Species Invasions Exceed Extinctions on Islands Worldwide: A Comparative Study of Plants and Birds

Dov F. Sax,[1,*] **Steven D. Gaines,**[1,†] **and James H. Brown**[2,‡]

1. Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California 93106;
2. Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131

abstract: Species richness is decreasing at a global scale. At subglobal scales, that is, within any defined area less extensive than the globe, species richness will increase when the number of nonnative species becoming naturalized is greater than the number of native species becoming extinct. Determining whether this has occurred is usually difficult because detailed records of species extinctions and naturalizations are rare; these records often exist, however, for oceanic islands. Here we show that species richness on oceanic islands has remained relatively unchanged for land birds, with the number of naturalizations being roughly equal to the number of extinctions, and has increased dramatically for vascular plants, with the number of naturalizations greatly exceeding the number of extinctions. In fact, for plants, the net number of species on islands has approximately doubled. We show further that these patterns are robust to differences in the history of human occupation of these islands and to the possibility of undocumented species extinctions. These results suggest that species richness may be increasing at subglobal scales for many groups and that future research should address what consequences this may have on ecological processes.

Keywords: naturalized species, extinctions, plants, birds, ecosystem stability, species richness.

Although biological invasions are clearly reducing species richness at a global scale, the impacts of these invasions at subglobal scales are far less certain (Rosenzweig 2001). This is because biological invaders, which are generally nonnative species, contribute to species loss by causing the extinction of natives and contribute to species gain by their own establishment. We define nonnatives here to include all species that were absent from a region before the arrival of humans, regardless of whether they were introduced by humans or arrived through their own power of dispersal. Among nonnatives we are interested in those that have become naturalized, that is, those that have established self-sustaining populations in the absence of human assistance (Richardson et al. 2000*a*; Sax and Brown 2000). Many of these naturalized species are distributed broadly across continents and islands, taking on geographical patterns of richness and range size that mimic native ones (Sax 2001). These same species often have strong and damaging effects on native biota, causing changes at the community, the ecosystem, and the landscape levels (e.g., Elton 1958; Carlton 1979; Mack 1981; Case and Bolger 1991; D'Antonio and Vitousek 1992; Simberloff and Stiling 1996). Indeed, as suggested above, naturalized species are undoubtedly contributing to a global decline in species richness by causing or facilitating the extinction of natives (e.g., Steadman 1995; Crawley 1997; Fritts and Rodda 1998).

At subglobal scales, the establishment of naturalized species necessarily causes a change in species composition, but the net outcome on species richness is uncertain. Diversity will increase, decrease, or remain unchanged within a region depending on the corresponding number of extinctions. In some cases, broad losses of native richness have followed the establishment of particular nonnative species; for example, the introduction of the brown tree snake *Boiga irregularis* Cogger led to the extinction of several bird species on Guam (Fritts and Rodda 1998). In other cases, many nonnative species have had no detectable effects on native biota (Simberloff 1981). Consequently, in systems where many nonnative species have become established without coincident extinctions, richness is presumed to have increased, for example, for subtidal invertebrates in San Francisco Bay as well as for plants and vertebrates in New Zealand (Atkinson and Cameron 1993; Valentine and Jablonski 1993; Carlton 1996).

A possible framework for understanding variation in likely responses to invasions comes from the theoretical

* E-mail: sax@lifesci.ucsb.edu.

† E-mail: gaines@lifesci.ucsb.edu.

‡ E-mail: jhbrown@unm.edu.

work of Rosenzweig (2001), who predicts that the establishment of nonnative species will commonly lead to a net increase in richness at subglobal scales. This prediction is based on the tenets of island biogeography theory (sensu MacArthur and Wilson 1967), which posits that an increase in the immigration rate of species (in this case, nonnative ones) should lead to an increase in richness. If this prediction is correct, then the relative change in richness of a region should be related to the relative change in rates of immigration. Groups of organisms with relatively low vagility that are poor natural dispersers should have the greatest increase in immigration rates when dispersal is human assisted. Consequently, low-vagility species should show dramatic increases in richness in formerly isolated regions. By contrast, groups of organisms with high natural vagility, such as birds, should show smaller relative increases in rates of immigration and consequently smaller increases in richness.

It is unclear, however, whether or not increases in species richness may lead to corresponding increases in extinction rates (Rosenzweig 2001). If extinction rates increase, then increases in richness could be offset, resulting in a dramatically changed species composition without a change in species number. If extinction rates increase enough (e.g., if invading species cause a cascade of extinction events), then richness could be reduced well below historic levels. However, even if rates of extinction are increased, the process of extinction itself may occur on a much longer timescale than invasions, which would make the perceived impact of invasions dependent on the timescale of observation. Finally, time lags may vary in duration among taxonomic groups because some taxa may be more susceptible to extinction once their population size has been depressed.

Here we explore net changes in species richness at subglobal spatial scales following the establishment of nonnative species. To do so, we examine the species richness of taxa on oceanic islands and archipelagos. Islands are particularly appropriate for addressing this question because of their discrete geographical boundaries and discrete periods of human occupation. Together these features facilitate determinations of species gain (via naturalization) and species loss (via extinction and extirpation). Of course, this approach can also be used within defined areas of a continent when adequate records of extinction and colonization exist (e.g., Newmark 1995). Islands, however, are noteworthy because it is the extinction of island endemics that has caused some of the most severe losses to the global richness of species (Steadman 1995). Finally, islands allow us to examine changes in richness at spatial scales that vary across seven orders of magnitude (from 0.25 to 265,000 km²), which provides variation that is

useful in evaluating whether changes in richness patterns are scale dependent.

We did not wish to focus here on changes in richness of taxonomic groups that were absent or poorly represented on oceanic islands before human influence because such groups, for example, nonvolant mammals and freshwater fishes, have clearly increased in richness since the introduction of nonnative species (e.g., Eldredge and Miller 1995). Instead, we examined groups that were diverse on islands before the arrival of humans and which therefore could have increased, remained unchanged, or decreased in richness. Similarly, we examined groups that we expected to vary in dispersal ability and susceptibility to extinction. To these ends, we examined the present-day patterns of species richness of two disparate taxonomic groups: vascular plants and land birds.

Methods

We surveyed the literature for information on the floras and faunas of oceanic islands. On these islands, we examined vascular plants (ferns, fern allies, flowering plants, and gymnosperms) that inhabit terrestrial or freshwater systems but excluded those found exclusively in marine environments, such as seagrasses. We also examined land birds, which include those found in terrestrial or freshwater habitats but exclude those that acquire the majority of their resources from the marine environment. This excluded most shorebird species except for those few that have expanded their niche on oceanic islands to include resource acquisition in terrestrial or freshwater habitats, for example, the Saint Helena wirebird *Charadrius sanctaehelenae* (Olson 1975). We examined these vascular plant and land bird species on oceanic islands and archipelagos that are currently inhabited by humans, where perturbation rates are presumably highest and the greatest numbers of nonnative species have been introduced (see app. A for a detailed list of the criteria used in selecting islands). We also noted which islands had been occupied by humans before European colonization; on these islands, the extinction of natives and the introduction of nonnatives may have gone unrecorded, occurring before Europeans arrived. Further, islands within an archipelago were not treated separately but instead as a single data point. Such islands often share a relatively common ecological setting and history of disturbance and, as such, could be considered to be pseudoreplicates if treated separately (Case 1996).

On all islands, we tallied the number of naturalized species that are extant as well as the number of native species that are extant and extinct (see table 1 for plants and table 2 for birds; see app. A for a detailed explanation of the criteria used to make these determinations). The

Table 1: Vascular plants on oceanic islands

Island (or archipelago)	Class	Natives (extant)	Natives (extinct)	Naturalized species (extant)	Total no. of extant species
Christmas Island (Indian Ocean)	B	201	2	151	352
Cocos (Keeling) Islands	B	61	1	53	114
Easter Island[a]	D	43	7	68	111
Hawaiian Islands[a]	D	1,223	71	1,090	2,313
Heron Island	B	27	…[b]	25	52
Lord Howe Island	A	219	2	202	421
Mangareva Island	D	85	…[b]	60	145
Nauru Island	D	50	1	85	135
New Zealand Islands[a]	D	2,065	3	2,069	4,134
Northern Line Islands	C	35	0	41	76
Norfolk Island	C	157	3	244	401
Pitcairn Island	C	40	4	40	80
Tristan da Cunha Island	A	70	0	54	124

Note: All islands are currently inhabited by humans but are split into one of four categories based on their history of human occupation before European contact. Class A islands have no evidence of human occupation or visitation before European contact and are otherwise unlikely to have been visited. Class B islands have evidence of human visitation, or are likely to have been visited, but have no evidence of human settlement and are unlikely to have been settled. Class C islands appear to have had human settlements but were abandoned before European contact. Class D islands had human settlements when European contact occurred. For our analyses, the first two classes of islands (A and B) were considered to be uninhabited, while the latter two (C and D) were considered to be inhabited before European contact.

[a] A fossil record exists.

[b] Insufficient information was available to determine whether any species had become extinct.

relationships between these values were examined by plotting the log-normalized data for each taxon in two ways. First, we plotted naturalized nonnative species versus extinct native species. This shows how richness of naturalized species is related to richness of extinct natives. The significance and explanatory power of these relationships were examined with ordinary least squares regression analyses. Second, we plotted the total number of species currently present on these islands (i.e., extant native and naturalized species) versus the total number of species that were historically present (i.e., extant and extinct native species). This relationship provides a graphical representation of how richness has changed for plants and birds across the islands and island archipelagos considered. This second set of comparisons was not examined with regression analyses because the axes are not independent.

Results

For vascular plants, the log numbers of extinct native species are not significantly correlated with the log numbers of naturalized species (fig. 1A). Instead, a goodness-of-fit test (using the Pearson statistic) shows that the null model of an equal number of points on either side of the line of equality is rejected because all of the points in this relationship are above the line of equality ($\chi^2 = 11.0$, df $\cong$ 1, $P < .001$). Thus, on all islands examined, more nonnative species have become naturalized than natives have

become extinct, and therefore, the number of species has consistently increased (fig. 1B). Moreover, the magnitude of increase is remarkably similar across islands; the total number of plant species has approximately doubled (i.e., points are tightly distributed along the dashed line that marks a twofold linear increase from the values present on the line of equality in fig. 1B). This doubling in species richness is a consequence of two factors. First, as stated above, few natives have become extinct (fig. 1A). Second, the log numbers of extant natives are highly correlated with the log numbers of naturalized species ($R^2 = 0.95$, slope $= 0.96$, $P < .001$). This second relationship is relatively unchanged by dividing the data into two groups—those islands that had human inhabitants before European colonization and those that did not (previously inhabited islands: $R^2 = 0.96$, slope $= 0.93$, $P < .001$; previously uninhabited islands: $R^2 = 0.99$, slope $= 0.96$, $P < .001$).

The number of species of naturalized plants on islands is significantly related to both the size of these islands and to the number of human inhabitants on these islands ($R^2 = 0.67$ and 0.71, respectively; fig. 2A, 2B). Both of these factors, however, explain less of the variation in numbers of naturalized species than do the numbers of native plant species. Further, the significance and amount of variance explained by these factors are strongly influenced by the presence of two extreme values, Hawaii and New Zealand. When these two extremes of island size are removed, both relationships become nonsignificant.

Table 2: Land birds on oceanic islands

Island (or archipelago)	Class	Natives (extant)	Natives (extinct)	Naturalized species (extant)	Total no. of extant species
Andaman/Nicobar Islands	D	104	…[a]	4	108
Ascension Island[b]	A	0	2	4	4
Chatham Islands[b]	D	15	21	18	33
Cook Islands[b]	D	11	14	5	16
Easter Island[b]	D	0	6	4	4
Fiji Islands[b]	D	53	7	11	64
Galápagos Islands[b]	A	36	0	2	38
Guam Island	D	6	12	7	13
Hawaii Islands[b]	D	39	64	55	94
Lord Howe Island[b]	A	6	9	11	17
Marquesas Islands[b]	D	12	9	6	18
Mauritius Island[b]	B	12	15	17	29
New Zealand Islands[b]	D	53	38	40	93
Norfolk Island[b]	B	11	6	14	25
Palau Islands	D	29	…[a]	4	33
Reunion Island[b]	B	11	22	21	32
Rodriquez Island[b]	B	3	11	7	10
Saint Helena Island[b]	A	1	5	8	9
Samoa Islands[b]	D	32	2	3	35
Society Islands[b]	D	14	11	12	26
Tonga Islands[b]	D	18	19	10	28
Tristan da Cunha Island	A	1	2	1	2
Wake Island	B	0	1	1	1

Note: "Classes" are the same as in table 1.

[a] Insufficient information was available to determine whether any species had become extinct.

[b] A fossil record exists.

The richness of naturalized land birds is significantly related to the total land area of islands and to their number of human inhabitants ($R^2 = 0.25$ and 0.34, respectively; fig. 2C, 2D). The amount of variance explained by these relationships, however, is much less than the amount of variance explained by characteristics of the native species, in this case by the number of native bird extinctions.

For land birds, the log numbers of species that have become extinct are closely correlated with the log numbers of naturalized species, with points distributed along the line of equality (fig. 1C). The amount of variance explained by this relationship is relatively high, and the slope is positive ($R^2 = 0.78$, slope $= 0.77$, $P < .001$). This relationship is relatively unchanged by dividing the data into two groups—those islands that had human inhabitants before European colonization and those that did not (previously inhabited islands, *filled triangles*, fig. 1: $R^2 = 0.79$, slope $= 0.89$, $P < .001$; previously uninhabited islands, *filled circles*, fig. 1: $R^2 = 0.76$, slope $= 0.78$, $P < .001$). This determination is important because if islands that were inhabited by humans before European colonization have a consistently different ratio of extinctions to naturalizations than islands that were not previously inhabited, then comparing these groups of islands together may be prob-

lematic. This determination is further corroborated by comparing the pattern of residuals of these two groups around their common regression line; the difference between the mean residual values is small (approximately one species) and not statistically significant (previously inhabited islands, *filled triangles*, fig. 1: mean $= -0.043$; previously uninhabited islands, *filled circles*, fig. 1: mean $= 0.047$, t value $= 1.14$, df $= 18$, $P > .27$). Finally, as a result of the relationship between extinct native species and extant naturalized species, there has been a remarkably precise correspondence between numbers of bird species before and after human occupation of these islands, with their total numbers having remained largely unchanged (i.e., points are distributed along the line of equality in fig. 1D). This relationship is remarkable because the mean percentage of native species that have become extinct on these islands is large ($\sim$57%) and the variation among islands is dramatic (from 0% to 100% loss of native bird species; table 2).

Discussion

Neither plants nor birds have seen a decline in species richness on oceanic islands. Instead, across all islands ex-
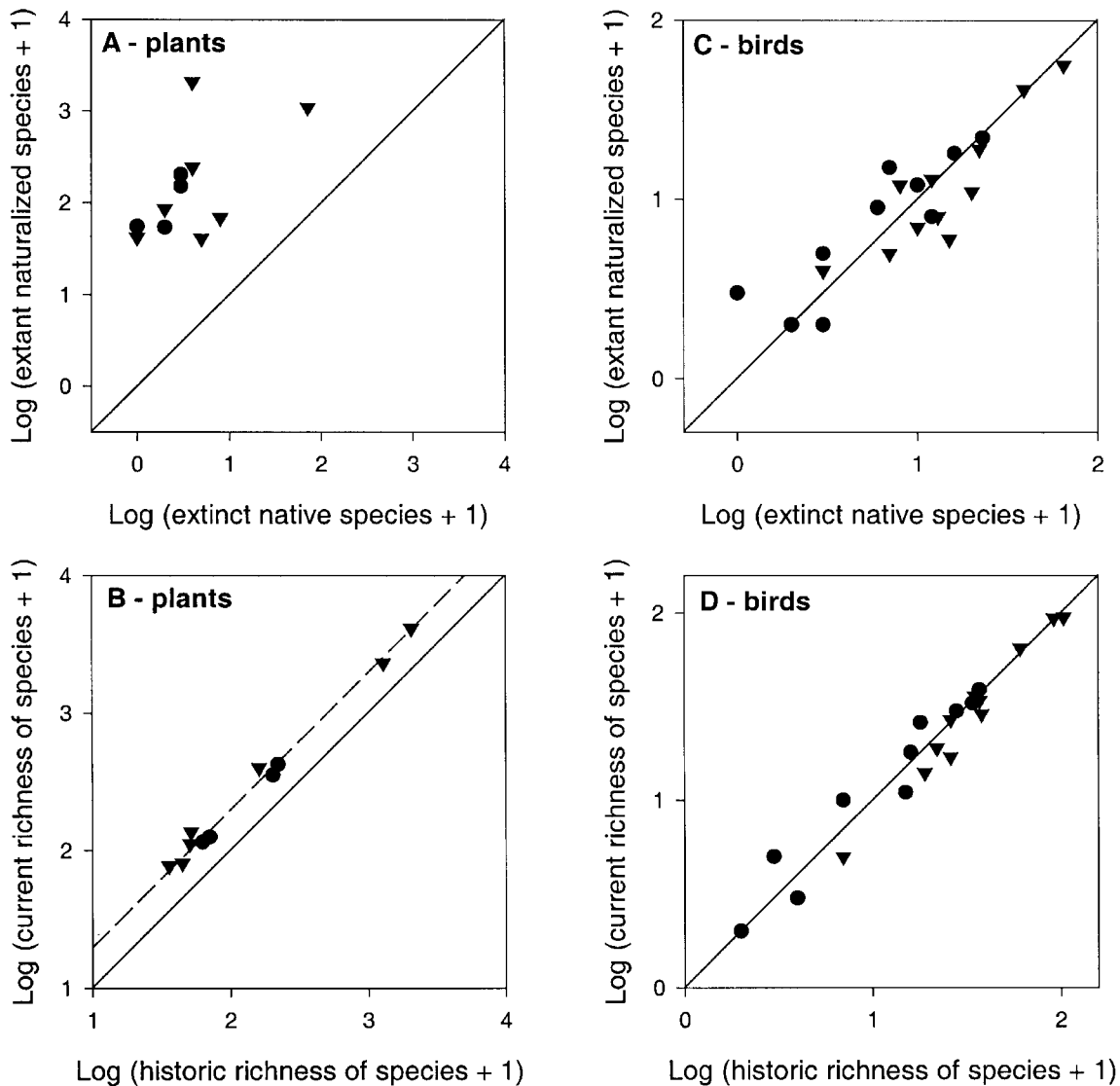
Figure 1: Species richness on islands. Filled triangles represent islands that were inhabited before European contact, while filled circles represent islands that were not. *A*, Many naturalized plants have been added relative to the number of extinctions (Pearson's statistic of an equal distribution about the line of equality rejects at *P* < .001). *B*, Net richness of plants has increased on all islands with naturalized species. The dashed line shows the approximate doubling (on a linear scale) of net richness. Note that this relationship is plotted as a visual aid and that a regression analysis is not appropriate since a portion of the data (namely, the number of extant natives) are incorporated to both the *X*- and *Y*-axes. *C*, Significant relationship between naturalized birds and extinct native birds ($y = 0.77x + 0.23$, $r^2 = 0.78$, *P* < .001). *D*, Net diversity of birds has remained approximately unchanged. Note that this relationship is plotted as a visual aid and that a regression analysis is not appropriate since portions of the data (namely, the number of extant natives) are incorporated to both the *X*- and *Y*-axes.

amined, the richness of plants has increased dramatically, while the richness of birds has remained relatively unchanged. For plants, this has occurred because few natives have become extinct, while many nonnatives have become naturalized. For birds, this has occurred because the number of natives that have become extinct are roughly equal to the number of nonnatives that have become naturalized.

This pattern with birds suggests the possibility that native species were driven to extinction by interactions with naturalized species (such as competition) on a nearly one-to-one basis. Although this hypothesis would seem to be credible, we know that such interactions have played, at most, a secondary role for at least two reasons. First, many native birds became extinct on these islands before the
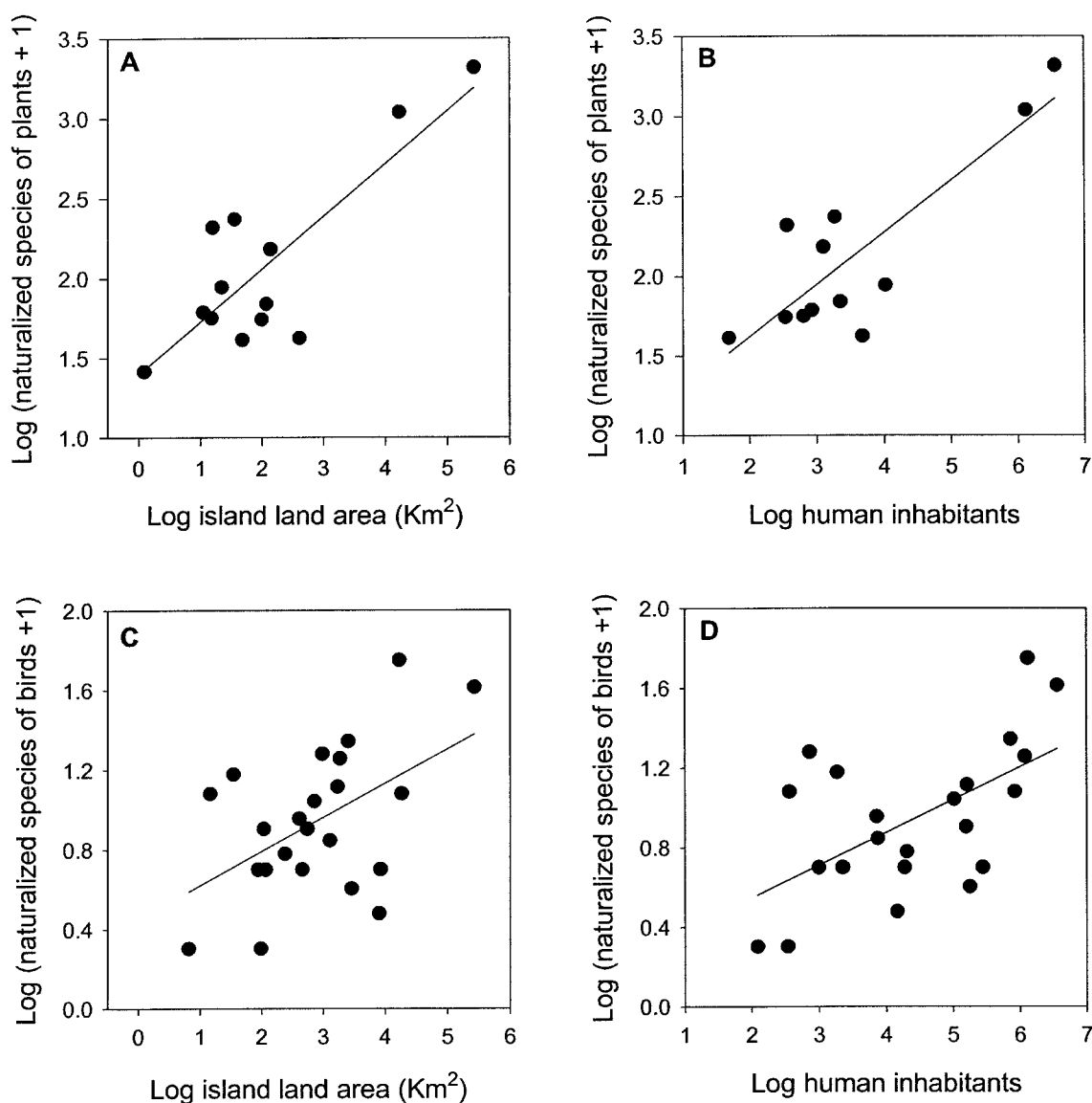
Figure 2: Island characteristics and richness of naturalized plant and bird species. *A*, Significant relationship between log island land area and richness of naturalized plant species ($y = 0.33x + 1.40$, $r^2 = 0.67$, $P < .001$). *B*, Significant relationship between log number of human inhabitants and richness of naturalized plant species ($y = 0.33x + 0.96$, $r^2 = 0.71$, $P < .001$). *C*, Significant relationship between log island land area and richness of naturalized bird species ($y = 0.17x + 0.45$, $r^2 = 0.25$, $P < .05$). *D*, Significant relationship between log number of human inhabitants and richness of naturalized bird species ($y = 0.16x + 0.22$, $r^2 = 0.34$, $P < .01$).

establishment of naturalized birds (James 1995). Second, many native bird extinctions are directly attributable to the introduction of nonvolant predators and to the loss of native habitat (Ebenhard 1988). To what extent competition and other interactions between natives and nonnatives may have augmented these other sources of extinctions is difficult to know; only further research can address this question.

In addition to understanding what caused bird extinc-

tions, it is also prudent to consider what allowed nonnative species of both birds and plants to become naturalized. Although there are many possibilities, we will discuss four likely explanations. The first explanation posits that nonnative species have become established because of the extinction of native species, which has created vacant niches. The second explanation posits that nonnative species have become established because of the alteration of native habitats, which has created environments that are favorable

to nonnative species. These two explanations are tightly linked, and their relative importance is difficult to disentangle because most native habitats that have been altered have also lost native species. Diamond and Veitch (1981) provide evidence to support the conclusion that the presence of native species and intact forest are sufficient to exclude nonnative bird species on offshore islands of New Zealand. Other studies have also shown that habitat modification, particularly of ecosystem-level characteristics, can facilitate the invasion of nonnative species (e.g., Vitousek and Walker 1989; D'Antonio and Vitousek 1992). The third explanation posits that the creation of wholly new anthropogenic habitats favors the naturalization of nonnative species. This explanation is supported by the distribution and abundance of many nonnative species in anthropogenic environments; in New Zealand, for example, many naturalized species exclusively occupy agricultural landscapes (Robertson and Heather 1999). Indeed the importance of anthropogenic habitats for nonnative species cannot be understated because their occurrence in these environments is common (e.g., Sax and Brown 2000). The fourth explanation posits that nonnative species have become established because they are competitively superior to natives. Such a disparity in competitive ability could occur for a number of reasons: absence of predators, differences in evolutionary history, and so on. For a review of this topic, see Sax and Brown (2000). Of course, none of these explanations are mutually exclusive, and some combination of them has undoubtedly been important for each nonnative species that has become naturalized. So, on the one hand, understanding the mechanisms responsible for a particular species success can only be evaluated by carefully examining the details of its naturalization history. On the other hand, the consistent patterns found among islands for naturalizations of birds and plants suggest that these processes may not be completely idiosyncratic and instead that a limited set of interacting mechanisms may be responsible. Comprehensive work to determine the underlying mechanisms will undoubtedly benefit most by examining both case-specific examples and broad-scale patterns of naturalization.

Data Quality

Before further considering the patterns shown here, we need to address potential inadequacies in the data. The largest concern is undocumented extinctions. Because thousands of birds are estimated to have become extinct on oceanic islands, we expect some portion of these to have gone undocumented (Pimm et al. 1994; Steadman 1995). Similarly, some number of plant extinctions may also have gone undocumented. If these numbers of undocumented extinctions were large, then the qualitative

conclusions reached here would be suspect. This concern is particularly relevant on islands colonized by Polynesians, or other seafaring peoples, where few records of early extinction events exist and our knowledge of species extinctions is dependent on fossil and archaeological records. However, three lines of evidence (the first for birds and plants and the remaining two exclusively for plants) suggest that the qualitative conclusions drawn from the data presented in figure 1 are robust and not due to inadequacies in the data. First, many of the islands used in this study were not inhabited before European colonization. Such differences in island history allow us to contrast those islands that had pre-European inhabitants with those that did not (represented by triangles and circles, respectively, in fig. 1). If undocumented extinctions seriously compromise the findings, then there should be marked differences between these two island types. We would expect relatively more recorded extinctions on islands that were not inhabited before European arrival, where presumably a greater proportion of the total number of extinctions caused by anthropogenic activities would have been recorded. However, we found no such differences. Data from both sets of islands are strikingly similar. This suggests that a significant portion of the extinctions that have occurred are accounted for in the data set.

For land birds, specifically, an examination of the regression of extinct native species versus extant naturalized species (fig. 1*C*) shows that the mean difference in residual values between islands that were inhabited before European colonization and those that were not is only one species. On average, then, this suggests that we are only missing approximately one more extinct species of bird on islands that were inhabited by humans before European colonization than on those that were not. This suggests that the fossil record on these islands may be more complete than expected and that we are aware of most of the bird species that have become extinct since human occupation of these particular islands. This may seem to be at odds with Steadman's (1995) estimate of the extinction of over 1,000 species of birds on oceanic islands. On careful inspection, however, these findings are not inconsistent; Steadman's estimate is based on the loss of only a few unique species from each of thousands of islands. So, in this case, the existing fossil evidence of extinct species together with the estimate (from the difference in residual values) of an average of approximately one additional missing species per island may, in fact, be a fairly accurate estimate of bird extinctions on these islands. This reasoning does make an assumption, namely, that our count is correct for the number of bird species that have become extinct on islands that were not inhabited before the arrival of Europeans. Fortunately, this assumption seems to be relatively sound. On these islands, early visitors or natu-

ralists often recorded species of birds that were later driven to extinction. Further, on eight of the 10 islands in our database that were not inhabited before European contact, an extensive fossil record supplements our knowledge of bird extinctions. Therefore, it seems unlikely that a great number of species that became extinct have gone unrecorded on these islands. In summary, for birds, then, it seems likely that the qualitative nature of the conclusions reached is robust. However, for the purposes of this article, it really is not critical that the richness of birds has remained stable. Future work may discover more fossil species of birds on these islands. Our point here, however, is simply that the richness of birds appears to be changing in a way that differs from that of plants and that these differences may be instructive in and of themselves. We leave it to plants to drive home the principal message of this study.

For plants, as stated above, species richness increased in a qualitatively similar way on all islands, regardless of whether they were or were not inhabited before European colonization; this suggests that the patterns observed are robust to differences in pre-European occupation and that great numbers of plant extinctions have not gone undetected. Of course, for most islands, the quality of the fossil record for plants is not as good as that for birds. As a result, the probability of a plant species becoming extinct and being unrecorded would also seem to be higher. Two additional lines of evidence for plants, however, mitigate these concerns. First, despite the incomplete nature of the fossil record, a record does exist, and it strongly suggests that there have been relatively few plant extinctions since the arrival of humans (James 1995). The best fossil evidence comes from New Zealand where numerous studies have examined the Quaternary fossil record (Clarkson et al. 1992, 1995; Burrows et al. 1993; Ogden et al. 1993; Burrows 1995, 1997*a*, 1997*b*; Newnham et al. 1995; Elliot et al. 1998). These studies describe local and regional paleofloras and, in each case, find that all of the fossil species identified are still extant in New Zealand. Among these studies a total of 118 species have been identified. If there had been a wholesale extinction of plant species in New Zealand since the arrival of humans, then we would expect some significant portion of these fossil species to now be extinct. Since none of them is extinct it suggests that, while extinctions of plant species in New Zealand have undoubtedly occurred, their relative numbers since human arrival must be few. Similar evidence is available from Hawaii, where paleobotanists have specifically looked for evidence in the fossil record of recent plant extinctions (Selling 1946, 1947, 1948). This directed effort, while identifying many fossil species, found only one extinct fossil species. Therefore, at least on the larger islands, as indicated by New Zealand and Hawaii, it does not appear that

there have been recent mass extinctions of plant species. On smaller islands, however, there may have been relatively greater numbers of plant extinctions, although the total numbers are still likely to be small; for example, Easter Island lost seven arborescent taxa following the island's deforestation (Flenley et al. 1991).

Beyond the fossil evidence itself (which is consistent with the conclusion that there have been few plant extinctions), a second line of evidence (or, in this case, reasoning) further suggests that the conclusions reached are robust. Namely, we can ask the question of just how incomplete the existing data on plant extinctions would have to be in order to alter the conclusions reached from figure 1. Clearly, with respect to net changes in species richness, the magnitude of increase in the number of species trivializes any concerns about a few undocumented extinctions. For example, New Zealand has gained ∼2,000 naturalized species; so, if there were an additional 1,000 or even 1,900 plant extinctions that we had no record of, our conclusions would still be the same, that is, that the total number of plants in New Zealand has increased. Given that New Zealand has ∼2,000 native plant species, half of the original native flora would need to have become extinct without detection to change the qualitative conclusion that plant diversity has increased. Since none of the 118 plant species with a fossil record that we identified in the Quaternary have become extinct, the likelihood of such massive undetected extinctions is exceedingly remote. Although the large flora of New Zealand provides an extreme example, the same relative magnitude of undetected loss of native plant species from other islands, that is, a number equal to the current number of known extant species of native plants, would be required to change the conclusion that richness of plants has increased. For plants, then, all available evidence suggests that the total number of plant species on islands has increased substantially.

Implications for Ecology

In addition to the implicit interest and importance inherent in the net changes in plant and bird richness, these changes also provide evidence for the debate on the fundamental processes that regulate the species richness of a focal place or region. Recently, Brown et al. (2001) and Sax (2002*a*) have argued that richness should be stable temporally, or spatially, when a number of conditions are met. Among these conditions (see Brown et al. 2001 for a complete list) is the requirement that the focal area has the opportunity for compensatory colonization and extinction events from a regional pool of species. They argue that stability of species richness will typically be greater in continental environments than in island systems because of their differences in access to a regional pool of species.

In this study, we show that richness of birds has been relatively stable, while richness of plants has not. Given the differences in the vagility of these two groups and the general differences in their ability to disperse over wide expanses of ocean, these results are consistent with the speculation of Brown et al. (2001). The high vagility of birds allows even remote oceanic islands to have regular access to a larger regional pool of species, allowing for the possibility of regular colonization events. This view is supported by the great number of species that migrate to, but do not breed on, oceanic islands and by the equally great number of bird species that are reported on these islands as "accidentals," "stragglers," or "irregular migrants" (i.e., they are observed sporadically but not regularly enough to be considered established members of the avifauna; see avifauna references in app. B). Indeed, since anthropogenic disturbances to islands began, some of these birds have been highly successful at becoming naturalized in newly created habitats. For example, on Lord Howe Island, at least eight of the 11 naturalized bird species have dispersed to Lord Howe under their own power, and many of these are most abundant within anthropogenic habitats (Fullagar et al. 1974; Hutton 1990). The high number of "natural"-dispersal events suggests that species richness of birds on many oceanic islands has not historically been limited by a shortage of colonists (i.e., that adequate numbers of birds have been able to disperse to islands) and instead that richness has been regulated primarily by local ecological processes on each island (Lack 1970). This interpretation is consistent with the low explanatory power of the number of human inhabitants observed in this study (fig. 2D), which might have been expected to be more important in determining migration pressure but which, here, appears to be, at most, a secondary consideration. Regardless, however, of the exact mechanism, the net effect of human activities on birds has been to change their composition dramatically, without substantially changing their total richness.

In contrast, low rates of transoceanic dispersal of vascular plants have apparently limited their richness on oceanic islands. Therefore, human-assisted dispersal has increased the richness of plants on those islands. This hypothesis is supported by comparing plant groups with different dispersal capacities. Ferns and their allies, which disperse long distances by wind-borne spores, have increased in richness following human settlement by only 4% (a marginal change in diversity that is comparable to the consistency seen in birds); in contrast, flowering plants, whose seeds are not dispersed as efficiently by wind, have increased in richness by ∼150%. Of course, some portion of this variation between ferns and flowering plants may be due to differential introduction efforts by humans. However, the interpretation that these differences are due to differential dispersal abilities is consistent with results observed in other studies where the role of human-assisted dispersal is reduced; for example, nearly 25% of the fern species occurring on Java have colonized Krakatau, while fewer than 10% of the flowering species have done so (Whittaker et al. 1997). Additional evidence for the differential capacity of ferns and flowering plants to colonize oceanic islands can probably be evaluated by contrasting species-area relationships for these two groups on islands and continents, although potential differences in speciation rates on islands may also need to be considered.

As a final example of the importance of dispersal capacity in determining these patterns, we present an extreme case—the freshwater fishes. These species are extremely unlikely to cross wide expanses of ocean and undoubtedly have low richness values on islands, at least, in part, because of a lack of dispersal opportunities. In fact, most native freshwater fishes on islands originated as marine species that secondarily invaded freshwater environments, including the five freshwater fishes that are native to Hawaii (Resh and De Szalay 1995). Consequently, the richness of freshwater fishes on oceanic islands has increased dramatically following the introduction of nonnative species, for example, by 800% on Hawaii (Eldredge and Miller 1995). We expect the qualitative nature of these dispersal-related processes to be similar for many taxonomic groups on islands and island-like environments, where we predict that the magnitude of increase in species richness will be inversely proportional to the vagility of the group in question.

An unexpected result of this study was the highly consistent, approximately twofold, increase in the species richness of plants on oceanic islands (fig. 1B). The consistency of this increase across islands that vary in size by more than seven orders of magnitude is striking, with the number of native species accounting for 95% of the variation in the number of nonnative species. Other studies, at a variety of spatial scales, have shown positive relationships between the number of native and naturalized species of plants (e.g., Chown et al. 1998; Lonsdale 1999; Stohlgren et al. 1999; Stadler et al. 2000; Sax 2002b). Lonsdale (1999), Sax (2002b), and others have suggested that the positive relationship between native and naturalized species may not be causal and that both groups of species are likely to be responding similarly to environmental variables that favor species richness (such as productivity or heterogeneity). Alternatively, the correspondence between native and naturalized species could be due to some interaction between island size and number of human inhabitants, which have been linked to species richness in other studies (e.g., Chaloupka and Domm 1986; Chown et al. 1998). Here, however, these variables are only weakly associated with the number of naturalized plants, particularly when

the outlying points of Hawaii and New Zealand are excluded (fig. 2). Of course, all islands examined in this study are occupied by humans, so the relative explanatory power of number of human inhabitants may be expected to be reduced. It should be noted, however, that had we included uninhabited islands in this study the precision of this two-fold increase in richness would have been reduced because uninhabited islands have increased in plant richness but not by the same proportion (see data in Chown et al. 1998). Still, it seems unlikely that island size, number of human inhabitants, or a similar response between native and naturalized species to environmental variables can, alone, account for the precision of the relationship shown here, where the number of native species explained 95% of the variation in the number of naturalized species. Undoubtedly, further work will be necessary to elucidate the mechanisms that can account for such a pattern.

Regardless of the mechanism, the consistency of this pattern begs the question of how this relationship will change in the future. We envision two principal alternatives. First, a new "carrying capacity" for plant species may have been reached, and few additional changes in richness will occur (although changes in composition could continue). This would be consistent with the pattern of bird richness, whose relatively unchanged values are consistent with the hypothesis that bird richness is at a carrying capacity on each island. Second, the current richness of plant species could be transient, increasing or decreasing in the future (Rosenzweig 2001). Richness could increase if the rate of extinctions remains low and the addition of nonnative species continues unabated. Alternatively, richness could ultimately decrease, if extinction rates of plants are inherently slow, and there is a long lag time before species en route to extinction actually become extinct. In the former case, species richness could conceivably continue to increase to levels that matched or even exceeded those on equal-sized areas of continents, while, in the latter case, species richness could conceivably decrease substantially. Further, if there were cascading extinction events, then species diversity could decline to levels well below those that existed before human arrival. Which of these alternatives are most likely is difficult to ascertain at this time, but the possibility of forthcoming extinctions in response to current patterns of invasions warrants considerable attention.

Although this study has examined changes in species richness on islands, it appears that qualitatively similar patterns occur on continents. At subglobal scales, the richness of plant species has increased substantially, while the richness of bird species has remained relatively unchanged. For example, in California, richness of plant species has increased; ~28 species have become extinct, while over 1,000 species have become naturalized (Hickman 1993;

Skinner and Pavlik 1994). In contrast, for birds in North America, richness has remained relatively unchanged; approximately seven to 12 species have gone extinct (depending on the inclusion of species lost to offshore islands and species only surviving in captivity) and ~22 nonnative species have become naturalized (Groombridge 1992; Sax 1999). Unfortunately, at spatial scales smaller than large political and geographic units, changes in richness are difficult to detect because detailed records of species extirpations are generally lacking. This precludes us from making absolute determinations about how richness has changed at many mesoscales on continents. Nevertheless, the positive relationships identified between native and naturalized richness of plants (Lonsdale 1999; Stohlgren et al. 1999; Stadler et al. 2000; Sax 2002b), together with the relatively few recorded plant extinctions on continents, suggests that species richness has increased at many mesoscales.

If species richness is decreasing at global scales and increasing at mesoscales, then how is richness changing at microscales or local scales? At these smallest scales, we imagine that idiosyncratic processes may often determine the outcome of changes in richness. However, if there were a general pattern, then we imagine that it would be consistent with that of mesoscales. We suspect this because the available evidence for plant richness at local scales is consistent with the patterns observed for islands. Stohlgren et al. (1999), Levine (2000), and Sax (2002b) have all shown positive relationships between native and nonnative plant richness at local scales. So, while we are not certain how richness has changed locally, it seems likely that, at least in some cases, richness has increased. Validating this conjecture is important because this information could lead to a reorientation of much ecological research. Currently, many research projects are conducted with the tacit assumption that species richness has declined at local scales. Consequently, many studies examine the ecological effects of a reduction in species richness (e.g., Naeem et al. 1994, 1996; McGrady-Steed et al. 1997; Hector et al. 1999; Tilman 1999; Petchey 2000). In contrast to these conventional studies of declining richness, Richardson et al. (2000b) have shown that increases in richness may also be important. They show that increasing richness can initiate a feedback mechanism, through the role of mutualisms, which facilitates invasions, and further promotes additional increases in richness; similarly, other studies have demonstrated that plant invasions may be facilitated by mutualistic interactions with established biota (e.g., Schiffman 1997). Besides Richardson et al. (2000b), few other studies have explicitly examined the effects of wholesale increases in richness on ecological processes, despite the likelihood that this commonly occurs and despite the effects that these changes may cause. Instead, studies have

focused on the effects of individual species invasions, thoroughly documenting these affects on community and ecosystem-level processes (e.g., Vitousek and Walker 1989). The effects of wholesale increases in species richness, however, may conceivably be much more significant, if not in type than certainly in magnitude. These effects could include the disruption of species interactions, the modification of successionary processes, the weakening of ecosystem stability, and the alteration of other ecosystem-level processes (such as productivity and nutrient cycling). Further, these impacts may not be restricted to an ecological context but may also affect future patterns of evolution (Mooney and Cleland 2001). Undoubtedly, the field of ecology would be advanced by better understanding the potential consequences of increasing richness, and we hope that a body of theoretical and empirical work can be developed that will examine these issues.

On a final note, this work bears on the field of conservation biology in at least three ways. First, a direct consequence of the establishment of nonnative species around the globe, coupled with the loss of some to many native species, is an increasing homogenization of floras and faunas (Harrison 1993; Brown 1995; Vitousek et al. 1996; Wilson 1997; McKinney 1998). This loss of distinctive biotas is particularly problematic given its application on both islands and continents. Second, as articulated by Angermeier (1994) and empirically demonstrated in this study, counts of species richness that do not distinguish between native and nonnative components of that richness are poor metrics of a system's ecological integrity. Third, it is unclear at this time whether the increases in species richness of plants on oceanic islands are ephemeral; it is not unlikely that many plant species will become extinct in the future as a direct consequence of current processes. Future ecological research should address how changes in species number and identity affect natural ecosystems and whether mass extinction events on islands are likely to occur.

Acknowledgments

APPENDIX A

Detailed Methods

Island Selection

Island and island archipelagos were selected if they met four criteria. First, they had to be oceanic, that is, not land bridge islands. Second, they had to currently be inhabited by a permanent human settlement (note that islands occupied by only a scientific or weather station were not included). Third, the vascular flora or avifauna of the island had to have been surveyed multiple times. Fourth, the most recent survey had to have been published within the past 22 years, that is, since 1980. In addition, three exceptions to these criteria were made for specific islands. First, New Zealand was included in the data set despite its former land connection with Australia. This was done because of its long period of isolation (∼80 million years), its submergence of over 80% of its existing land area during periods with higher sea levels, and its extensive glaciations. Together these factors have caused the loss of much of its archaic or continental flora and fauna, making it largely comparable with true oceanic islands. Second, the Chatham Islands (a continental land fragment of Gondwanaland) were included since available evidence suggests that the islands were entirely submerged, or nearly so, ∼4 million years ago; therefore, the islands' current flora and fauna were gained through geologically recent dispersal events, such that, for all practical purposes, its biota are truly oceanic (Campbell 1998; Trewick 2000). Third, Iceland was not included in the data set, since its long period of contact with Europeans makes it difficult to determine whether species are native or nonnative. Note that most islands that met these criteria did so for either plants or birds, with only a few meeting the criteria for both groups. Note also that several apparently obvious midsized islands were excluded because they did not meet one or more of the listed criteria. This does not imply that these islands did not fit the pattern described for other islands but, instead, that we followed our set of a priori criteria. For example, the vascular flora of Guam was last described in 1974, so it was excluded by our fourth criterion, even though that publication listed the island as having 282 native plants and 187 nonnative ones (numbers that are generally consistent with those described for other islands in the results; Lee 1974). The vascular flora of the Society Islands was excluded since recent information was only available on the flowering plants (Welsh 1998), even though that publication listed the islands as having 301 extant native and 210 naturalized species. Similarly, the vascular flora of the Galápagos and the biota of New Caledonia, both with many naturalized species, were excluded

for failure to meet the above criteria (Galápagos: A. Tye, personal communication; New Caledonia: MacKee 1994; Gargominy et al. 1996). Note further that, unlike values used for islands in some previous compilations, none of the values for individual islands or island archipelagos used here are based solely on regional field guides but, instead, include published critical examinations of an individual island or archipelago.

Species Status

Species on each island (or island archipelago) were identified as native or nonnative and extant or extinct. For birds, these values are generally consistent with those reported in the literature (table B1). Some small alterations of these reported values were necessary, however, because not all studies used the same operational definitions of native, nonnative, and naturalized. Here we consider all species that have arrived to an island following human settlement to be nonnative, regardless of whether or not they arrived with human assistance. Further, birds were considered to be established, whether they were natives or nonnatives, only if there was evidence of successful reproduction on multiple occasions. Thus, species that were only known to have reproduced once, or not at all, were not considered to be established and were not considered further here. Note that this criterion excludes most migrants, vagrants, waifs, and so forth. Further, only currently established nonnative species were considered to be extant; nonnative species that had formerly been established but apparently become extinct were not considered here. On Hawaii and New Zealand, no exact consensus has been reached for these numbers due to differences in taxonomy and the extent of the archipelagos considered. For Hawaii, taxonomy follows James and Olson (1991) and Olson and James (1991) for all species described by them and Pratt et al. (1987) otherwise. Further, the Hawaiian Islands considered in this study include all of the main islands, as well as the northwestern islands as far from the main islands as Laysan. For New Zealand, taxonomy follows Turbott (1990), and the islands considered include North, South, Stewart, and all land bridge islands but not islands that are geographically isolated from the mainland but within its political jurisdiction.

For plants, applying operational definitions of species status (and, subsequently, using values altered from those reported in the literature) may seem unnecessary because the qualitative pattern of few native extinctions and many naturalizations is robust to the definitions used. Nevertheless, we did this to facilitate comparisons between islands. We began by using the same definitions for plants as those defined above for birds. However, given the differences that exist between birds and plants, we also invoked several additional criteria. First, plants that are cultivated, or that are otherwise directly aided by humans (e.g., through watering), were not considered to be naturalized and were not considered further here. This includes a very large number of species on some islands; for example, in New Zealand, more than 20,500 plant species are known to be cultivated or grown as garden ornamentals (Landcare Research Herbarium at Lincoln [CHR], personal communication, 1999). Second, species that were only observed once, regardless of whether they were presumed to be native or nonnative, were not considered to be established. Similarly, there were a small number of species (fewer than 20) that were observed more than once but sporadically in time and/or space, for example, being seen only twice in 150 yr. These species were not considered to be established because their presence was likely to be the result of repeated introduction events. Third, species were considered to be extinct if they had not been observed within 50 yr of the most recent survey. Note that, in some cases, insufficient information was available to determine whether any native species had become extinct, in which case these islands were not used in determining relationships between extant and extinct species (tables 1, 2). The only exceptions to the application of these operational definitions are for Hawaii and New Zealand, for which species values are taken directly from cited sources. For Hawaii, the number of nonnative species and the number of extant natives were taken directly from the literature, while the number of plant species presumed to be extinct were taken from an on-line database at the Bishop Museum (1999); for New Zealand all plant values were from a personal communication with the Landcare Research Herbarium at Lincoln (CHR; table 1).

APPENDIX B

Table B1: Data references

Island (or archipelago)	References
Andaman/Nicobar Islands	Mathur 1968; Lever 1987; Ripley and Beehler 1989
Ascension Island	Blair 1989; Ashmole and Ashmole 1997
Chatham Islands	Lever 1987; Freeman 1994; Millener 1999
Christmas Island (Indian Ocean)	Bailey 1977; Du Puy 1993
Cocos (Keeling) Islands	Telford 1993
Cook Islands	Holyoak and Thibault 1984; Pratt et al. 1987; Steadman 1989, 1991, 1995, 1997; Kirch et al. 1995
Easter Island	Johnson et al. 1970; Flenley et al. 1991; Zizka 1991; Steadman et al. 1994; Marticorena and Rodriguez 1995; Steadman 1995
Fiji Islands	Steadman 1989; Beckon 1993
Galápagos Islands	Harris 1973; Kramer 1984; Steadman et al. 1991
Guam Island	Jenkins 1983; Fritts and Rodda 1998
Hawaiian Islands	James and Olson 1991; Olson and James 1991; Eldredge and Miller 1995, 1998; Pyle 1997; Bishop Museum 1999
Heron Island	Rogers and Morrison 1994; Rowland 1995, 1996
Lord Howe Island	Cassels 1984; Hutton 1990; Green 1994
Mangareva Island	St. John 1988
Marquesas Islands	Holyoak and Thibault 1984; Pratt et al. 1987; Steadman and Rolett 1996
Mauritius Island	Cheke 1987; Mourer-Chauvire et al. 1999
Nauru Island	Thaman et al. 1994
New Zealand Islands	Cassels 1984; Turbott 1990; Robertson and Heather 1999; Landcare Research Herbarium at Lincoln (CHR), personal communication, 1999
Norfolk Island	Schodde et al. 1983; Ritchie 1989; Green 1994; Anderson 1996
Northern Line Islands	Webster 1985; Webster et al. 1992
Palau Islands	Pratt et al. 1980
Pitcairn Island	Hiroa 1945; Florence et al. 1995
Reunion Island	Cheke 1987; Mourer-Chauvire et al. 1999
Rodriquez Island	Cheke 1987; Mourer-Chauvire et al. 1999
Saint Helena Island	Olson 1975; Lever 1987; Brooke et al. 1995; Oldfield and Sheppard 1997
Samoa Islands	Watling 1982; Milberg and Tyrberg 1993; Steadman 1993*b*
Society Islands	Pratt et al. 1987; Walters 1988; Steadman 1989, 1997
Tonga Islands	Steadman 1993*a*; Steadman and Freifeld 1998
Tristan da Cunha Island	Groves 1981; Richardson 1984; Watkins and Furness 1986
Wake Island	Cassels 1984; Jones 1995

Note: References to the flora, avifauna, and archaeological history of each island or island archipelago by locality. Note that this list of references is sufficient to generate the data used in this study (tables 1, 2). This list does not include the numerous additional references that exist for these islands because these older references are generally cited within the ones presented here.

Literature Cited

Anderson, A. 1996. Discovery of a prehistoric habitation site on Norfolk Island. Journal of the Polynesian Society 105:479–486.

Angermeier, P. L. 1994. Does biodiversity include artificial diversity? Conservation Biology 8:600–602.

Ashmole, N. P., and M. J. Ashmole. 1997. The land fauna of Ascension Island: new data from caves and lava flows, and a reconstruction of the prehistoric ecosystem. Journal of Biogeography 24:549–589.

Atkinson, I. A. E., and E. K. Cameron. 1993. Human influence on the terrestrial biota and biotic communities of New Zealand. Trends in Ecology & Evolution 8:447–451.

Bailey, E. 1977. The Christmas Island story. Stacey, London.

Beckon, W. N. 1993. The effect of insularity on the diversity of land birds in the Fiji Islands: implications for refuge design. Oecologia (Berlin) 94:318–329.

Bishop Museum. 1999. Hawaiian flowering plant checklist database. http://www.bishopmuseum.org/bishop/HBS/plantchecksearch.html.

Blair, M. 1989. The RAFOS expedition to Ascension Island. Royal Air Force Ornithological Society 19:1–35.

Brooke, R. K., J. L. Lockwood, and M. P. Moulton. 1995. Patterns of success in passeriform bird introductions on Saint Helena. Oecologia (Berlin) 103:337–342.

Brown, J. H. 1995. Macroecology. University of Chicago Press, Chicago.

Brown, J. H., S. K. M. Ernest, J. M. Parody, and J. P. Haskell. 2001. Regulation of diversity: maintenance of species richness in changing environments. Oecologia (Berlin) 126:321–332.

Burrows, C. J. 1995. A macrofossil flora from sediments in a lagoon marginal to Lake Coleridge, Canterbury, New Zealand. New Zealand Journal of Botany 33: 519–522.

———. 1997a. An interglacial macrofossil flora from Schulz Creek, north Westland, New Zealand. New Zealand Journal of Botany 35:187–194.

———. 1997b. A macrofossil flora from early Aranuian lake-bed deposits, Doubtful River, Waiau-uha catchment, North Canterbury, New Zealand. New Zealand Journal of Botany 35:545–553.

Burrows, C. J., P. Randall, N. T. Moar, and B. G. Butterfield. 1993. Aranuian vegetation history or the Arrowsmith Range, Canterbury, New Zealand. III. Vegetation changes in the Cameron, upper South Ashburton, and Paddle Hill Creek catchments. New Zealand Journal of Botany 31:147–174.

Campbell, H. J. 1998. Fauna and flora of the Chatham Islands: less than 4 m.y. old? Geology and Genes 97: 15–16.

Carlton, J. T. 1979. Introduced invertebrates of San Francisco Bay. Pages 427–444 in T. J. Conomos, ed. San Francisco Bay, the urbanized estuary. American Association for the Advancement of Science, Pacific Division, San Francisco.

———. 1996. Biological invasions and cryptogenic species. Ecology 77:1653–1655.

Case, T. J. 1996. Global patterns in the establishment and distribution of exotic birds. Biological Conservation 78: 69–96.

Case, T. J., and D. T. Bolger. 1991. The role of introduced species in shaping the abundance and distribution of island reptiles. Evolutionary Ecology 5:272–290.

Cassels, R. 1984. The role of prehistoric man in the faunal extinctions of New Zealand and other Pacific Islands. Pages 741–767 in P. S. Martin and R. G. Klein, eds. Quaternary extinctions: a prehistoric revolution. University of Arizona Press, Tucson.

Chaloupka, M. Y., and S. B. Domm. 1986. Role of anthropochory in the invasion of coral cays by alien flora. Ecology 67:1536–1547.

Cheke, A. S. 1987. An ecological history of the Mascarene Islands, with particular reference to extinctions and introductions of land vertebrates. Pages 5–89 in A. W. Diamond, ed. Mascarene Island birds. Cambridge University Press, Cambridge.

Chown, S. L., N. J. M. Gremmen, and K. J. Gaston. 1998. Ecological biogeography of southern ocean islands: species-area relationships, human impacts, and conservation. American Naturalist 152:562–575.

Clarkson, B. R., B. D. Clarkson, and R. N. Patel. 1992. The pre-Taupo eruption (c. AD 130) forest of the Benneydale-Pureora district, central North Island, New Zealand. Journal of the Royal Society of New Zealand 22:61–76.

Clarkson, B. R., M. S. McGlone, D. J. Lowe, and B. D. Clarkson. 1995. Macrofossils and pollen representing forests of the pre-Taupo volcanic eruption (c. 1850 yr BP) era at Pureora and Benneydale, central North Island, New Zealand. Journal of the Royal Society of New Zealand 25:263–281.

Crawley, M. J. 1997. Biodiversity. Pages 595–632 in M. J. Crawley, ed. Plant ecology. Blackwell Science, Oxford.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23:63–87.

Diamond, J. M., and C. R. Veitch. 1981. Extinctions and introductions of the New Zealand avifauna: cause and effect? Science (Washington, D.C.) 211:499–501.

Du Puy, D. J. 1993. Christmas Island. Flora of Australia 50:1–30.

Ebenhard, T. 1988. Introduced birds and mammals and their ecological effects. Swedish Wildlife Research 13: 1–107.

Eldredge, L. G., and S. E. Miller. 1995. How many species are there in Hawai'i? Bishop Museum Occasional Papers 41:3–18.

———. 1998. Numbers of Hawaiian species: supplement 3, with notes on fossil species. Bishop Museum Occasional Papers 55:3–15.

Elliot, M. B., J. R. Flenley, and D. G. Sutton. 1998. A late Holocene pollen record of deforestation and environmental change from the Lake Tauanui catchment, Northland, New Zealand. Journal of Paleolimnology 19: 23–32.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Methuen, London.

Flenley, J. R., A. S. M. King, J. Jackson, and C. Chew. 1991. The Late Quaternary vegetational and climatic history of Easter Island. Journal of Quaternary Science 6: 85–115.

Florence, J., S. Waldren, and A. J. Chepstow-Lusty. 1995. The flora of the Pitcairn Islands: a review. Biological Journal of the Linnean Society 56:79–119.

Freeman, A. N. D. 1994. Landbirds recorded at the Chatham Islands, 1940 to December 1993. Notornis 41: 127–141.

Fritts, T. H., and G. H. Rodda. 1998. The role of introduced species in the degradation of island ecosystems: a case history of Guam. Annual Review of Ecology and Systematics 29:113–140.

Fullagar, P. J., J. L. McKean, and G. F. Van Tets. 1974. Pages 55–72 *in* H. F. Recher and S. S. Clark, eds. Environmental survey of Lord Howe Island: a report to the Lord Howe Island Board. Government Printer, Sydney.

Gargominy, O., P. Bouchet, M. Pascal, T. Jaffré, and J. Tourneur. 1996. Conséquences des introductions d'espèces animales et végétales sur la biodiversité en Nouvelle-Calédonie. Revue d'Ecologie la Terre et la Vie 51:375–402.

Green, P. S. 1994. Norfolk Island and Lord Howe Island. Flora of Australia 49:1–25.

Groombridge, B., ed. 1992. Global biodiversity: status of the Earth's living resources. Chapman & Hall, London.

Groves, E. W. 1981. Vascular plant collections from the Tristan da Cunha group of islands. Bulletin of the British Museum (Natural History) Botany Series 8:333–420.

Harris, M. P. 1973. The Galápagos avifauna. Condor 75: 265–278.

Harrison, S. 1993. Species diversity, spatial scale, and global change. Pages 388–401 *in* P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, eds. Biotic interactions and global change. Sinauer, Sunderland, Mass.

Hector, A., B. Schmid, C. Beierkuhnlein, M. C. Caldeira, M. Diemer, P. G. Dimitrakopoulos, J. A. Finn, et al. 1999. Plant diversity and productivity experiments in European grasslands. Science (Washington, D.C.) 286: 1123–1127.

Hickman, J. C., ed. 1993. The Jepson manual: higher plants of California. University of California Press, Berkeley.

Hiroa, T. R. 1945. An introduction to Polynesian anthropology. Bernice P. Bishop Museum Bulletin 187:1–133.

Holyoak, D. T., and J.-C. Thibault. 1984. Contribution à l'étude des oiseaux de Polynesie orientale. Memoires du Museum National d'Histoire Naturelle 127:1–209.

Hutton, I. 1990. Birds of Lord Howe Island: past and present. Lithocraft Graphics, Melbourne.

James, H. F. 1995. Prehistoric extinctions and ecological changes on oceanic islands. Pages 88–102 *in* P. M. Vitousek, L. L. Loope, and H. Adersen, eds. Islands: biological diversity and ecosystem functioning. Springer, Heidelberg.

James, H. F., and S. L. Olson. 1991. Descriptions of thirty-two new species of birds from the Hawaiian Islands. II. Passeriformes. Ornithological Monographs 46:1–88.

Jenkins, J. M. 1983. The native forest birds of Guam. Ornithological Monographs 31:1–61.

Johnson, A. W., W. R. Millie, and G. Moffet. 1970. Notes on the birds of Easter Island. Ibis 112:532–538.

Jones, H. L. 1995. Bird observations on Wake Atoll. Western Birds 26:65–75.

Kirch, P. V., D. W. Steadman, V. L. Butler, J. Hather, and M. I. Weisler. 1995. Prehistory and human ecology in eastern Polynesia: excavations at Tangatatau Rockshelter, Mangaia, Cook Islands. Archaeology in Oceania 30: 47–65.

Kramer, P. 1984. Man and other introduced organisms. Biological Journal of the Linnean Society 21:253–258.

Lack, D. 1970. Island birds. Biotropica 2:29–31.

Lee, M. A. B. 1974. Distribution of native and invader plant species on the island of Guam. Biotropica 6: 158–164.

Lever, C. 1987. Naturalized birds of the world. Longman, Essex.

Levine, J. M. 2000. Species diversity and biological invasions: relating local process to community pattern. Science (Washington, D.C.) 288:852–854.

Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522–1536.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, N.J.

Mack, R. N. 1981. Invasion of *Bromus tectorum* into western North America: an ecological chronicle. Agro-Ecosystems 7:145–165.

MacKee, H. S. 1994. Catalogue des plantes introduites et cultivées en Nouvelle-Calédonie. Museum National D'Histoire Naturelle, Paris.

Marticorena, C., and R. Rodriguez. 1995. Flora de Chile. Vol. 1. Pteridophyta-Gymnospermae. Universidad de Concepcion, Concepcion.

Mathur, L. P. 1968. History of the Andaman and Nicobar Islands, 1756–1966. Sterling, Delhi.

McGrady-Steed, J., P. M. Harris, and P. J. Morin. 1997. Biodiversity regulates ecosystem predictability. Nature 390:162–165.

McKinney, M. L. 1998. On predicting biotic homogenization: species-area patterns in marine biota. Global Ecology and Biogeography Letters 7:297–301.

Milberg, P., and T. Tyrberg. 1993. Naive birds and noble savages—a review of man-caused prehistoric extinctions of island birds. Ecography 16:229–250.

Millener, P. R. 1999. The history of the Chatham Islands' bird fauna of the last 7000 years—a chronicle of change and extinction. Smithsonian Contributions to Paleobiology 89:85–109.

Mooney, H. A., and E. E. Cleland. 2001. The evolutionary

impact of invasive species. Proceedings of the National Academy of Sciences of the USA 98:5446–5451.

Mourer-Chauvire, C., R. Bour, S. Ribes, and F. Moutou. 1999. The avifauna of Reunion Island (Mascarene Islands) at the time of the arrival of the first Europeans. Smithsonian Contributions to Paleobiology 89:1–38.

Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton, and R. M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. Nature 368:734–737.

Naeem, S., K. Håkansson, J. H. Lawton, M. J. Crawley, and L. J. Thompson. 1996. Biodiversity and plant productivity in a model assemblage of plant species. Oikos 76:259–264.

Newmark, W. D. 1995. Extinction of mammal populations in western North American national parks. Conservation Biology 9:512–526.

Newnham, R. M., P. J. de Lange, and D. J. Lowe. 1995. Holocene vegetation, climate and history of a raised bog complex, northern New Zealand based on palynology, plant macrofossils and tephrochronology. Holocene 5:267–282.

Ogden, J., R. M. Newnham, J. G. Palmer, R. G. Serra, and N. D. Mitchell. 1993. Climatic implications of macro- and microfossil assemblages from late Pleistocene deposits in northern New Zealand. Quaternary Research 39:107–119.

Oldfield, S., and C. Sheppard. 1997. Conservation of biodiversity and research needs in the UK Dependent Territories. Journal of Applied Ecology 34:1111–1121.

Olson, S. L. 1975. Paleornithology of St. Helena Island, South Atlantic Ocean. Smithsonian Contributions to Paleobiology 23:1–49.

Olson, S. L., and H. F. James. 1991. Descriptions of thirty-two new species of birds from the Hawaiian Islands. I. Non-passeriformes. Ornithological Monographs 45:1–88.

Petchey, O. L. 2000. Species diversity, species extinction, and ecosystem function. American Naturalist 155:696–702.

Pimm, S. L., M. E. Moulton, and L. J. Justice. 1994. Bird extinctions in the central Pacific. Philosophical Transactions of the Royal Society of London B, Biological Sciences 344:27–33.

Pratt, H. D., J. Engbring, P. L. Bruner, and D. G. Berrett. 1980. Notes on the taxonomy, natural history, and status of the resident birds of Palau. Condor 82:117–131.

Pratt, H. D., P. L. Bruner, and D. G. Berrett. 1987. The birds of Hawaii and the tropical Pacific. Princeton University Press, Princeton, N.J.

Pyle, R. L. 1997. Checklist of the birds of Hawaii—1997. Elepaio 57:129–138.

Resh, V. H., and F. A. De Szalay. 1995. Streams and rivers of Oceania. Pages 717–736 *in* C. E. Cushing, K. W. Cummins, and G. W. Minshall, eds. River and stream ecosystems. Elsevier, Amsterdam.

Richardson, D. M., P. Pyšek, M. Rejmánek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000*a*. Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6:93–107.

Richardson, D. M., N. Allsopp, C. M. D'Antonio, S. J. Milton, and M. Rejmánek. 2000*b*. Plant invasions—the role of mutualisms. Biological Reviews of the Cambridge Philosophical Society 75:65–93.

Richardson, M. E. 1984. Aspects of the ornithology of the Tristan Da Cunha group. Cormorant 12:123–201.

Ripley, S. D., and B. M. Beehler. 1989. Ornithogeographic affinities of the Andaman and Nicobar Islands. Journal of Biogeography 16:323–332.

Ritchie, N. 1989. Archaeology and history of Norfolk Island. Archaeology in New Zealand 32:118–134.

Robertson, H. A., and B. D. Heather. 1999. The hand guide to the birds of New Zealand. Penguin, Auckland.

Rogers, R. W., and D. Morrison. 1994. Floristic change on Heron Island, a Coral Cay in the Capricorn-Bunker Group, Great Barrier Reef. Australian Journal of Botany 42:297–305.

Rosenzweig, M. L. 2001. The four questions: what does the introduction of exotic species do to diversity? Evolutionary Ecology Research 3:361–367.

Rowland, M. J. 1995. Indigenous water-craft use in Australia: the "big picture" and small experiments on the Queensland coast. Bulletin of the Australian Institute for Maritime Archaeology 19:5–18.

———. 1996. Prehistoric archaeology of the Great Barrier Reef province—retrospect and prospect. Pages 191–212 *in* P. Veth and P. Hiscock, eds. Archaeology of northern Australia. University of Queensland Anthropology Museum, St. Lucia.

Sax, D. F. 1999. Native and exotic species distributions: implications for general models of diversity, from community to biogeographic scales. Ph.D. diss. University of New Mexico, Albuquerque.

———. 2001. Latitudinal gradients and geographic ranges of exotic species: implications for biogeography. Journal of Biogeography 28:139–150.

———. 2002*a*. Equal diversity in disparate species assemblages: a comparison of native and exotic woodlands in California. Global Ecology & Biogeography 11:49–58.

———. 2002*b*. Native and naturalized plant diversity are positively correlated in scrub communities of California and Chile. Diversity and Distributions 8:193–210.

Sax, D. F., and J. H. Brown. 2000. The paradox of invasion. Global Ecology & Biogeography 9:363–372.

Schiffman, P. M. 1997. Animal-mediated dispersal and disturbance: driving forces behind alien plant naturaliza-

tion. Pages 87–94 *in* J. O. Luken and J. W. Thieret, eds. Management of plant invasions. Springer, New York.

Schodde, R., P. Fullagar, and N. Hermes. 1983. A review of Norfolk Island birds: past and present. Australian National Parks and Wildlife Service, Canberra.

Selling, O. H. 1946. Studies in Hawaiian pollen statistics. I. The spores of Hawaiian pteridophytes. Special Publication of the Bishop Museum 37:1–87.

———. 1947. Studies in Hawaiian pollen statistics. II. The pollens of the Hawaiian phanerogams. Special Publication of the Bishop Museum 38:1–430.

———. 1948. Studies in Hawaiian pollen statistics. III. On the late Quaternary history of the Hawaiian vegetation. Special Publication of the Bishop Museum 39: 1–154.

Simberloff, D. 1981. Community effects of introduced species. Page 53–81 *in* M. H. Nitecki, ed. Biotic crises in ecological and evolutionary time. Academic Press, New York.

Simberloff, D., and P. Stiling. 1996. Risks of species introduced for biological control. Biological Conservation 78:185–192.

Skinner, M. W., and B. M. Pavlik, eds. 1994. California native plant society's inventory of rare and endangered vascular plants of California. 5th ed. California Native Plant Society, Sacramento.

Stadler, J., A. Trefflich, S. Klotz, and R. Brandl. 2000. Exotic plant species invade diversity hot spots, the naturalized flora of northwestern Kenya. Ecography 23:169–176.

Steadman, D. W. 1989. Extinction of birds in eastern Polynesia: a review of the record, and comparisons with other Pacific Island groups. Journal of Archaeological Science 16:177–205.

———. 1991. Extinct and extirpated birds from Aitutaki and Atiu, southern Cook Islands. Pacific Science 45: 325–347.

———. 1993*a*. Biogeography of Tongan birds before and after human impact. Proceedings of the National Academy of Sciences of the USA 90:818–822.

———. 1993*b*. Bird bones from the To'aga site: prehistoric loss of seabirds and megapodes. Pages 217–228 *in* P. V. Kirch and T. L. Hunt, eds. The To'aga site: three millennia of Polynesian occupation in the Manu'a Islands, American Samoa. University of California Archaeological Research Facility, Berkeley.

———. 1995. Prehistoric extinctions of Pacific Island birds: biodiversity meets zooarchaeology. Science (Washington, D.C.) 267:1123–1130.

———. 1997. The historic biogeography and community ecology of Polynesian pigeons and doves. Journal of Biogeography 24:737–753.

Steadman, D. W., and H. B. Freifeld. 1998. Distribution, relative abundance, and habitat relationships of land-
birds in the Vava'u Group, kingdom of Tonga. Condor 100:609–628.

Steadman, D. W., and B. Rolett. 1996. A chronostratigraphic analysis of landbird extinction on Tahuata, Marquesas Islands. Journal of Archaeological Science 23: 81–94.

Steadman, D. W., T. W. Stafford, Jr., D. J. Donahue, and A. J. T. Jull. 1991. Chronology of Holocene vertebrate extinction in the Galápagos Islands. Quaternary Research 36:126–133.

Steadman, D. W., P. V. Casanova, and C. C. Ferrando. 1994. Stratigraphy, chronology, and cultural context of an early faunal assemblage from Easter Island. Asian Perspectives 33:79–96.

St. John, H. 1988. Census of the flora of the Gambier Islands, Polynesia. Privately published, Honolulu.

Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. Ecological Monographs 69:25–46.

Telford, I. R. H. 1993. Cocos (Keeling) Islands. Flora of Australia 50:30–42.

Thaman, R. R., F. R. Fosberg, H. L. Manner, and D. C. Hassall. 1994. The flora of Nauru. Atoll Research Bulletin 392:1–223.

Tilman, D. 1999. Diversity and production in European grasslands. Science (Washington, D.C.) 286:1099–1100.

Trewick, S. A. 2000. Molecular evidence for dispersal rather than vicariance as the origin of flightless insect species on the Chatham Islands, New Zealand. Journal of Biogeography 27:1189–1200.

Turbott, E. G. 1990. Checklist of the birds of New Zealand. 3d ed. Ornithological Society of New Zealand, Auckland.

Valentine, J. W., and D. Jablonski. 1993. Fossil communities: compositional variation at many time scales. Pages 341–349 *in* R. E. Ricklefs and D. Schluter, eds. Species diversity in ecological communities. University of Chicago Press, Chicago.

Vitousek, P. M., and L. R. Walker. 1989. Biological invasion by *Myrica faya* in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. Ecological Monographs 59: 247–265.

Vitousek, P. M., C. M. D'Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. American Scientist 84:468–478.

Walters, M. 1988. Probable validity of *Rallus nigra* Miller, an extinct species from Tahiti. Notornis 35:265–269.

Watkins, B. P., and W. Furness. 1986. Population status, breeding and conservation of the Gough Moorhen. Ostrich 57:32–36.

Watling, D. 1982. Birds of Fiji, Tonga and Samoa. Mill-wood, Wellington.

Webster, L. 1985. Checklist of the vascular plants of the northern Line Islands. Atoll Research Bulletin 287:1–38.

Webster, L., J. O. Juvik, and P. Holthus. 1992. Vegetation history of Washington Island (Teraina), northern Line Islands. Atoll Research Bulletin 358:1–50.

Welsh, S. L. 1998. Flora societensis: a summary revision of the flowering plants of the Society Islands: Mehita, Tahiti, Moorea, Tetiaroa (iles du vent); Huahine, Raiatea, Tahaa, Bora Bora, Tupai, Maupiti, and Mopelia (iles sous le vent). Brigham Young University, Orem, Utah.

Whittaker, R. J., S. H. Jones, and T. Partomihardjo. 1997. The re-building of an isolated rain forest assemblage: how disharmonic is the flora of Krakatau? Biodiversity and Conservation 6:1671–1696.

Wilson, K. 1997. Extinct and introduced vertebrate species in New Zealand: a loss of biodistinctiveness and gain in biodiversity. Pacific Conservation Biology 3:301–305.

Zizka, G. 1991. Flowering plants of Easter Island. Palmengarten, Frankfurt.

Associate Editor: Daniel F. Doak