of species invasions on the extinction of native species. We begin by examining the International Union for Conservation of Nature database for patterns of extinction in plants and terrestrial vertebrates that have occurred

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[†]To whom correspondence should be addressed. E-mail: dov.sax@gmail.com.

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worldwide over the past 500 years. We then focus on patterns of invasion and extinction on islands over the past few hundred years. Next, we consider, with a focus on plants, whether islands are saturated with respect to the total number of species they can support. We also consider what the implications of species saturation are for future plant extinctions. Finally, we explore several research gaps that currently limit our ability to forecast species extinctions.

General Drivers of Extinction. Humans have caused or contributed to many plant and animal extinctions. Over the past 15,000 years, humans have contributed to extinctions of large fauna on most continents of the world (11). Over the past few thousand years, human colonists and their commensals (such as the Polynesian rat) have contributed to the extinction of thousands of bird species across oceanic islands of the world (3). Over the past 500 years, humans have reduced the amount of natural habitat worldwide, directly exploited species, introduced exotic species and exotic pathogens, and created many other conditions conducive to species extinction. The total number of recent extinctions is unknown, because many species have likely gone extinct before ever being recorded by science (12). Estimates of global species loss vary, but based on rates of tropical deforestation and the species-area relationship a fairly typical estimate is 27,000 species lost per year; this is based on a species-area relationship with a z value of 0.15 and an estimate of 10 million species globally (12). Even with a more conservative estimate of 5 million species on the planet (13), this would still equate to $\approx 13,500$ species lost, or at least committed to extinction, per year. In sharp contrast to such estimates, the number of documented extinctions during the past 500 years is much lower; the International Union for Conservation of Nature, as of November 2007, reports 785 extinctions worldwide. Many other extinctions, not included in this number, have likely occurred, but they have not yet been documented adequately enough to be listed as extinct by the International Union for Conservation of Nature. Consequently, although species listed as extinct by the International Union for Conservation of Nature are likely an underestimate of the total number of extinctions over the past 500 years, those listed provide the most detailed evidence on extinction available.

There has been recent disagreement in the literature about how best to interpret extinction data from the International Union for Conservation of Nature, particularly with regards to the role species invasions play in causing extinctions (1, 14, 15). This disagreement has largely been due to the difficulty in ascribing precise causes to species extinctions. The precise mechanisms for any individual extinction are difficult to confidently determine for two reasons. First, extinctions are often caused by multiple factors, such as species invasions, habitat destruction, human exploitation, pollution, and infectious disease (16). Second, most “documented” extinctions actually involve some speculation about the factors responsible (because few species have been carefully monitored from the point of initial population decline to the point of final extinction). Additionally, it is worth noting that disagreement over species concepts, and disagreement over phylogenetic classifications of individual species, although not an issue for most extinct species, is an important point of debate in some cases. Given these limitations, it seems most appropriate to (i) consider whether general trends in the data exist, as opposed to focusing on the details of any one extinction, and (ii) focus analyses on those taxonomic groups that have been best studied and documented. Consequently, here we examine general trends in extinction in two of the best studied groups: terrestrial vertebrates and plants.

An analysis of the International Union for Conservation of Nature database on species extinctions reveals several emerging patterns for terrestrial vertebrate and plant species. First, most

extinctions have been on islands as opposed to mainlands (Fig. 1A). This holds true generally when all causes of extinction are pooled (Fig. 1A) and specifically when only extinctions that exotic species are believed to have contributed to are considered (Fig. 1B). Second, terrestrial vertebrates have disproportionately gone extinct compared with plants (Fig. 1A), both in absolute terms and relative to the taxonomic richness of their respective groups. Third, the presumed causes of these extinctions are not evenly distributed among types of species interactions. Predation has been a far more important species interaction in causing extinctions than competition (Fig. 1C). Indeed, predation alone, i.e., in the absence of other factors like habitat destruction or pollution, is listed as being responsible for the extinction of $>30\%$ of vertebrate species (Fig. 1C). In contrast, competition is never listed as being the sole factor responsible for species extinction (Fig. 1C). Further, predation is listed as one of several contributing factors in $>40\%$ of terrestrial vertebrate extinctions, whereas competition is listed as a contributing factor in $<10\%$ of terrestrial vertebrate extinctions (Fig. 1C). This means that predation acting alone or in concert with other factors is believed to have contributed to the extinction of close to 80% of all terrestrial vertebrate species, whereas competition has contributed to $<10\%$ of these extinctions. This predominance of predation over competition in causing extinctions may be due in part to the broad range of processes that we classify here as “predation,” e.g., both human hunting and parasitism (see *Methods*). However, even if we consider predation in the strictest sense to include only carnivorous animal interactions, the qualitative patterns described here are maintained. Further, differences between the role of predation and competition are conserved when considering only those cases where exotic species are believed to have played a contributing role in species extinction (Fig. 1D); in these cases, the combined influence of predation acting alone and predation acting in concert with other factors is believed to account for 98% of all extinctions. These patterns suggest that terrestrial vertebrates are much more likely to go extinct from predation than competition. This interpretation is consistent with observational and theoretical work by Davis (17), who suggests that competition should rarely be an important factor in species extinctions. Finally, for plants, we did not evaluate the role of predation versus competition in causing species extinctions because the degree of certainty generally associated with listed causes of plant extinctions in the International Union for Conservation of Nature database seemed too speculative. Still, if predation is the true cause of most species-interaction-based extinctions then perhaps this can help to explain why competition from invasive plants has led to so few plant extinctions—at least so far.

Invasions and Extinctions on Islands. Patterns of species invasions and extinctions have been well documented across a wide variety of islands and for a number of taxonomic groups (2, 5, 18, 19). In general, many species of plants, vertebrates, and invertebrates have been introduced to islands (2, 18, 20). Many of these introduced species have become naturalized, i.e., they have formed self-supporting populations capable of perpetuating themselves. Islands have also lost many native species; among vertebrates, extinctions have been greatest for bird species, largely because most other vertebrate groups are relatively depauperate on islands (21). In contrast to birds, plants have generally suffered few extinctions on islands (2, 4). For example, in New Zealand, 38 of 91 native land bird species have become extinct, whereas only 3 of $>2,000$ native plant species have become extinct (2). Overall, these patterns of extinction and naturalization have led to large changes in net species richness on islands around the world. Bird richness on most oceanic islands has remained largely unchanged, because the number of extinctions has been largely matched by the number of exotic

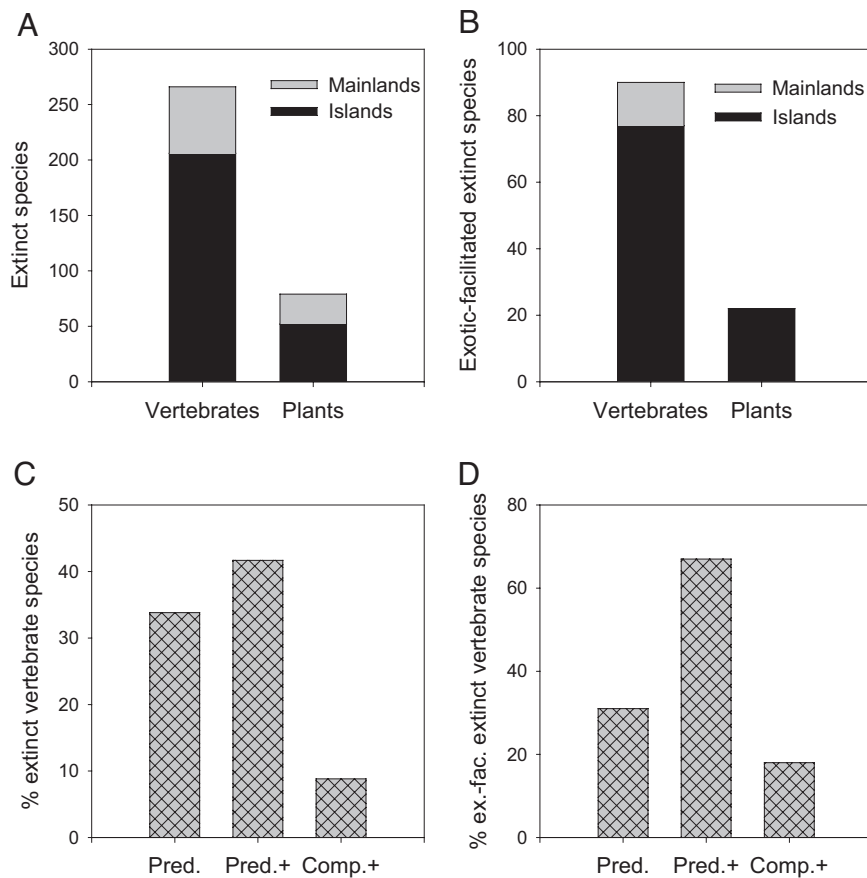


Fig. 1. Extinction patterns over the last 500 years, from the International Union for Conservation of Nature database. (A) The majority of documented extinctions have been on islands, as opposed to mainlands, for both terrestrial vertebrates (birds, mammals, reptiles, and amphibians) and plants. (B) Extinctions facilitated by exotic species (i.e., in which exotics are listed as at least one of the factors contributing to a species extinction) show the same pattern, with more extinctions on islands, as opposed to mainlands. (C) Among the 204 vertebrate species with listed causes of extinction, some form of predation (including human hunting, carnivory, and infectious disease) is cited as the sole factor responsible for species extinctions in 69 (33.8%) of extinctions, predation together with other contributing factors is cited for 85 (41.7%) of extinctions, and competition together with other factors is listed for 18 (8.8%) of extinctions. In no case is competition listed as the sole cause of species extinction. (D) Extinctions facilitated by exotic species show similar patterns, with predation listed alone in 31 of 100 extinctions, predation together with other factors listed in 67 extinctions, and competition together with other factors listed in 18 extinctions.

birds that have become naturalized (2). This relative consistency in net bird richness may be important in understanding and predicting future extinctions, but is not a “good” thing from a conservation perspective, because it means that many unique endemic species have been lost and replaced by more cosmopolitan species from mainlands (22). In contrast to birds, mammal richness has increased dramatically, particularly on oceanic islands, which have few native mammal species (5). Freshwater fish richness has also increased, because few native fishes have gone extinct (at least so far), whereas many exotic species have become naturalized (19). Invertebrate richness may also have increased, because many invertebrates have become naturalized on islands, e.g., >2,500 species on Hawaii alone (20), but records of extinction are less certain, so it is difficult to know how net richness has changed without additional investigation. Finally, vascular plants have seen dramatic increases in richness across both continental and oceanic islands, because many exotics have become naturalized, whereas few native species have gone extinct (23).

Increases in plant richness show several distinct patterns. First, comparisons between mainlands and islands and among island types (land-bridge versus oceanic) show repeatable quantitative differences; mainland areas have increased in plant species richness least, land-bridge islands have increased more, and oceanic islands have increased the most. For example, counties

in California have increased on average by 17%, the California Channel Islands have increased by 44%, and oceanic islands have increased by 104% in richness (23). Second, increases in richness on some islands have been sufficiently large that these isolated systems now approximate the richness of continental areas. For example, the addition of naturalized plants to Hawaii has pushed its net plant richness up to levels typical for an area of equal size in mainland Mexico (23). Third, the average increase in richness observed across oceanic islands is highly regular, with most islands showing a strikingly consistent doubling in net plant richness (2).

The doubling in plant richness on oceanic islands is due to a tightly correlated one-to-one relationship between native and naturalized plant species, with 96% of the variation in naturalized plant richness explained solely by native plant richness (Fig. 2). Other island characteristics individually explain far less variation in the richness of naturalized species. For example, human population size (79%), island area (71%), island maximum elevation (49%), and date of European settlement (31%) explain significant amounts of the variation but account for far less than that of native species richness. Indeed, even a multiple regression analysis with these and other island characteristics generates a model that accounts for less of the variation in naturalized species richness than is explained by native richness alone (see *Methods*). It is unclear why native plant richness is

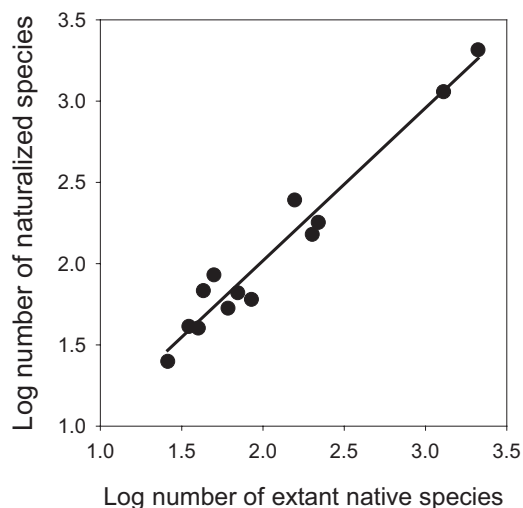


Fig. 2. Native and naturalized plant richness are highly correlated across oceanic islands. The log number of extant native plant species explains 96% of the variation in the log number of naturalized plant species. See [Table S1](#) for a list of islands and richness values.

such a good predictor of naturalized plant richness, but the strength of the relationship suggests that it may provide clues into understanding how richness patterns are likely to change in the future.

Plant invasion patterns provide several lines of evidence that suggest islands might be “filling-up” or becoming “saturated” with species. First, the most species-poor islands (oceanic as opposed to continental) have increased in plant richness the most. Second, many islands are now coming close to matching the species richness levels of continental environments. Third, patterns of increase are highly consistent among oceanic islands, where a close to perfect doubling in species richness of plants has occurred. This doubling might represent a new saturation point for species richness. If this has occurred and a saturation point has been reached, then it would be valuable to know the mechanism by which it has done so, e.g., whether it arose from colonization-based or extinction-based saturation. Alternatively, it would be valuable to know whether no saturation point has been reached. Distinguishing among these alternatives is critical, because they paint very different pictures for the future for plant biodiversity on islands.

Evaluating Colonization-Based Saturation. Colonization-based saturation will occur if the probability of adding new species to an area decreases over time as net richness increases—at some point, as an area fills up, the probability of adding any additional species will become so low that an effective saturation point will be reached (10). In some ways, this is a special case of Elton’s invasion hypothesis (24), which postulated that species-rich regions would be more difficult to invade than species-poor ones. In regards to islands, if a colonization-based saturation point has been reached, then new species cannot be added unless existing species are removed. This situation appears to have occurred for birds on islands, where native birds that were driven extinct (largely by naturalized mammal predation and human hunting) have been replaced by an approximately similar number of naturalized bird species [most of which invaded after the natives were already extinct (2)]. The importance of colonization-based saturation for birds is further corroborated by patterns of invasion in Hawaii, where birds introduced earlier were more likely to become established and persist than those introduced later, when naturalized richness was higher (25). For groups like

plants, which have had few extinctions and many introductions, islands were presumably not saturated by colonization-based mechanisms before species introductions. If, however, oceanic islands have now reached a colonization-based saturation point for plants, then the probability of introduced plant species becoming naturalized on islands should have decreased over the past two hundred years as more and more of these species became naturalized. One way this could manifest is as an asymptote in the cumulative number of exotic plant species that became naturalized over time.

We evaluate the possibility that plants have reached a colonization-based saturation point on oceanic islands by examining time-series of exotic species additions to individual islands through time (see *Methods*). A complete list of analyzed islands and their naturalized richness values through time are described in the [supporting information \(SI\) Text](#). Our results show no evidence of an asymptote in number of plant species that have become naturalized through time on any of the islands analyzed, which we illustrate with patterns of naturalization on six individual islands (Fig. 3). Instead, the number of naturalized plant species has increased in an approximately linear manner over time, with some potential evidence for exponential increases in a few cases (Fig. 3). Also in a few cases, and most notably for Heron Island, there appears to be a slight leveling-off in the number of naturalized species for the very last date recorded; this leveling-off is due to a procedural artifact in how naturalizations are tallied. Because exotic species that are recorded for the first time are typically not classified as being naturalized (because there is no evidence yet that they have established self-perpetuating populations), the total number of naturalized species will generally be underestimated in the last time step (see *Methods*).

In addition to change within individual islands, we also analyzed patterns of change across islands. To do this, we constructed 20-year bins as points of comparison through time (see *Methods*). Currently, the average ratio across islands of naturalized-to-native plant species is $\approx 1:1$. Our results show that this ratio has changed fairly steadily through time, from 1860 to 2000, with no evidence for an asymptote in the rate of change (Table 1). Only the final time step shows a leveling-off, but this is due to a procedural artifact (see *Methods*). A second way to illustrate change across islands is with comparisons of regressions through time between the log number of native and naturalized species. To do this, we used the same 20-year bins. Our results show that the slope of these log-log relationships has been fairly consistent through time, which we illustrate with all of the statistically significant regression lines for 20-year bins (Fig. 4A). Nonsignificant regression lines for 1860, 1940, and 1960 occurred in periods when relatively few historical surveys were conducted on these islands such that few data points are available for analysis (*SI Text*). The regressions from 2000 and 1880, when a relatively large number of individual data points are available, illustrate the consistency in slope among these periods (Fig. 4B). The consistency in the slope but change in intercept implies that the proportion of naturalized-to-native species has generally been consistent across islands within any given time interval but different among time intervals. This suggests two things. First, it suggests that there is something uniform about the relationship between native and naturalized species across these islands. Second, it suggests that the particular 1:1 relationship observed today is transient. At the current rate of change, the average ratio between naturalized-to-native species on oceanic islands should be $\approx 3:2$ by the year 2060.

There is no evidence of a decrease in the rate of exotic addition of plants to individual islands or across islands over the past 200 years. This suggests that more plant species will continue to be added to these islands in the future. On first consideration, this could be interpreted as strong evidence against the operation of

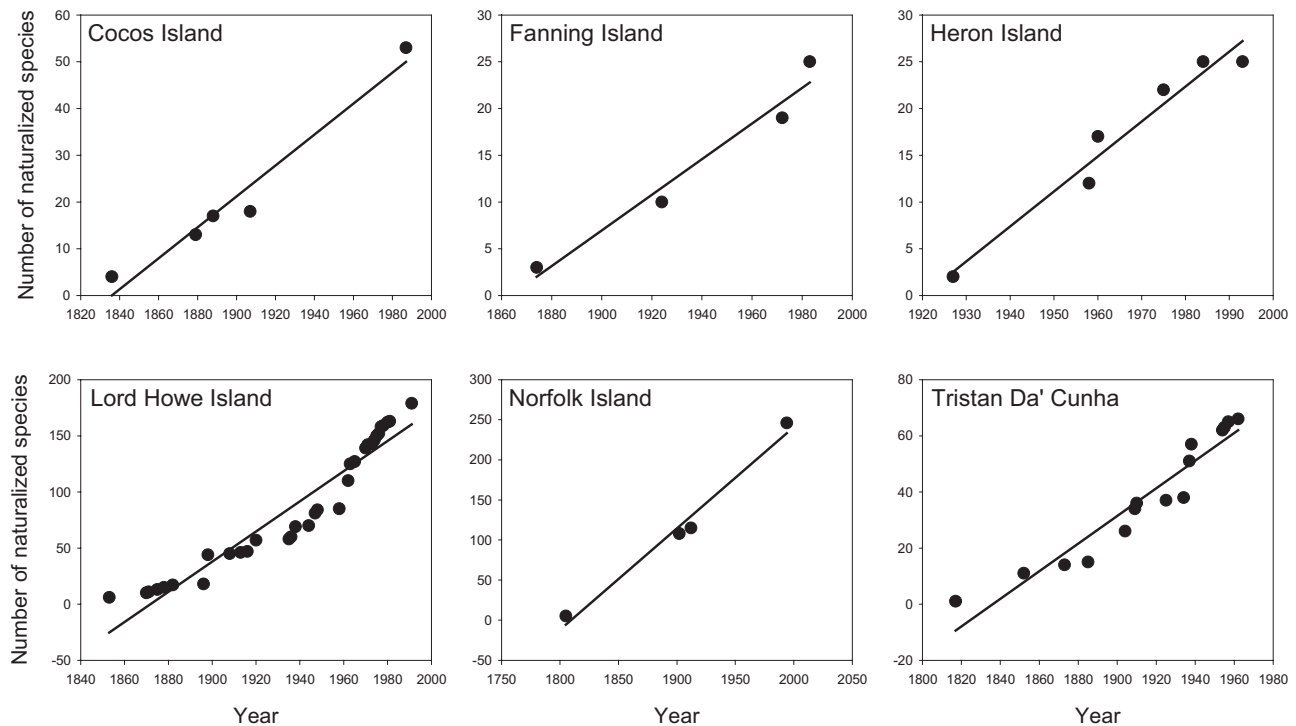


Fig. 3. Naturalized plant richness has increased on oceanic islands in an approximately linear fashion over the past 200 years. Regression lines are all highly significant. None of these islands show evidence of an asymptote in cumulative richness of naturalized species over time.

colonization-based saturation for plant species on these islands. However, because the rate of exotic propagule pressure, i.e., the total number of exotic species being introduced per unit time, is unknown, we cannot assess whether the probability of colonization is declining. It is conceivable, and perhaps not unlikely, that propagule pressure of exotic species has been increasing exponentially. If this were true, then the observed linear increase in the total number of naturalized plant species would actually signal a declining probability of naturalization through time—which would be consistent with colonization-based saturation. Therefore, data on rates of propagule pressure over time are needed to fully evaluate the importance of colonization-based saturation for plants.

Evaluating Extinction-Based Saturation. Extinction-based saturation occurs when the per species extinction rate on the island increases to match the rate of new colonizations. Unlike colonization-based saturation, where an island at saturation will experience little change in species composition, extinction-based saturation necessarily involves species turnover. To date, native plants show no evidence of extinction-based saturation on islands, because thousands of exotic plant species have become

naturalized, whereas relatively few native species have been lost (2). Likewise, previously established naturalized species also appear not to be pushed out by the establishment of additional naturalized plant species. For example, on Lord Howe Island, only 4 of 183 species that have become naturalized have been lost through time. So, with an important caveat, neither natives nor already established exotic species show evidence to support extinction-based saturation.

The caveat to the conclusion that extinction-based saturation is not prevalent in plants is tied to the time course of extinctions. There is enormous uncertainty in how long extinctions may take

Table 1. Ratio (and standard error) of naturalized to native plant species on oceanic islands

Year	Ratio	SE
2000	1.07	0.11
1980	1.07	0.14
1960	0.70	0.13
1940	0.52	0.15
1920	0.44	0.09
1900	0.31	0.09
1880	0.15	0.03
1860	0.07	0.04

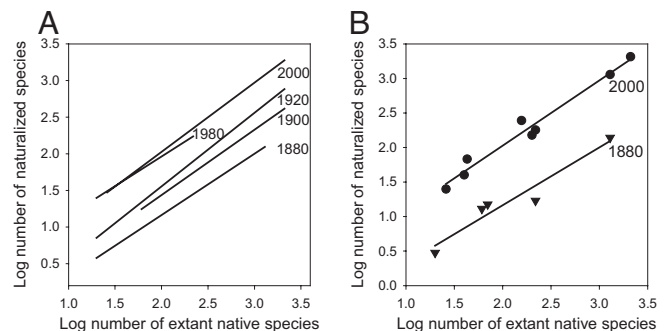


Fig. 4. Across 20-year time intervals from 1880 to the present, the slope of log-log regressions between native and naturalized richness has been relatively constant, whereas the intercepts have changed; this implies that the 1:1 relationship currently observed between native and naturalized richness is a recent phenomenon but that, at repeated points during the past 120 years, there has been a consistent ratio of native-to-naturalized species across islands. (A) Regression lines are illustrated for each 20-year interval that had a significant relationship; limited data reduced the statistical power for the 1860, 1940, and 1960 time intervals. (B) The regression lines and individual data points are shown for the two time intervals with the greatest amount of data.

Table 2. Alternative forecasts of exotic naturalizations and native extinctions of plant species on islands

Scenario	Naturalizations	Extinctions
No saturation	Many	Few
Colonization-based saturation	Few	Few
Extinction-based saturation	Many	Many

to manifest. It is conceivable that extinctions already set in motion by existing alterations of island biotas could take hundreds or thousands of years to come to completion. Such time-lags to extinction could create a large “extinction-debt” (26) that will be paid in the future even without future exotic introductions. Therefore, as with colonization-based extinction hypotheses, we cannot fully evaluate whether extinction-based saturation is in operation. There is little evidence to suggest that species richness of plants on islands is saturating at this time, but this conclusion may need to be revised in the future.

Future of Plant Diversity on Islands. The composition of plant species on islands has been in a rapid state of flux during the past two centuries, because thousands of exotic plant species have been added to island floras. Despite efforts in some regions to control new introductions, we expect that still more exotic plant species will be added to islands over the next century. Even if colonization-based saturation is occurring and the probability of establishment is decreasing, ample introductions may have already occurred to compensate for a declining probability of naturalization. In fact, we see little evidence to support the conclusion that the flow of propagules to islands will be reduced in the near-future. Many countries, such as the United States, currently lack or fail to enforce regulations ample to prevent many invasions from occurring (27). Even in those cases where rigorous importation laws exist and are enforced, as in New Zealand, there will generally be a large “bank” of potentially invading species that are already present. For example, in New Zealand, >22,000 exotic plant species that have not yet become naturalized are grown in the country (28). Many of these plants have the potential to escape cultivation and become naturalized components of the flora (29, 30). Further, global warming and changing environmental conditions many promote the establishment of many species that previously were unlikely to establish naturalized populations. The total number of plant species already present (but not yet naturalized) on most islands around the world has not been tallied, but the numbers are likely to be substantial [e.g., the estimate for Hawaii is $\approx 8,000$ plant species (20)]. Given the substantial size of these species banks and the likely continued import of additional species, it seems likely that most islands will continue to see the addition of exotic species to their naturalized floras in the future.

The ultimate consequence of these exotic species additions for native diversity is still difficult to determine with certainty. We see three primary alternatives with respect to exotic plant invasions and their impact on native species. First, saturation may be unimportant for plant species or, at least, not important at or near the levels of diversity currently present on islands. If this is true, then we might expect many more exotic species to be added without consequent extinctions of native plant species (Table 2). Second, if colonization-based saturation points are being approached then we might expect rapid declines in the rate at which exotic species become naturalized in the future; importantly, we would also then expect few of the native plant species on these islands to go extinct (Table 2). Third, if extinction-based saturation points are being approached or have been exceeded but are masked by long times to extinction, then we would expect newly introduced exotics to continue to become

naturalized and many native species to be on a pathway to extinction (Table 2). In each case, we predict an increase in naturalized plant richness but with different magnitudes and vastly different outcomes for native species extinctions. Unfortunately, on the basis of current data, we cannot distinguish among these dramatically different views of future change in island biotas. Fortunately, there are key types of data that could be acquired and key theoretical questions that could be explored that can help to distinguish among these alternatives. Such insight is critical to advancing ecological theory and informing our understanding of how best to use a limited number of conservation resources in preserving the unique biota of islands worldwide.

Gaps in Extinction Research. We believe that there are four research gaps that must be addressed to improve our understanding of the consequences of species invasions for the future of native biodiversity. First, propagule pressure of exotic species must be better understood. To date, propagule pressure has been poorly studied in nearly all ecosystems. Some important attention has been paid to records of bird introductions (31), but few other groups have received the same attention (32). In part, this is due to the difficulty of reconstructing records for groups where introductions have not been well documented. Nevertheless, for plants, a careful historical survey of seed catalogs and import records could undoubtedly provide critical insight on rates of introductions. Second, time-lags for species extinction must be better studied. Time lags to extinction have received very limited attention. Some important work was done by Diamond (33), and a smattering of more recent papers exist (e.g., ref. 34), but here too the bulk of attention has been on birds. A greater effort is needed to understand dynamics of time-lags to extinction, particularly how these may vary across taxonomic groups and geographic areas. Third, we need to more carefully consider and examine how exotic invasions change the abundance patterns of native species. Although abundance for most native species is expected to decline after invasions, the patterns of these declines may be very important in predicting whether extinctions are likely in the future. In particular, it is important to know which species pay the largest cost; the long term consequences will differ greatly if most of the abundance declines in native species are borne by those species that were previously most abundant, as opposed to those species that were already naturally rare. Fourth, we need to understand how the transformation of large areas into exotic-dominated ecosystems influences extinction of native species through reduction in total available habitat. The species-area relationship is currently one of the most actively used tools for predicting species loss (13), yet its application to exotic-dominated habitat loss has been poorly studied. It is unclear whether the species-area relationship can be used in such circumstances to predict future species loss and, if so, then how accurate such predictions are likely to be. The answer is likely to depend on the extent to which patterns of area loss are congruent with species distributions (35) and on the degree to which natives are excluded from exotic-dominated habitats. Collectively, these gaps in our knowledge create large uncertainty in forecasts of the future responses of island biotas to species introductions. Certainly, there is a pressing need for new data and insights if we cannot distinguish among the polar extremes of (i) there is little risk to native plant species on islands from future exotic introductions and (ii) a large fraction of native plant species on islands are already on a path to extinction. Hopefully, future work on the interplay between species invasions and extinctions can more fully resolve these issues and, in the process, help us to develop a more comprehensive theory of species extinctions.

Methods

International Union for Conservation of Nature Extinction Analysis. Accounts of all 785 species listed as “extinct” were downloaded from the International

Union for Conservation of Nature database (www.iucnredlist.org) in November 2007. Those species comprising the terrestrial vertebrate groups (birds, mammals, reptiles, and amphibians; 258 species) and plants (87 species) were considered further. Species accounts were used to classify each species as being from a mainland or island. Only species restricted to islands were listed as “island” species. Included in these tallies are three marine mammals, which we listed as “mainland” for the purposes of these analyses. Species accounts were also used to tally the factors listed as having contributed to species extinction. To do so, both the annotated list of contributing factors, and the text description were examined for each species. We classified extinction factors into three categories: predation, competition, and other factors. Predation includes pairwise species interactions that are positive for one species and negative for the other; this included any of the following: human hunting (including any form of direct human exploitation of a species), carnivorous predation, herbivorous predation, parasitism, and infectious disease. “Competition” included interactions where species competed for resources. All other factors, such as habitat loss and pollution, were considered to be “other factors.” Tallies were compiled for species listed as (i) only being impacted by predation, (ii) impacted by predation together with other factors, and (iii) impacted by competition together with other factors. In no case was competition listed as the sole factor causing a species extinction. These same tallies were repeated for the subset of extinct species listed as having been impacted by an “alien,” i.e., nonnative or exotic, species.

Island Characteristics. Island characteristics are recorded in Table S1. Prehistoric occupancy, date of European settlement (for uninhabited islands) or first date of trade with Europeans (for islands already inhabited), latitude, island elevation, island area, human population size, and island occupation history are taken from references described in Sax *et al.* (2) and as cited in Table S1. Native and naturalized richness were tallied from the literature after applying a standardized set of criteria to published work. These criteria defined native and naturalized plant species as those believed to have self-supporting populations, such that species believed to be ephemeral were not included. Further, species that are “cryptogenic,” i.e., possibly native or exotic, were excluded from these tallies. See Sax *et al.* (2) for a complete discussion of these criteria and their application. Native and naturalized richness recorded in Table S1 reflect the most up-to-date values available; these values differ slightly from those recorded in Sax *et al.* (2), particularly where a more detailed accounting of historical records has provided additional information on species status.

Multiple Regression Analysis. A multiple regression analysis was performed to explain variation in the log number of naturalized plant species on islands. Predictor variables included history of occupation, time of European settlement/trade, latitude, log of island elevation, log of island area, and log of human population size (Table S1). Several variables (as indicated above) were log-transformed to meet the assumption of normally distributed data. Stepwise analyses were performed by using the backward and forward procedures for adding and removing variables. The probability for a variable to enter the model was set at 0.250, and the probability for a variable to leave was set at 0.100. The best model constructed (judged by lowest AIC value and statistically significant predictor variables) has three predictors: history of occupation, log of elevation, and log of human population size; the model has an adjusted R^2 value of 0.91. All statistical analyses were performed in JMP software, Version 5.0.1.

Historical Data on Naturalized Plants. Data were compiled from the literature, using the criteria described above in *Island Characteristics*. Because sampling efforts varied among historic accounts of the flora, the number of exotics recorded in *SI Text* are “range-through” data—such that species believed to be established at two points in time are recorded here as being established at all points of time between these. Therefore, if a survey in the 1800s and the

modern flora both list a plant as established, then it was assumed to occur on the dates between these, even if it was not recorded on one of the interim dates. In most cases, this resulted in relatively minor alterations from the number of species recorded at any one point in time. This standardization allowed islands where only range-through data were available to be compared with those where all counts were independent. This procedure is particularly appropriate for large, topographically complex islands where individual species are easily missed on any one survey of an island. The one island considered here where this procedure may not have been necessary is Heron Island—a small (19-ha) island in the Great Barrier Reef. However, the differences on Heron Island between range-through and point-time data are relatively small, as indicated in *SI Text*. Range-through data were not calculated for New Zealand; consequently, data from 1940 (when a range-through calculation is anticipated to make a substantial difference in recorded values) were not used in analyses of change in naturalized richness through time (see *SI Text*). Note that range-through and point-time data are always equivalent for the first and last time steps of any given island. The most recent (modern) publications used as data sources for islands are listed in Sax *et al.* (2); older records used to reconstruct the historical data are cited within these modern publications.

Analyzing Change in Naturalized Richness. Data on change in naturalized richness through time (*SI Text*) were analyzed in multiple ways. First, data were plotted on individual islands over time (Fig. 3). Second, the mean ratio of naturalized to native richness was calculated in 20-year intervals over the past 140 years (Table 1); e.g., the penultimate interval, 1980, extended from 1971 to 1990. Native richness was held constant across these ratio analyses, using the currently recorded values (Table S1); this was done because the actual number of native species on islands has changed very little over the past 140 years, because few species have been lost and presumably few native species gained during this time period. Naturalized richness values were taken from *SI Text*. When more than one date was available from a single 20-year time interval, then the date closest to the midpoint of the time period was used; if two dates were equally close to the midpoint, then the one closest to dates analyzed for other islands in that time period was used. Third, these same native and naturalized values were plotted by 20-year time intervals (Fig. 4).

Note that the last date recorded for any individual island is subject to a procedural artifact that reduces the total number of naturalized species. This artifact lowers the number of naturalized species not just for individual islands, but also for mean estimates of naturalized species across islands. This procedural artifact occurs because exotic species are only counted as “naturalized” if they are seen (i) in multiple places on an island within a single time step or (ii) within the same area across multiple time steps, i.e., across two or more survey periods that are separated sufficiently for at least one turnover in generation time to have occurred (see ref. 2 for a full discussion). Consequently, species seen in only one place on an island and recorded from only the most recent island survey will not be considered to be naturalized unless they persist to the next survey period, when the number of naturalized species from the previous time period would then be revised upwards.

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