CONCEPTS & SYNTHESIS
EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

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GLOBAL PATTERNS OF PLANT INVASIONS AND THE CONCEPT OF INVASIBILITY

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Abstract. With a simple model, I show that comparisons of invasibility between regions are impossible to make unless one can control for all of the variables besides invasibility that influence exotic richness, including the rates of immigration of species and the characteristics of the invading species themselves. Using data from the literature for 184 sites around the world, I found that nature reserves had one-half of the exotic fraction of sites outside reserves, and island sites had nearly three times the exotic fraction of mainland sites. However, the exotic fraction and the number of exotics were also dependent on site area, and this had to be taken into account to make valid comparisons between sites. The number of native species was used as a surrogate for site area and habitat diversity. Nearly 70% of the variation in the number of exotic species was accounted for by a multiple regression containing the following predictors: the number of native species, whether the site was an island or on the mainland, and whether or not it was a nature reserve.

After controlling for scale, there were significant differences among biomes, but not continents, in their level of invasion. Multiple biome regions and temperate agricultural or urban sites were among the most invaded biomes, and deserts and savannas were among the least. However, there was considerable within-group variation in the mean degree of invasion. Scale-controlled analysis also showed that the New World is significantly more invaded than the Old World, but only when site native richness (probably a surrogate for habitat diversity) is factored out. Contrary to expectation, communities richer in native species had more, not fewer, exotics. For mainland sites, the degree of invasion increased with latitude, but there was no such relationship for islands. Although islands are more invaded than mainland sites, this is apparently not because of low native species richness, as the islands in this data set were no less rich in native species than were mainland sites of similar area. The number of exotic species in nature reserves increases with the number of visitors. However, it is difficult to draw conclusions about relative invasibility, invasion potential, or the roles of dispersal and disturbance from any of these results. Most of the observed patterns here and in the literature could potentially be explained by differences between regions in species properties, ecosystem properties, or propagule pressure.

Key words: dispersal; disturbance; exotic species; extinction; immigration; invasibility; islands; nature reserves; plant invasions; propagule pressure; weeds.

INTRODUCTION

The invasion of natural communities by introduced plants constitutes one of the most serious threats to biodiversity (Heywood 1989), and it seems that there is now no nature reserve in the world outside Antarctica that is without introduced plant species (Usher 1988). Exotic weeds in conservation areas are increasingly recognized as representing a major threat to the preservation of biodiversity (Humphries et al. 1991, Cronk and Fuller 1995, Luken and Thieret 1997, Schmitz et al. 1997), and can profoundly alter ecosystem structure and function (e.g., Hobbs and Mooney 1986, Braithwaite and Lonsdale 1987, Vitousek et al. 1987, Braithwaite et al. 1989, Cronk and Fuller 1995).

Invasions have long fascinated ecologists, and considerable attention has been brought to bear on the question of whether some ecosystems are more invasible than others (e.g., Crawley 1986, Fox and Fox 1986, Usher et al. 1988, Vitousek 1988, Cronk and Fuller 1995: 8–11, Williamson 1996: 26). To ask

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whether a region is more ‘‘invasible’’ than another is clearly to ask not simply whether it has more exotic species, but whether it is intrinsically more susceptible to invasion. It is not, however, easy to determine intrinsic susceptibility to invasion. A simple model illustrates this. Successful invasion of a natural community requires dispersal, establishment, and survival (Hobbs 1989), with the number of species in an area being determined by a balance between immigration and extinction. Most invading species fail to establish (Williamson 1996). Consider this simple equation:

$$E = IS \tag{1}$$

which proposes that the number of exotic species E in a region is given by the product of the number of exotic species introduced, I, and the survival rate of exotic species in their new range, S. I and S can be further broken down into their components. For I,

$$I = I_a + I_i \tag{2}$$

where I_a is the number of accidental introductions (either as contaminants or by natural dispersal), and I_i is the number of intentional introductions (for agriculture, as ornamentals, etc.). For S,

$$S = S_v S_h S_c S_m \tag{3}$$

where S_v is the rate of species survival after extinctions due to competition from the native vegetation, S_h is the rate of species survival after extinctions due to herbivory and pathogens, S_c is the rate of species survival after extinctions due to chance events at establishment (droughts, etc.), and S_m is the rate of species survival after extinctions due to maladaptation (e.g., tropical species released into a temperate climate, terrestrial species released into an aquatic environment, etc.).

These simple equations provide a crude idea of the kind of mechanisms that contribute to determining the exotic richness of a region. When ecologists suggest that Region 1 is more invasible than Region 2, it seems self-evident that they are focusing on S in Eq. 1, and are proposing that the exotic species arriving in Region 1 are more likely to survive than those arriving in Region 2. From Eq. 1, however, it is clear that, to understand the underlying causes of exotic richness and to compare regions for invasibility, we need to know about both I and S. That is, we must control for the number of species introduced, I, before we can compare values of S. In practice, as I will show, this is often impossible, because we rarely know how many species have been introduced and have failed (see Simberloff 1989). As Williamson (1996: 55) pointed out, ‘‘Looking for real differences in invasibility requires looking at the residuals from the relationship between invasion success and propagule pressure.’’

Even if we could control for I, there are further complications before we can compare invasibilities. The invasibility of a region presumably consists of those properties of the region that affect exotic species survival S. The native biota affect S_v and S_h, by definition, but these are both affected by the exotic biota too, because they represent the outcome of interactions between the native and exotic species. Invasibility will also be affected by the degree of disturbance that the region has undergone (e.g., Crawley 1986, Hobbs 1989, 1991, Hobbs and Huenneke 1992, Burke and Grime 1996), because it reduces the ability of the native vegetation to compete and so obviously increases S_v for the invaders. Thus, an invaded region, relatively undisturbed and with a high native cover value, might be expected to give rise to a low S_v among the invading species through competition, but this might be counterbalanced if the invaders are good competitors (raising S_v) or repellent to herbivores (raising S_h). If feral animals become abundant, disturbance increases and S_v will rise, increasing E. The remaining quantities, S_c and S_m, are likely to be affected only by the qualities of the invading species. S_m is affected by definition, whereas S_c might be raised if, for example, the invading species have persistent seed banks, allowing them to survive chance periods of hardship. Another hypothetical determinant of a region’s invasibility is the ecosystem’s resistance to invasion (Table 1; Williamson 1996: 193–196). This is a system property, relating to the way in which the community is structured, the strength of the interactions between trophic levels, etc. Thus, invasibility is an emergent property of ecosystems, manifested in the rate of mortality of exotic species, but at the same time potentially affected by the climate, the properties of the native species, the level of disturbance, and the ecosystem’s resistance to invasion (Table 1).

Another concept that has been mooted in the literature is invasion potential (di Castri 1989), the ability of species to invade (Table 1). Presumably, an invasion by species with high invasion potential would give relatively high values of S. An example of how the rate of establishment of exotic species can be changed by the nature of the species is the intentional release of 466 pasture species into the savannas of northern Australia (Lonsdale 1994). These were predominantly selected to be vigorous competitors (i.e., high S_v) and hardy (high S_c), and were almost all savanna species (high S_m). About 13% of the introduced species survived in the wild to become weeds (Lonsdale 1994), in contrast to a general expectation on the order of ~0.1% for a random assortment of introduced species (Williamson and Fitter 1996).

Thus, there are apparently three contrasting themes in invasion ecology, emphasizing (1) ecosystem properties (henceforth referred to as EP), which may include ecosystem resistance to invasion and the degree of disturbance; (2) propagule pressure (PP) and the importance of dispersal rates; and (3) the properties of the exotic species (SPE), such as invasion potential, or those of the native species (SPN). The final column in Table 1 attempts to summarize all of this. Thus, in-

TABLE 1. Some concepts in invasion studies redefined in terms of Eqs. 1–3. The final column shows how factors implicated in the invasion terms can be classified as ecosystem properties (EP), native species properties (SPN), exotic species properties (SPE), or propagule pressure (PP). See the *Introduction* for more details.

Term in invasion ecology	Conventional definition	Definition in terms of Eqs. 1–3	Factors implicated
Disturbance	removal of competing vegetation (Hobbs 1991)	disturbance raises S_v	EP, SPN
Native species resistance to invasion	competitive ability of native species	high resistance → low S_v	SPN
Resistance to disturbance	ability of native ecosystems or species to recover from disturbance	high resistance → low S_v	EP, SPN
Ecosystem resistance to invasion	intrinsic resistance of native ecosystem to invasion through community structure (Williamson 1996: 193–196)	high resistance → low S_v, or low S_h	EP
Invasibility	overall susceptibility of sites to invasion (Williamson 1996: 55)	high invasibility → higher S	EP, SPN†
Invasion potential	intrinsic ability of species to invade (di Castri 1989)	high invasion potential → higher S_v, S_h, or S_c	SPE
Propagule pressure	number of propagules arriving at a site (Williamson 1996: 45)	propagule pressure varies I	PP

† Invasibility emerges from the region's climate, level of disturbance, ecosystem resistance to invasion, and native species' competitive ability and resistance to disturbance.

vasibility is potentially determined by the level of disturbance (EP), the competitive abilities of the native species and their resistance to disturbance (SPN), and by the way the native community is assembled (EP). Invasion potential, by contrast, is a property of the invading species only (SPE). The impact of disturbance is affected by the amount of disturbance (EP) and the ability of the individual species to withstand disturbance (SPN *and* SPE, because the exotics must be able to withstand disturbance if we are to invoke the latter as a facilitator of invasion). Lastly, we have the number of propagules arriving at a site (PP). It is not unusual to find invasion studies focusing on one of these aspects only. However, as we have seen, to explore rigorously the effects of any one factor, we need to be able to take account of the potential effects of the others.

In addition to these logical difficulties in determining differences in intrinsic properties of ecosystems and species, we also need to consider the kind of data that we use to measure the degree of invasion. The number of species at a site always increases with site area, even before we start considering intrinsic site properties (e.g., Rosenzweig 1995: Chapter 2). The values of E and I in Eqs. 1–3 are, therefore, all scale dependent, so to compare regions for invasibility, we need to establish some basis of comparison that controls for size. Many comparative studies (e.g., Crawley 1986, Usher 1988, Vitousek 1988, di Castri 1989, Heywood 1989, Cowie and Werner 1993, U.S. Congress OTA 1993: Table 3.3, Planty-Tabacchi et al. 1995, Butterfield et al. 1997) have used *percentage exotic*, i.e., the number of exotics divided by the total number of species (exotic and native), expressed as a percentage, or simply the number of exotics in comparisons. This exotic fraction was perhaps used in the expectation that it controls for scale, but this cannot be assumed, and the methodology for its use has to be explored.

The study that follows is an attempt to collate and analyze data on exotic plant invasions from around the world, to try to tease out the dominant processes underlying plant invasions, and to test generalizations from the literature on invasions in the most appropriate way after controlling for scale. The data analysis begins by exploring a large data set on the incidence of exotic plant species naturalized in various sites around the world, to quantify the scale dependency of exotic species richness. I then compare the degree of invasion between different continents and biomes. Next, I retest various generalizations about plant invasions and invasibility from the literature. Lastly, in the light of the results, the *Discussion* reappraises the roles of ecosystem properties such as invasibility, species properties such as invasion potential, and propagule pressure, in determining the degree of invasion.

Generalizations tested

I list here various hypotheses from the invasion literature, and classify them according to whether they are exploring the EP, PP, or SP themes.

a) The Old World is less susceptible to invasion than the New World (Crosby 1986, di Castri 1989). Di Castri (1989) proposed that Old World species have greater invasion potential than New World species (SPE), suggesting that this was because the Old World flora had been more exposed in the past to natural and anthropogenic disturbance.

b) Richer communities are less invasible (EP; Elton 1958, Fox and Fox 1986, Holdgate 1986).

c) Temperate ecosystems are more invasible than tropical ecosystems (EP/SP; Holdgate 1986).

TABLE 2. Summary of data sources on exotic richness at 184 sites used in the analyses.

Source	Types of sites	*n* (no. sites)
Brockie et al. (1988)	islands	6
Macdonald and Frame (1988)	savannas	5
Crawley (1986)	U.K. counties	14
Crawley (1986)	Northeast USA	1
Hussey et al. (1992)	Culeenup Island, Western Australia	1
Humphries et al. (1991)	various	20
Vitousek (1988)	U.S. national parks	9
Kruger et al. (1989)	South African fynbos reserves	14
Macdonald et al. (1988)	Mediterranean-biome reserves	4
Loope et al. (1988)	arid land reserves	4
Mooney et al. (1986)	Californian local floras	14
Cowie and Werner (1993)	regions of northern Australia	7
Macdonald et al. (1989)	South African reserves	36
Macdonald et al. (1989)	North American reserves	16
Rejmanek et al. (1991)	Californian islands	11
U.S. Congress OTA (1993)	North American states and regions	10
Dafni and Heller (1990)	Israel	1
Le Floc'h (1990)	North Africa	1
Heywood (1989)	various national floras	10

d) Islands in Europe and North America are less invaded than are tropical islands (EP/SPE/SPN; Brockie et al. 1988).

e) Islands are more invasible than the mainland because they are species-poor by comparison (EP; Elton 1958, Simberloff 1997), the corollary of (b).

f) An increase in the number of human visitors to an area leads to an increase in the number of exotic species (PP; Macdonald et al. 1989). All of these ideas were previously either untested, or tested in ways that were probably not immune to scale problems. I will explore them here with a larger data set than any previously available.

The generalizations were obviously never couched in terms of Eq. 1, but they are mostly attempting to distinguish between degrees of invasibility or invasion potential and, consequently, they implicitly focus on factors affecting *S*. The exception is generalization (f). This was based on an empirical result, which has been taken to indicate the importance of transport of plant species into reserves by tourists (Usher 1988) and, more widely, as evidence of the dominant role of propagule pressure (as opposed to ecosystem properties) in determining exotic richness (Williamson 1996: 48, 55). This implies variation in *I*.

METHODS

The data

Data on the number of exotic and native plant species from sites around the world came from various sources, mostly compilations (Table 2). Where sites were duplicated between data sets, the more recent reference was used. Data extracted were as follows: the number of native species (N), the number of exotic species (E), the fraction of the total flora that was exotic (X), and the area of the site (A). The full data set consisted of 184 sites. However, area values were unavailable for 80 sites, most notably those of Kruger et al. (1989; 14 sites) and Macdonald et al. (1989; 52 sites). Data were extracted from Macdonald et al. (1989) by measuring the coordinates from their Figs. 9.1 and 9.2. Sites were coded for biome or land use and continent using Cox and Moore (1985: 51–67) and the Times Atlas (Anonymous 1990). Large regions such as continents, containing a range of biomes, were classified as ''multiple biomes.''

Exotic species are ''species coming from outside the area in question,'' invaders sensu Williamson (1996: 58). However, it is impossible to judge from the present data set the percentages of the exotic species that actually cause pest problems, or that are naturalized but have no harmful effect.

Statistical analyses

Variables were examined for normality and were log- or arcsine-transformed as necessary. Relationships between variables were tested for significance by correlation (Snedecor and Cochran 1980: 361–363) and, where the correlation proved significant, trend lines were fitted by least squares linear regression. For multiple regressions, independent variables were first tested to ensure that they were not autocorrelated prior to their inclusion in the model. The strengths of regression relationships were measured by their adjusted r^2 values (Seber 1977). This corrects for the number of independent variables in the model. An overall indication of the accuracy with which the fitted regression predicts the dependence of y on x is given by the standard error of the estimate, expressed as a percentage of the mean of y (Zar 1996: 327–328).

Differences between groups of sites were compared using ANOVAs of standardized residuals from the regressions. The use of residuals controls for the most important explanatory variables, so that one may cautiously assume that one is comparing sites of different types on something approaching an equivalent basis.

TABLE 3. Regression models used to explore global patterns of exotic richness, showing adjusted r^2 and the percentage standard errors of estimates. For every independent variable, the coefficient, its standard error (1 SE) and the significance of its t test are given.

			Independent variables					
			Intercept		log A		log N	
Model	Dependent variable	n	Coefficient	1 SE	Coefficient	1 SE	Coefficient	1 SE
1	arcsine $X^{0.5}$	104	0.58***	0.04	−0.04***	0.01		
2	log E	108	1.56***	0.11	0.18***	0.03		
3	log N	104	1.96***	0.06	0.27***	0.01		
4	log E	177	−0.27	0.23			0.82***	0.07
5	log E	104	1.59***	0.16	0.17***	0.03		
6	log E	104	1.44***	0.14	0.20***	0.03		

Notes: The model variables are site area, A; native species richness, N; island status, I ($I = 1$ for islands, $I = 0$ for mainland); reserve status, R ($R = 1$ for reserves, $R = 0$ for nonreserves); fraction of exotic species, X; and exotic richness, E. Levels of statistical significance are indicated as: *$P < 0.05$, **$P < 0.01$, and ***$P < 0.001$. Cells are left blank where not applicable.

For example, if we are interested in comparing differences between groups of sites in variable y, but we know that much of the variation in y depends on x, we can use ANOVAs of the residuals from a regression of y on x. Essentially, one is then comparing the vertical displacement of the data points from the central trend of y on x, to see whether groups differ, on average, in being above or below the trend. This avoids confounding the effects due to site factors with the effects due to x.

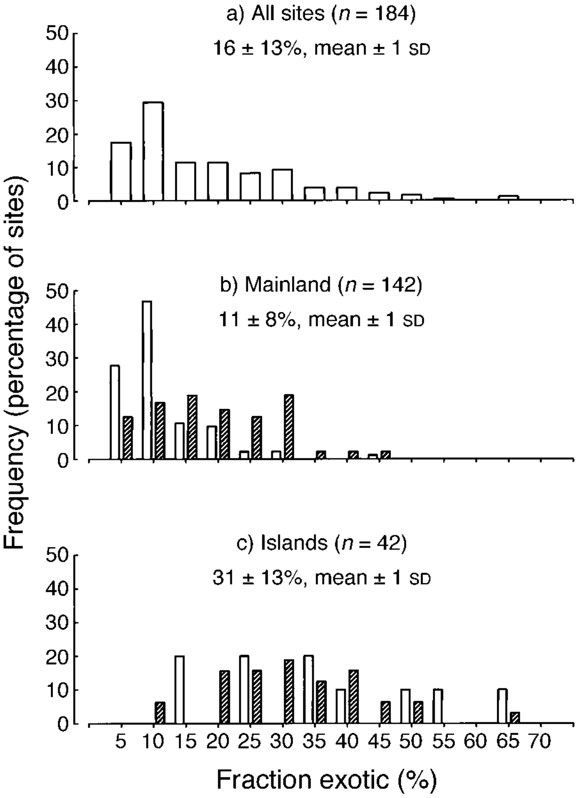

FIG. 1. Frequency distributions of exotic fractions for a global set of 184 sites, showing (a) all sites combined, (b) mainland, and (c) island sites (reserves are shown as open columns, and nonreserves as hatched columns).

RESULTS

Global patterns of exotic plant richness

Across all sites, the mean value of X, the fraction of the flora that was exotic, was 16%, but there was considerable variation about this mean, the minimum value being 1.3% (Zachariashoek reserve in South Africa; Kruger et al. 1989), and the maximum being 64% (Hawaii Volcanoes; Vitousek 1988). The frequency distribution of exotic fractions was right skewed, with 18% of all sites having fractions of $\leq$5% (Fig. 1a). Island sites (Fig. 1c) had almost three times as large an exotic fraction as mainland sites (Fig. 1b), whereas reserves had less than half of the exotic fraction of nonreserve sites (Figs. 1b, c). Furthermore, the exotic fraction X, and the number of exotic species E, were significantly related to site area A (Models 1 and 2 in Table 3; Fig. 2).

As a consequence of all this systematic variation, invasion patterns across the world could only be compared after controlling for several site descriptors that were the source of much variation: reserve and island status, and site size. The most obvious measure of site size in the present data set is area. However, area data are available only for 104 out of the 184 sites in the data set. An alternative measure of scale that maximizes the available data is the number of native species ($n = 177$ sites), but a prerequisite for the use of native species richness to measure scale is that it be strongly correlated with area. This is, in fact, the case: log A accounted for 78% of the variance in log N (Model 3 in Table 3; Fig. 3). I therefore used log N to control for scale in the full data set. A plot of log E against log N gives an overall positive relationship, within which two roughly parallel clouds of data points are apparent (Fig. 4), the lower one consisting largely of mainland sites, the upper one largely of islands and nonreserve sites. Therefore, a linear regression model was fitted for log E, using the explanatory variable

TABLE 3. Extended.

Independent variables							
I		*R*		Residuals from Model 3			SE of estimate as percentage of mean
Coefficient	1 SE	Coefficient	1 SE	Coefficient	1 SE	Adjusted r^2	
						0.12	37
						0.28	22
						0.78	8
0.42***	0.07	−0.35***	0.06			0.69	15
0.28*	0.10	−0.41***	0.10			0.46	19
0.36***	0.09	−0.28**	0.09	0.22***	0.04	0.61	16

log N, with island status indicated by the coding variable I (for islands, $I = 1$; for mainland, $I = 0$), and reserves by the variable R (for reserves, $R = 1$; for nonreserves, $R = 0$). The model explained 69% of the variance in log E (Fig. 4; Model 4 in Table 3). Thus, a simple model involving only three explanatory variables (the number of native species, and whether the site is an island or a park) can account reasonably well for most of the variation in the number of exotic species around the world. The coefficients 0.42 for I and −0.35 for R indicate that (taking antilogs) islands, on average, possess 2.6 times as many exotics as mainland sites of similar native diversities, whereas nonreserve sites have 2.2 times as many exotics as reserves.

Separating effects of native species richness from those of site area

Although native species richness effectively describes much of the variation in exotic richness, it is still informative to partition this effect into two components: the effect due to the area of the site, and that due to its native species richness. To do this, I first fit the model for log exotic richness against log area, and park and island status, to examine the explanatory power of area alone (for the 104 sites for which area data exist). All of the parameters were significant, but the model explained a comparatively unimpressive 42% of the variance in log E (Model 5 in Table 3; Fig. 5).

We can now add the standardized residuals from Model 3 (Table 3), the regression of native species richness on area, as an indication of the degree to which each site differs from the central area trend in native richness. In this way, we are partitioning the variance in exotic species richness between the effects due to native richness and those due to the area of the site. A multiple regression of log E against log A, island and park status, and the native richness residuals from Model 3 accounted for 62% of the variance in log E (Model 6 in Table 3). All of the coefficients for the explanatory variables were highly significant (Table 3). This model explained significantly more of the overall variance than that explained in terms of area alone ($F_{1,103} = 38.7$, $P < 0.001$ for the contribution of native richness residuals to the explanatory power of the model). Indeed, the native richness residuals explained about the same amount of variation as did site area (Table 4). The positive coefficient for native richness residuals in Model 6 indicates that alien species richness was positively related to native species richness (Fig. 6). This

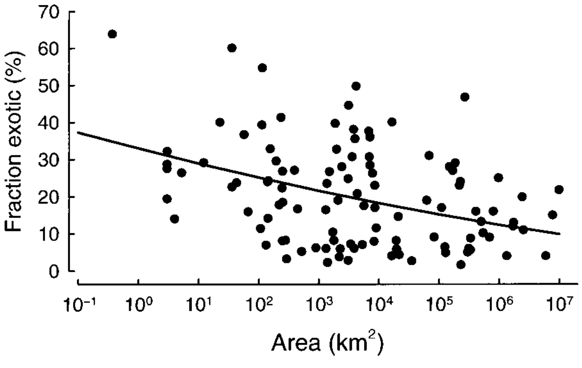

FIG. 2. The relationship between the fraction of the flora that is exotic, X, and the area of the site, A ($r = 0.35$, $n = 104$, $P = 0.00027$). The fitted regression line is Model 1 in Table 3. Note the log scale of the x-axis.

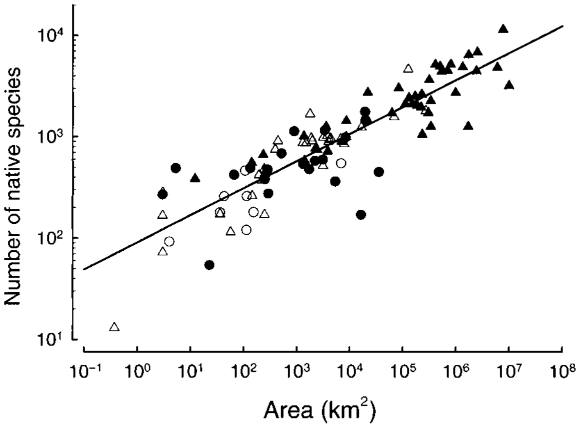

FIG. 3. The relationship between the number of native species and site area for 104 sites around the world, broken down into island reserves (○), island nonreserves (△), mainland reserves (●), and mainland nonreserves (▲). The fitted line is Model 3 (Table 3). Note the log scale of both axes.

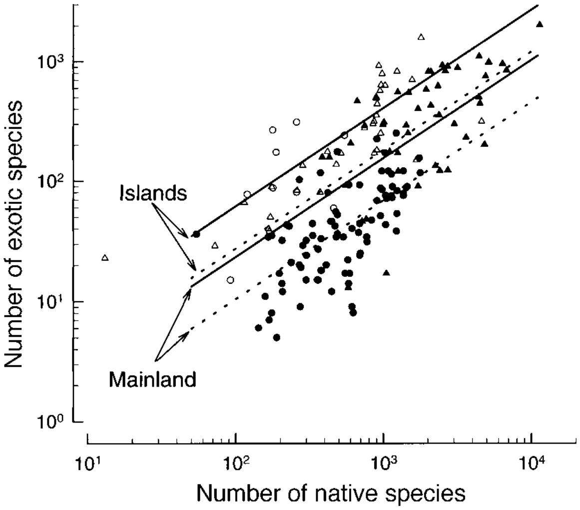

FIG. 4. The relationship between the number of exotic plant species (E) and the number of native plant species (N) for 177 sites and regions around the world, broken down into island reserves (○), island nonreserves (△), mainland reserves (●), and mainland nonreserves (▲). The fitted lines shown are from Eq. 4 (see also Model 4 in Table 3): solid lines are for nonreserve sites, and broken lines are for reserves. Both axes are log scales.

TABLE 4. Proportions of total variance in exotic species richness ($n = 104$ sites) accounted for by the various explanatory variables in Model 6 (see Table 3), and the possible factors implicated in each variance component from Table 1 (see *Discussion*).

Source of variance	Percentage of total variance accounted for	Factors implicated
Native richness residual	23	EP, SPN
Log area	22	EP
Island/mainland	13	EP, SPN, PP
Reserve status	9	EP, PP
Residual	34	EP, SPN, SPE, PP, interactions, chance, error
Total	100	

is an important result, with implications for the diversity/invasibility hypothesis. In summary, then, the reason for the strong explanatory power of native species richness in the larger data set (Model 4) is probably that it embodies site area and site native diversity.

Regional and biome patterns of invasion

In this section, I will first present raw comparisons between regions and biomes simply using exotic fractions, uncorrected for scale. Next, I will control for scale and will compare continents or biomes by one-way ANOVAs of the residuals from Model 5 (Table 3). Model 6 has native richness as an explanatory variable (see Table 3), which means that its residuals include little of the variation due to native richness. By contrast, a comparison of regions using Model 5 residuals includes any effects due to native richness. Because native richness could be an important cause of any regional differences in invasibility, Model 5 residuals are the logical choice. If there are significant differences between regions after controlling for site size and island and reserve status, the implication is that these differences must result from interregional variation in factors such as propagule pressure, native diversity, and invasibility. Unfortunately, there is no way to go further with the current data and tease out the effect of invasibility alone.

1. *Raw comparisons (before controlling for scale, etc.).*—Continents varied at least twofold in their exotic fractions, from oceanic islands at 43% ($n = 4$; these islands were treated separately as being not attributable

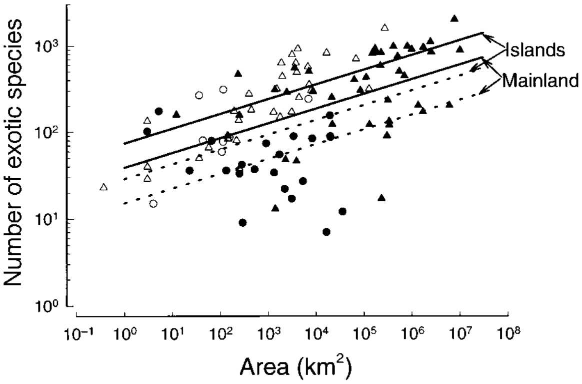

FIG. 5. The relationship between the number of exotic species (E) and site area (A) for 104 sites around the world, broken down into island reserves (○), island nonreserves (△), mainland reserves (●), and mainland nonreserves (▲). The fitted lines are from Model 5 (Table 3): solid lines are for nonreserve sites, and broken lines are for reserves. Both axes are log scales.

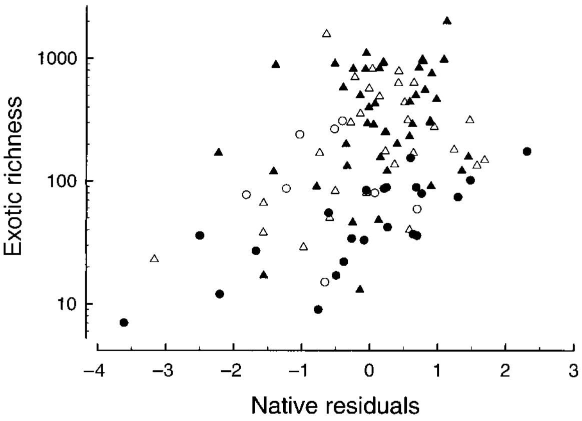

FIG. 6. The effect on exotic richness (E) of the residuals from Model 3 in Table 3 (a regression of native richness on area) for 104 sites around the world, broken down into island reserves (○), island nonreserves (△), mainland reserves (●), and mainland nonreserves (▲). Note the log scale of the y-axis.

TABLE 5. The fraction of the flora that is exotic for 184 sites around the world, broken down by continent, and before controlling for site scale and type.

Continent	Mean (%)	1 SD	n
Oceanic islands	43	10	4
Britain	31	10	15
North America	19	11	69
Australia	17	15	29
South America	13	4	3
Europe	9	3	5
Africa	7	6	57
Asia	7	1	2

Notes: Oceanic islands are presented separately, as being unattributable to any continent. Britain is shown separately from the rest of Europe because the means are very different.

TABLE 6. The fraction of the flora that is exotic for 184 sites around the world, broken down by biome, and before controlling for site scale and type.

Biome	Mean (%)	1 SD	n
Temperate agricultural/urban	31	9	24
Temperate forest	22	16	13
Multiple	19	11	26
Mediterranean shrubland†	17	13	43
Alpine	11	8	26
Savanna	8	6	33
Wet tropics	6		1
Desert‡	6	3	18

† Of mediterranean type rather than location.
‡ Exclusively reserves.

to any continent), to Asia ($n = 2$) at 7% (Table 5). For biomes, the fraction varied from temperate agricultural/urban sites at 31%, down to deserts at 6% (Table 6). The one datum for the wet tropics was similar to that for deserts (Table 6).

2. *Patterns after controlling for site size and site descriptors (i.e., island and reserve status).*—The analyses were carried out on the subset of the data analyzed in Model 5. I also excluded continents or biomes for which the number of sites was less than four: Asia ($n = 2$), South America ($n = 2$), and the wet tropics ($n = 1$). Comparing standardized residuals of log E from Model 5 showed that there were differences between continents (Fig. 7a), but considerable variation within continents meant that these were not significant ($F_{5,99} = 2.2$, $P = 0.06$). By contrast, there were significant differences between biomes ($F_{6,102} = 5.9$, $P < 0.001$). The relative values of these scale-controlled data were somewhat changed from the uncontrolled values. For biomes (Fig. 7b), the multiple biome and temperate agricultural/urban sites were all above the central trend, and deserts and savannas below, with mediterranean shrubland, temperate forest, and alpine habitats close to the trend. Three groups were recognizable by least significant differences (LSD), but with less overlap between groups than for continents (Fig. 7b). Nevertheless, there was considerable variation within biomes. For example, the Australian savannas (mean residual $= -1.3$) were much less invaded than were the African (-0.3), whereas the Australian mediterranean habitats (0.7) were much more invaded than those of North America (-0.4) or Europe (-0.6).

Testing generalizations about plant invasions

The generalizations (a–f) can now be tested after controlling for the effect of scale dependency and, where appropriate, native richness and island or reserve status. The basic approach here will be to explore the differences in mean residuals for groups of sites, as was done for the previous biome and continent comparisons. Except where otherwise stated, I will use the residuals from Model 5 (Table 3), for the reasons pre-

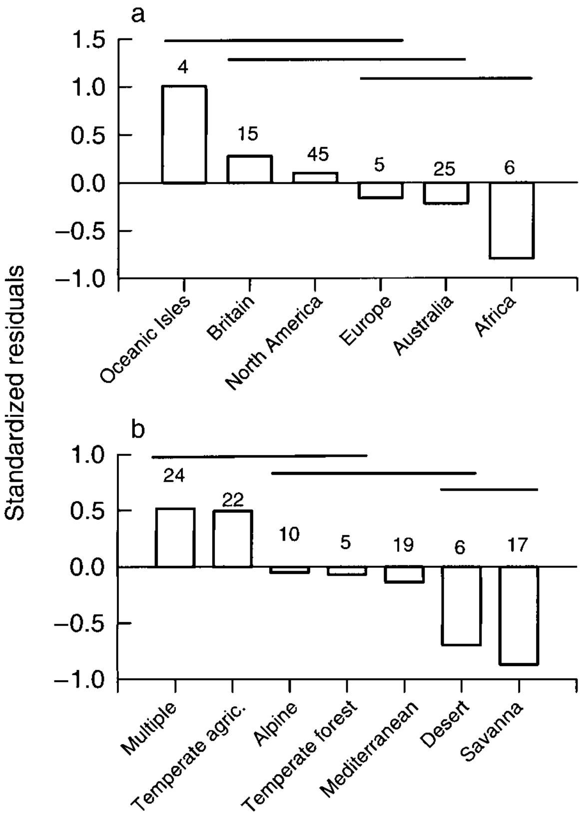

FIG. 7. Degree of invasion compared between different continents (a) and biomes (b). The invasion index is given by the standardized residuals from Model 5 (see also Fig. 5), averaged for the various continent or biome groups. The residuals are an indication of the degree to which a particular biome or continent diverges from the norm after controlling for site scale, and for whether sites are reserves or islands. They are arranged from positive (i.e., more invaded than the norm) on the left to negative on the right; compare these with the uncorrected values in Tables 5 and 6. The horizontal lines show groups not significantly different by least significant differences (LSD). Note that, for continents, the overall F test was not significant, and the LSD bars are therefore provided only as an indication of variation between groups. The number of cases in each group is shown above the columns.

TABLE 7. Statistics for the regression models used to explore literature hypotheses about exotic richness.

			Independent variables					
			Intercept		log N		Residuals from Model 9	
Model	Dependent variable	n	Coefficient	1 SE	Coefficient	1 SE	Coefficient	1 SE
7	exotic residuals from model 6: islands	39	−0.10***	0.37				
8	exotic residuals from model 6: mainland	64	−1.09**	0.36				
9	Log V	52	−2.86*	1.25	2.68***	0.46		
10	log E	52	−1.14***	0.29	1.00***	0.11	0.12***	0.03

Notes: See Table 3 and *Methods* for statistical details. Cells are left blank where not applicable.

viously given (see *Regional and biome patterns of invasion*).

a) *Old World vs. New World sites.*—From the available data, the Old World sites ($n = 13$) represented by Britain (a single geometric mean for all sites), Europe, Africa, and Asia can be separated from the New World sites ($n = 47$) represented solely by North America, and their mean standardized residuals from Model 4 then can be compared by t test. The mean residual for New World sites was close to the central trend, being 0.08 ± 0.13 (mean ± 1 SE), whereas that for Old World sites was well below at -0.45 ± 0.30, but as a consequence of the great variation about the means, the two groups did not differ significantly ($t_{58} = 1.8$, $P = 0.075$). If, by contrast, we remove the effect due to native species richness from the comparison, by using the residuals from Model 6, the New World is more invaded than the Old ($t_{58} = 2.3$, $P = 0.027$). This conclusion is further strengthened if we examine the residuals from the larger data set of Model 4 ($t_{127} = 4.3$, $P < 0.001$). Thus, there is evidence to support the generalization that the New World is more invaded than the Old, but only when we factor out the effect of site differences in native species richness.

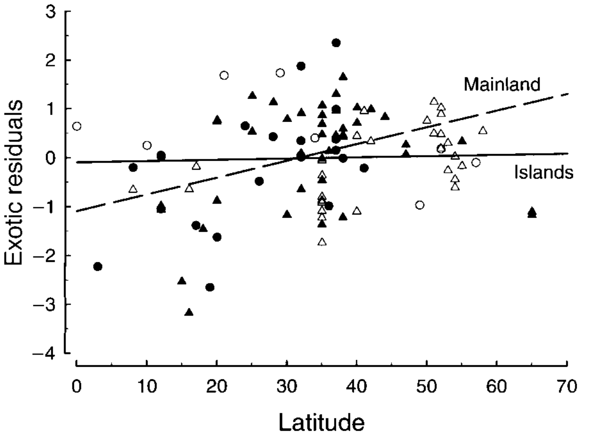

FIG. 8. Effect of latitude on the divergence of exotic richness from the norm represented by Model 5 in Table 3. There was no significant trend for islands (open symbols, solid line; Model 7 in Table 7), but a significant positive trend for mainland sites (solid symbols, broken line; Model 8 in Table 7). The sites are broken down into island reserves (○), island nonreserves (△), mainland reserves (●), and mainland nonreserves (▲).

b) *The effect of increasing native community richness on weediness.*—In this case, scale is central to the question being addressed. In order to accept the prediction that invasion success declines with increasing native richness, we would need to be able to show that the number of exotic species declines as the number of native species increases for a given area of site. In fact, from Model 5 (Table 3), exotic richness increases as the native richness/area residuals increase (Fig. 6). Given that these residuals are already controlling for area, this indicates that there is a positive, not a negative, relationship between exotic richness and native richness. This conclusion needs to be qualified, however (see *Discussion: Diversity, invasibility, and invasion potential*).

c) and d) *Temperate vs. tropical mainland sites and temperate vs. tropical islands.*—I maximized the sensitivity of these analyses by testing for a latitudinal trend in the residuals from Model 5 using linear regression. There was a slight positive trend for mainland sites, but none for islands (Models 7 and 8 in Table 7; Fig. 8). These results were not changed if exotic residuals were used to control for native richness (i.e., those from Models 4 and 6). Thus, the predictions in their modified forms are upheld for mainland sites, but not for islands. Even for mainland sites, however, the results are not very convincing: the relationship accounts for only 14% of the variance and does not accurately predict the effect of latitude (Table 7).

e) *Islands are more invasible because they are species poor.*—At any given area, islands tend to have more exotic species than equivalent mainland sites (Fig. 5), implying that they may be more invasible (or may suffer a higher propagule pressure). However, the native species density for this data set was not noticeably less in islands (Fig. 3). Comparing the residuals from the regression of native species richness against density (Model 3) showed that there was no significant difference between islands and mainland sites ($t_{102} = 0.69$, $P = 0.49$). Thus, the higher level of invasion seen on islands is not explained by low native species density in this data set of 104 sites.

f) *The effect of visitors on exotic richness.*—The test

TABLE 7. Extended.

Independent variables			
Latitude		Adjusted r^2	SE estimate as percentage of mean
Coefficient	1 SE		
0.003	0.009	0.00	123
0.034**	0.011	0.14	119
		0.40	23
		0.68	15

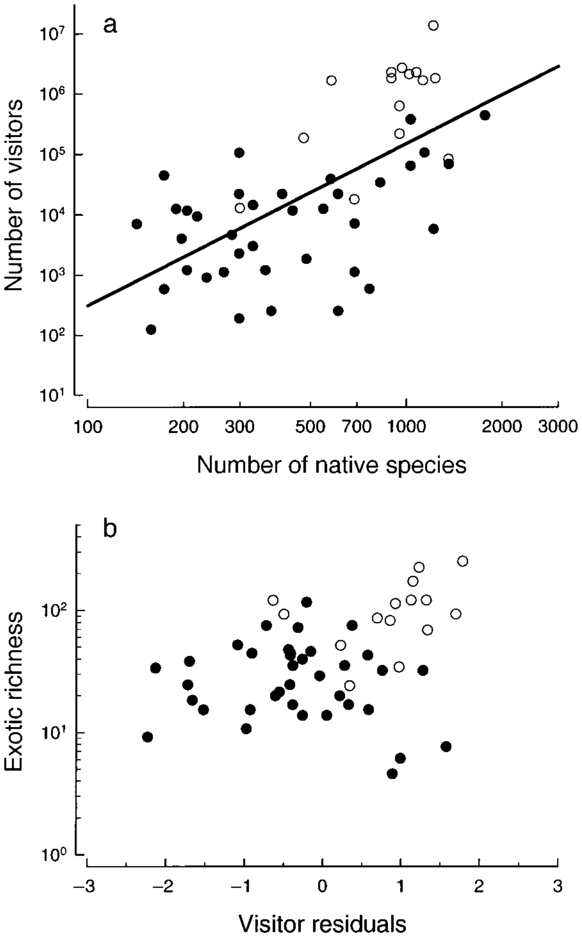

FIG. 9. (a) The positive relationship (Model 9 in Table 7) between the number of visitors and the number of native species, for 52 national parks in the United States (open symbols) and South Africa (solid symbols). (b) The effect on exotic richness of the residuals from the relationship in (a); see Model 10 in Table 7. All data are replotted from graphs 9.1 and 9.2 of Macdonald et al. (1989). Log scales are used for the y-axes, and for the x-axis in panel (a).

of the relationship between the number of exotics and the number of visitors risks being heavily confounded. Exotic richness increases with native richness; larger parks have more native species and can potentially hold more visitors; therefore, exotic richness is automatically likely to be positively related to the number of visitors, without necessarily indicating a causal relationship. We must take account of the change in exotic species number with the size and richness of the site, using the number of native species. This I did, by first regressing the log number of visitors (log V) on the log of native species richness (log N) to remove any dependence of visitor rate on reserve size. The data used were the combined South African and United States data from Macdonald et al. (1989) that originally demonstrated the visitor relationship; these formed a subset of my larger data set, as noted in Table 2. Log N and log V were strongly, positively correlated (r = 0.64, $n = 52$, $P < 0.001$), and the regression explained 40% of the variance in log V (Model 9 in Table 7; Fig. 9a). The standardized residuals from this regression represent the variation in log V that is not explained by log N. I used these residuals and log N as the independent variables in a multiple regression with exotic richness. This was essentially asking whether exotic richness varies with visitation rate, after controlling for log N. The number of exotics was significantly positively related to the visitor residuals (Model 10 in Table 7; Fig. 9b), indicating that weeds increased with the number of visitors, above any site size effect.

DISCUSSION

Interpreting exotic richness data

Past investigations of the invasion properties of different regions have often relied on comparisons of their exotic fractions or their numbers of exotic species (e.g., Crawley 1986, Usher 1988, Vitousek 1988, di Castri 1989, Heywood 1989, Fox 1990, Cowie and Werner 1993, U.S. Congress OTA 1993: Table 3.3, Planty-Tabacchi et al. 1995, Butterfield et al. 1997). This study has shown, however, that these quantities are better used to compare regions after being corrected for scale. The relationship between exotic and native richness (Model 4) does this, as well as correcting for habitat diversity and island and reserve status, and allows sites to be compared on a more equivalent basis. Native richness describes much of the variation in exotic richness, because it embodies not just the area of the site, but also its habitat diversity (cf. Macdonald et al. 1986). After correcting for scale and habitat diversity in this way, the results show some clear patterns of degree of invasion. Some of the predictions from the literature are supported by these corrected data (see the summary in Table 8). I will now briefly discuss their implications, using insights from Eqs. 1–3 and Table 1.

Reserves, islands, biomes, and continents

Nonreserves are more invaded than reserves, which has led to the suggestion that, being presumably less disturbed (Usher 1988), reserves are less invasible and give rise to lower values of S_V. On the other hand, immigration of exotic seeds (I) is likely also to be generally lower for reserves. Thus, to get at the effect

TABLE 8. Summary of invasion generalizations tested, explanations originally proposed, evidence for or against them from the present study, and alternative explanations deduced from Eqs. 1–3 and Table 1.

Generalization tested (with source)	Original explanation proposed (with implication in terms of EP, SPN, SPE, and PP)	Actual results from present study	Alternative explanations for actual results
Old World less invasible than New World (di Castri 1989)	Old World species have higher invasion potential than New World (SPE)	not consistent ($P = 0.075$) unless native diversity is factored out ($P = 0.027$)	immigration rates greater toward New World than Old World (PP) Old World less invasible than New (EP, SPN)
Richer communities are less invasible (Elton 1958, Fox and Fox 1986, Holdgate 1986)	richer communities are more stable and have fewer vacant niches (EP)	not consistent; opposite is true ($P < 0.0001$)	richer plant communities are evidence of greater habitat diversity (EP)
Temperate ecosystems are more invasible than tropical ecosystems (Holdgate 1986)	temperate ecosystems are less rich and therefore more invasible (EP)	consistent ($P < 0.0024$)	temperate ecosystems are more resistant to invasion (EP) temperate invaders have greater invasion potential (SPE) temperate natives have less resistance to invasion or disturbance (SPN) seed immigration is higher in the temperate zone (PP)
Islands in Europe and North America are less invaded than tropical islands (Brockie et al. 1988)	none offered	no significant effect	not applicable
Islands are more invaded than the mainland (Elton 1958)	islands are species-poor (EP) and therefore more invasible	consistent with generalization ($P < 0.0001$), but not with explanation	island ecosystems are less resistant to invasion (EP) islands are more disturbed (EP) island invaders have greater invasion potential (SPE) or resistance to disturbance island natives have less resistance to invasion or disturbance (SPN) average propagule pressure higher on islands (PP)
An increase in the number of human visitors to an area leads to an increase in the number of exotic species (Macdonald et al. 1989).	visitors increase the propagule pressure (PP)	consistent ($P = 0.0003$)	visitors increase disturbance (EP)

of the invasibility of reserves, we would have to tease out two confounded factors, EP and PP (we can perhaps discount SP in this case, because there would not necessarily be systematic differences in SP for native species between reserves and nonreserves). Similarly, there are real differences in the degree of invasion between biomes, which might lead one to conclude, for example, that deserts and savannas are less invasible, but they are uninterpretable without evidence on PP at least.

The line of evidence provided by islands is similarly confounded. Islands are much more invaded than mainland sites, but again we have no information on propagule pressure on islands relative to mainland sites. We know that islands were ''seeded'' with pigs by explorers, pirates, and whalers, to provide a source of meat (Crosby 1986: 175), and that the pigs rapidly became abundant and did enormous damage to the native vegetation. Perhaps, also, evolutionary isolation may lead to a less competitive native flora, or one less able to compete under grazing (SPN). However, all of this is speculation (Simberloff 1997) and is difficult to explore scientifically.

Diversity, invasibility, and invasion potential

The previous data confirm the generalization (Crosby 1986, di Castri 1989) that New World sites have a higher number of exotic species than Old World sites, but only when variation due to differing native diversities is factored out of the comparison. One explanation of this might be that the ''noise'' created by variation in native richness obscures the underlying pattern. Di Castri (1989) proposed that Old World species had greater invasion potential (ability to invade) than New World species. This is, in fact, an SPE factor (see Table 1), and implies that Old World invaders would have a higher S_v or S_h. Before we could invoke this, however, we would have to control for the immigration rate I, as well as accounting for any difference between New World and Old World species and ecosystems, in causing extinction among newcomers (SPN, EP), which would also affect S_v and S_h. The immigration rate I was probably much greater in the direction of the New World than toward the Old World (di Castri 1989), which would tend to give a higher E in the New World, even if the characteristics of ecosystems and species were identical (see Eq. 1). This, together with the fact that we have no index of relative ecosystem invasibility, means that we can draw no conclusions at all about the relative invasion potential of Old and New World species.

Moreover, although one may conclude that the degree of invasion for mainland sites increases with latitude, we can only infer that one climatic zone is more invasible than another if we assume that there is no latitudinal change in immigration rate, nor in the invasion potential of the species (cf. Eqs. 1–3). Thus, the invasibility of ecosystems is again confounded with immigration and with species' characteristics.

The idea that richer communities are less invasible has been a central one in invasion theory since Elton (1958) first proposed it (Law and Morton 1996). Although May (1973) opposed it on theoretical grounds, a more recent study involving experimental grassland communities supported it (Tilman 1997), and it is a commonly accepted ecological truism (e.g., Fox and Fox 1986, Holdgate 1986). In the sites studied here, however, as in the experiment of Robinson et al. (1995), exotic richness *increases* with native species density. Furthermore, Elton's (1958) argument that islands are more invasible than the mainland because they are comparatively species-poor seems to be falsified. It is true that islands seem to be more invaded (again, we cannot be sure about their invasibility), but the island sites in this study were not noticeably impoverished in their native flora, compared with the mainland sites.

I suggest, then, that there is no causal relationship between native and exotic diversities when these are measured at the community scale, as in the present data set. Rather, exotic species richness responds to greater habitat diversity in the same positive way that native species richness does (see Pickard 1984) and, thus, exotic and native richness are positively correlated without a causal link. However, the relationship is likely to be more complex (Robinson et al. 1995) at the much smaller scale at which plant competition operates. At this scale, no simple relationship would necessarily exist between the degree of invasion and native richness; a third axis, that of competition intensity, which is not a simple function of native richness, would probably be involved.

Propagule pressure vs. invasibility

The concepts that have received most attention in surveys of invasion ecology are invasibility, disturbance, and invasion potential (see Table 1). However, immigration rates (propagule pressures) are also an important force shaping the exotic biota (Newsome and Noble 1986, Pimm 1991, Simberloff 1989, Williamson 1989, Green 1997). Indeed, Williamson (1996: 55), speaking of invasions in general, believes that much of the variation between regions comes from variation in propagule pressure. For plants, there is surprisingly little evidence for or against this. A recent experiment (Tilman 1997: Fig. 4b) found that 70% of the variance in number of species gained in plots was accounted for by propagule pressure (expressed as the number of species added). However, this was within a single habitat type, over just four years, and is probably not applicable globally. One can estimate from Table 4 that propagule pressure is potentially implicated in up to 56% of the variance in exotic richness, being a possible contributor to the variance due to island status, reserve status, and to the residual variance. This is really an upper estimate, because all these are also factors where properties of native species and ecosystems (such as invasibility) are implicated, and the residual variance obviously includes the effects of chance, of measurement error, and of any interactions as well. Nevertheless, it is clear that differences in propagule pressure are probably a major source of variation in the data. If dispersal were unimportant, weed floras on different continents would be a random assortment of species, whereas weed species composition is clearly related to the colonial history of the region (e.g., di Castri 1989).

Just as conclusions about invasibility are inevitably confounded by our ignorance of immigration rate I, so can the reverse happen. My re-analysis here of the results of Macdonald et al. (1989) confirmed their finding that there is a positive relationship between E and the visitation rate. This might lead to the conclusion that visitors are increasing accidental introductions, I_a. However, this could equally be a result of tourists as agents of disturbance (effects on S_v in Eq. 3). In any case, it appears that the density of seeds on tourist vehicles can be so low that the efforts of nature reserve managers are better directed at searching for and eradicating new weed outbreaks than on finding and removing the seeds as they are brought in (Lonsdale and Lane 1994).

This is the largest data set yet brought to bear on the subject of plant invasions. Despite its imperfections (e.g., poor coverage of South America and Asia), it has revealed some intriguing global patterns. It would also be interesting in future to determine whether similar patterns exist in global data for exotic vertebrates. As an indication, a scale-controlled re-plot of data on exotic amphibians and reptiles (Butterfield et al. 1997) confirmed the previous findings that Hawaii and Florida

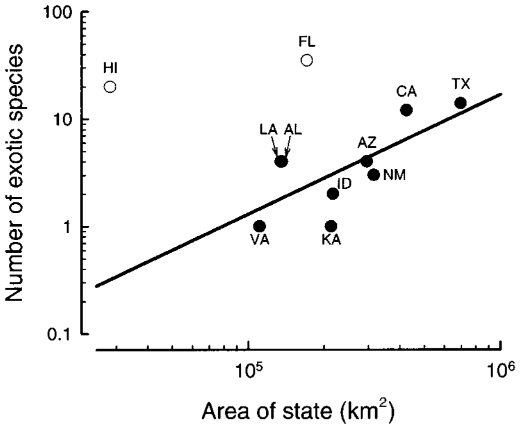

FIG. 10. Relationship between richness of exotic reptiles and amphibians and area for 11 U.S. states, replotted from Butterfield et al. (1997). The regression line is fitted to all states except Florida and Hawaii ($\log E = -5.46 + 1.11 \log A$; $r = 0.71$, $n = 9$, $P = 0.03$). The state abbreviations are: AL, Alabama; AZ, Arizona; CA, California; FL, Florida; HI, Hawaii; ID, Idaho; KS, Kansas; LA, Louisiana; NM, New Mexico; TX, Texas; and VA, Virginia. Both axes are log scales.

were the most invaded states of 11 studied, but also emphasized just how extraordinary the data are for those two states (Fig. 10). Florida is an order of magnitude above the species–area regression for the remaining states, and Hawaii is two orders of magnitude above.

Data sets on exotic richness may be useful for determining the priority of control efforts. However, they will not easily allow conclusions about the fundamental questions in invasion ecology (the relative roles of species properties, disturbance, invasibility, and propagule pressure) because they represent a single time slice through a dynamic process, such that multiple explanations are usually possible for the same result (Table 8). Only those studies in which experimental ecosystems of differing diversities are invaded by the same suite of species would allow one to tackle the more fundamental question of whether high-diversity systems are more or less invasible.

CONCLUSIONS

Nearly 70% of the variation in exotic plant richness among sites around the world is explained by native richness and by whether or not the site is an island or a reserve. Native richness has such explanatory power because it embodies the area of the site and its habitat diversity. The relationship between the degree of invasion and native richness is positive, rather than negative, at the geographical scale of these sites, again probably because both are positively correlated with habitat diversity. Exotic richness results from a flux between propagule pressure and extinction, but the relative contributions of these two factors are not known. Propagule pressure is implicated in up to 56% of the variance in exotic richness, and extinction rates in no less than 44%. Invasibility is an emergent property of invaded ecosystems and their established species that affects only the extinction rates of the invaders, and not their immigration rates. Given the uncertainties about the relative importance of invasibility, conclusions about the invasibilities of different regions are difficult to draw from samples of exotic richness.

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LITERATURE CITED

Anonymous. 1990. The Times atlas of the world. Eighth edition. Times Books, London. UK.

Braithwaite, R. W., and W. M. Lonsdale. 1987. The rarity of *Sminthopsis virginiae* in relationship to natural and unnatural habitats. Conservation Biology **1**:341–343.

Braithwaite, R. W., W. M. Lonsdale, and J. A. Estbergs. 1989. Alien vegetation and native biota in tropical Australia: the impact of *Mimosa pigra.* Biological Conservation **48**:189–210.

Brockie, R. E., L. L. Loope, M. B. Usher, and O. Hamann. 1988. Biological invasions of island nature reserves. Biological Conservation **44**:9–36.

Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. Ecology **77**:776–790.

Butterfield, B. P., W. E. Meshaka, and C. Guyer. 1997. Nonindigenous amphibians and reptiles. Pages 123–138 *in* D. Simberloff, D. C. Schmitz, and T. C. Brown, editors. Strangers in paradise—impact and management of nonindigenous species in Florida. Island Press, Washington, D.C., USA.

Cowie, I. D., and P. A. Werner. 1993. Alien plant species invasive in Kakadu National Park, tropical northern Australia. Biological Conservation **63**:127–135.

Cox, C. B., and P. D. Moore. 1985. Biogeography. Fourth edition. Blackwell Scientific, Oxford, UK.

Crawley, M. J. 1986. What makes a community invasible? Pages 429–453 *in* A. J. Gray, M. J. Crawley, and P. J. Edwards, editors. Colonization, succession and stability. Blackwell Scientific, Oxford, UK.

Cronk, Q. B., and J. L. Fuller. 1995. Plant invaders. Chapman and Hall, London, UK.

Crosby, A. W. 1986. Ecological imperialism: the biological expansion of Europe, 900–1900. Cambridge University Press, New York, New York, USA.

Dafni, A., and D. Heller. 1990. Invasions of adventive plants in Israel. Pages 135–160 *in* F. Di Castri, A. J. Hansen, and M. Debussche, editors. Biological invasions in Europe and the Mediterranean basin. Kluwer Academic, Dordrecht, The Netherlands.

di Castri, F. 1989. History of biological invasions with special emphasis on the old world. Pages 1–30 *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions: a global perspective. John Wiley, Chichester, UK.

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

Fox, M. D. 1990. Mediterranean weeds: exchanges of invasive plants between the five Mediterranean regions of the world. Pages 179–200 *in* F. Di Castri, A. J. Hansen, and M. Debussche, editors. Biological invasions in Europe and the Mediterranean basin. Kluwer Academic, Dordrecht, The Netherlands.

Fox, M. D., and B. J. Fox. 1986. The susceptibility of natural communities to invasion. Pages 57–66 *in* R. H. Groves and

J. J. Burdon, editors. Ecology of biological invasions. Cambridge University Press, Cambridge, UK.

Green, R. E. 1997. The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand. Journal of Animal Ecology **66**:25–35.

Heywood, V. H. 1989. Patterns, extents and modes of invasions by terrestrial plants. Pages 31–60 *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions: a global perspective. John Wiley, Chichester, UK.

Hobbs, R. J. 1989. The nature and effects of disturbance relative to invasions. Pages 389–405 *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions: a global perspective. John Wiley, Chichester, UK.

———. 1991. Disturbance a precursor to weed invasion in native vegetation. Plant Protection Quarterly **6**:99–104.

Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology **6**:324–337.

Hobbs, R. J., and H. A. Mooney. 1986. Community changes following shrub invasion of grassland. Oecologia **70**:508–513.

Holdgate, M. W. 1986. Summary and conclusions: characteristics and consequences of biological invasions. Philosophical Transactions of the Royal Society of London **B314**:733–742.

Humphries, S. E., R. H. Groves, and D. S. Mitchell. 1991. Plant invasions of Australian ecosystems: a status review and management directions. Kowari **2**:1–134.

Hussey, B. M. J., D. Anderson, and S. Loney. 1992. A checklist of plants found growing in a native or naturalised state on Culeenup Island, Yunderup, Western Australia. West Australian Naturalist **19**:35–43.

Kruger, F. J., G. J. Breytenbach, I. A. W. Macdonald, and D. M. Richardson. 1989. The characteristics of invaded Mediterranean-climate regions. Pages 389–405 *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions: a global perspective. John Wiley, Chichester, UK.

Law, R., and R. D. Morton. 1996. Permanence and the assembly of ecological communities. Ecology **77**:762–775.

Le Floc'h, E., H. N. Le Houerou, and J. Mathez. 1990. History and patterns of plant invasion in Northern Africa. Pages 105–133 *in* F. Di Castri, A. J. Hansen, and M. Debussche, editors. Biological invasions in Europe and the Mediterranean basin. Kluwer Academic, Dordrecht, The Netherlands.

Lonsdale, W. M. 1994. Inviting trouble: introduced pasture species in Northern Australia. Australian Journal of Ecology **19**:345–354.

Lonsdale, W. M., and A. M. Lane. 1994. Tourist vehicles as vectors of weed seeds in Kakadu National Park, Northern Australia. Biological Conservation **69**:277–283.

Loope, L. L., P. G. Sanchez, P. W. Tarr, W. L. Loope, and R. L. Anderson. 1988. Biological invasions of arid land nature reserves. Biological Conservation **44**:95–118.

Luken, J. O., and J. W. Thieret. 1997. Assessment and management of plant invasions. Springer-Verlag, New York, New York, USA.

Macdonald, I. A. W., and G. Frame. 1988. The invasion of introduced species into nature reserves in tropical savannas and dry woodlands. Biological Conservation **44**:67–93.

Macdonald, I. A. W., D. M. Graber, S. DeBenedetti, R. H. Groves, and E. R. Fuentes. 1988. Introduced species in nature reserves in Mediterranean type climatic regions of the world. Biological Conservation **44**:37–66.

Macdonald, I. A. W., L. L. Loope, M. B. Usher, and O. Hamann. 1989. Wildlife conservation and the invasion of nature reserves by introduced species: a global perspective. Pages 215–255 *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions: a global perspective. John Wiley, Chichester, UK.

Macdonald, I. A. W., F. J. Powrie, and W. R. Siegfried. 1986. The different invasion of southern Africa's biomes and ecosystems by alien plants and animals. Pages 205–225 *in* I. A. W. Macdonald, F. J. Kruger, and A. A. Ferrar, editors. The ecology and management of biological invasions in southern Africa. Oxford University Press, Oxford, UK.

May, R. M. 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton, New Jersey, USA.

Mooney, H. A., S. P. Hamburg, and J. A. Drake. 1986. The invasion of plants and animals into California. Pages 250–272 *in* H. A. Mooney and J. A. Drake, editors. The ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York, New York, USA.

Newsome, A., and I. R. Noble. 1986. Ecological and physiological characters of invading species. Pages 1–20 *in* R. H. Groves and J. J. Burdon, editors. Ecology of biological invasions. Cambridge University Press, Cambridge, UK.

Pickard, J. 1984. Exotic plants on Lord Howe Island: distribution in time and space 1853–1981. Journal of Biogeography **11**:181–208.

Pimm, S. L. 1991. The balance of nature? University of Chicago Press, Chicago, Illinois, USA.

Planty-Tabacchi, A.-M., E. Tabacchi, R. J. Naiman, C. Deferrari, and H. Decamps. 1995. Invasibility of species-rich communities in riparian zones. Conservation Biology **10**:598–607.

Rejmanek, M., C. D. Thomsen, and I. D. Peters. 1991. Invasive vascular plants of California. Pages 81–101 *in* R. H. Groves and F. di Castri, editors. Biogeography of Mediterranean invasions. Cambridge University Press, Cambridge, UK.

Robinson, G. R., J. F. Quinn, and M. L. Stanton. 1995. Invasibility of experimental habitat islands in a California winter annual grassland. Ecology **76**:786–794.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, UK.

Schmitz, D. C., D. Simberloff, R. H. Hofstetter, W. Haller, and D. Sutton. 1997. The ecological impact of nonindigenous plants. Pages 39–61 *in* D. Simberloff, D. C. Schmitz, and T. C. Brown, editors. Strangers in paradise: impact and management of nonindigenous species in Florida. Island Press, Washington, D.C., USA.

Seber, G. A. F. 1977. Linear regression analysis. John Wiley, New York, New York, USA.

Simberloff, D. 1989. Which insect introductions succeed and which fail? Pages 61–75 *in* J. A. Drake, H. A. Mooney, F. Di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions: a global perspective. SCOPE 37. John Wiley, Chichester, UK.

———. 1997. The biology of invasions. Pages 3–17 *in* D. Simberloff, D. C. Schmitz, and T. C. Brown, editors. Strangers in paradise: impact and management of nonindigenous species in Florida. Island Press, Washington, D.C., USA.

Snedecor, G. W., and W. G. Cochran. 1980. Statistical methods. Seventh edition. Iowa State University Press, Ames, Iowa, USA.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. Ecology **78**:81–92.

U.S. Congress OTA (Office of Technology Assessment). 1993. Harmful non-indigenous species in the United States, OTA-F-565. U.S. Government Printing Office, Washington, D.C., USA.

Usher, M. B. 1988. Biological invasions of nature reserves:

a search for generalizations. Biological Conservation **44**: 119–135.

Usher, M. B., F. J. Kruger, I. A. W. Macdonald, L. L. Loope, and R. E. Brockie. 1988. The ecology of biological invasions into nature reserves: an introduction. Biological Conservation **44**:1–8.

Vitousek, P. M. 1988. Diversity and biological invasions of oceanic islands. Pages 181–189 *in* E. O. Wilson and F. M. Peter, editors. Biodiversity. National Academy Press, Washington, D.C., USA.

Vitousek, P. M., L. R. Walker, L. D. Whiteaker, D. Mueller-Dombois, and P. A. Matson. 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. Science **238**:802–804.

Williamson, M. 1989. Mathematical models of invasion. Pages 329–350 *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions: a global perspective. John Wiley, Chichester, UK.

———. 1996. Biological invasions. Chapman and Hall, London, UK.

Williamson, M., and A. Fitter. 1996. The varying success of invaders. Ecology **77**:1661–1665.

Zar, J. H. 1996. Biostatistical analysis. Third edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.