HUMAN IMPACTS, PLANT INVASION, AND IMPERILED PLANT SPECIES IN CALIFORNIA

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Abstract. Invasive species are one of the fastest growing conservation problems. These species homogenize the world's flora and fauna, threaten rare and endemic species, and impose large economic costs. Here, we examine the distribution of 834 of the more than 1000 exotic plant taxa that have become established in California, USA. Total species richness increases with net primary productivity; however, the exotic flora is richest in low-lying coastal sites that harbor large numbers of imperiled species, while native diversity is highest in areas with high mean elevation. Weedy and invasive exotics are more tightly linked to the distribution of imperiled species than the overall pool of exotic species. Structural equation modeling suggests that while human activities, such as urbanization and agriculture, facilitate the initial invasion by exotic plants, exotics spread ahead of the front of human development into areas with high numbers of threatened native plants. The range sizes of exotic taxa are an order of magnitude smaller than for comparable native taxa. The current small range size of exotic species implies that California has a significant "invasion debt" that will be paid as exotic plants expand their range and spread throughout the state.

Key words: California, USA; dispersal; exotic plants; extinction; global biodiversity hotspot; habitat loss; invasive species; rare species; species richness; structural equation models.

INTRODUCTION

A major focus of current research in conservation biology is directed at understanding the patterns and effects of habitat conversion and exotic invasion on native biodiversity. Currently, many continental flora contain >20% exotic species. In the United States, the flora of individual states contain 8–47% exotic species (Rejmanek and Randall 1994, Vitousek et al. 1997, Westbrooks 1998). These invasive species cause billions of dollars of damage to agricultural crops (Westbrooks 1998, Pimentel et al. 2000), alter basic ecosystem processes (Vitousek et al. 1987, Jackson et al. 1988, D'Antonio and Vitousek 1992, Christian and Wilson 1999, Dyer and Rice 1999), and threaten global biodiversity (Mills et al. 1994, Vitousek et al. 1997, Lodge et al. 1998, Stein et al. 2000). The already grave situation may worsen as invasion rates increase in the coming decades (Westbrooks 1998, Levine and D'Antonio 2003). Nevertheless, we still have little ability to make general predictions about landscape- to regional-scale distribution of exotic species and the threat that these invasions pose to native communities.

Predicting invasions is difficult because of the large spatial scale of the problem and the correlated suite of factors that determine the diversity and abundance of invasive species. While exotic invasion can be studied experimentally at the local scale (Love 1944, Robinson 1954, Stachowicz et al. 1999, Levine 2000, Seabloom et al. 2003, Corbin and D'Antonio 2004), regional-scale studies of invasion rely on observational datasets. In these large-scale data sets, invasion rates and human-generated patterns emerge from complex feedback between the environment, spatial distribution of human impacts, and the distribution of native diversity (Dobson et al. 2001, Scott et al. 2001, Seabloom et al. 2002, Williams et al. 2005, Schwartz et al. 2006, Harrison et al. 2006*a*).

For example, the positive correlation between native diversity and exotic invasion among U.S. states has received particular attention (Stohlgren et al. 2003). However, it is unclear whether this positive correlation demonstrates that similar natural factors drive the distribution of native and exotic diversity, because states with high native and exotic diversity also tend to have large human populations (Rejmanek 2003). Furthermore, heavily populated states also tend to be located on coasts, and coastal states and cities are important foci of plant invasions in the United States (Forcella 1985, Mensing and Byrne 1998, Mack and Erneberg 2002,

Mack 2003). Highly invaded coastal states have also been colonized for longer periods of time, and have higher levels of human impact than inland states (Rejmanek and Randall 1994, Seabloom et al. 2002, Rejmanek 2003, Schwartz et al. 2006). Thus, it is difficult to determine whether observed exotic diversity is driven by (1) concordant processes that increase both native and exotic diversity, (2) long-term high levels of propagule pressure in coastal areas, or (3) human activities such as habitat conversion that are most intense in low elevation areas near the coast.

Here we use a comprehensive, floristic survey of California, USA to explore the large-scale interrelationships among environmental factors, human conversion of habitat, and the number of native, exotic, and imperiled species. California is of particular interest because it is a global biodiversity hotspot and contains 20% of all vascular plant species in the United States and 4% of the worldwide pool of species (Stein et al. 2000). The diverse California flora has been invaded by more than 1000 species of exotic plants (Rejmanek and Randall 1994, Rejmanek 2003, Stohlgren et al. 2003). Fourteen vascular plant species have gone extinct and 709 are listed or are proposed for listing by state or federal agencies as being at risk of extinction. The Nature Conservancy lists 1679 species as being at risk of extinction (Stein et al. 2000).

The floristic data used here have several advantages for resolving underlying relationships between human impact, invasion, and the number of imperiled species. The database lists of native, exotic, and imperiled species in 234 contiguous regions are unique in their spatial scope, resolution, and richness (Williams et al. 2005, Viers et al. 2006). We have supplemented these detailed distributional data with spatial data on potential environmental correlates of diversity and invasion (e.g., productivity and climate) and measures of human impact (population density and cover of urban and agricultural land uses). Furthermore, in California, there is no underlying relationship between distance to the coast (where propagule pressure is presumably highest) and native diversity, as is the case nationally (Seabloom et al. 2002, Rejmanek 2003, Dark 2004). This covariance structure allows us to isolate the effects of human impact, environmental constraints, and native diversity on invasion.

We first consider a null model in which native and exotic species are functionally identical species and are at equilibrium with the environment. We then determine the degree to which the observed pattern deviates from the null prediction and identify factors acting on the introduction, establishment, and spread of exotic species that may cause their distribution to deviate from the null prediction. Finally, we examine the relationships among human impact, invasion, and the number of imperiled plant species.

Null model: overall correlation between native and exotic species

We first consider the simple case in which native and exotic species are functionally similar and exotics are not limited by dispersal or competitive exclusion by established species. In this case, diversity of natives and exotics should be driven by the same processes and should be highly positively correlated at large spatial scales (Stohlgren et al. 2003, Fridley et al. 2004).

Environmental constraints on the distribution of exotic species

Positive correlations between native and exotic species can arise from common responses to environmental gradients, such as fertility or disturbance. If common responses to environmental gradients are the primary driver of the relationship between native and exotic richness, we would expect there to be little correlation among the residuals of environmental models fit separately to native and exotic richness.

Functional and phylogenetic constraints on the distribution of exotic species

Functional or phylogenetic lineage differences between the native and exotic species pools may cause species to respond differently to natural or anthropogenic environmental gradients (e.g., productivity or human disturbance). For example, if the exotic species pool is biased toward annual species, we might expect exotic species richness to be higher in disturbed areas while perennial or woody species may achieve higher diversity in stable habitats. Similarly, certain taxonomic families may be overrepresented in the exotic species pool, and these taxa may differ in their distributions (e.g., the distribution of Fabaceae relative to soil nitrogen). As a result, biases in the representation of functional or phylogenetic groups may cause the correlation between native and exotic diversity to be lower than expected under the null model. If the effects of functional or phylogenetic differences between native and exotic species strongly alter the distribution of exotic species, we expect the correlation between native and exotic diversity to be higher within groups of functionally or phylogenetically related lineages, than in the overall species pool.

Dispersal constraints on the distribution of exotic species

There is often a lag between the time of introduction and the spread of introduced species (Sakai et at. 2001), such that the current distribution of exotic species reflects the spatial location of introduction sources rather than environmental tolerances (e.g., coastal areas or transportation corridors; Forcella 1985, Rejmanek and Randall 1994, Mensing and Byrne 1998, Gelbard and Harrison 2003, Mack 2003). This lag may arise from either ecological (e.g., the initial phase of exponential growth) or evolutionary (e.g., adapting to a new habitat) processes (Forcella 1985, Mack 1985, Sakai et al. 2001).

If the current distribution of exotic species is strongly affected by time lags, we would predict that (1) exotic species should have higher diversity in areas that have high levels of introductions (e.g., coastal port areas or areas with high levels of human impact), (2) mean range size of exotics should be smaller than for functionally similar native species (e.g., native and exotic annuals), and (3) the distribution and range size of fast-dispersing native and exotic species (i.e., those with a shorter generation time, such as annuals) should be more similar than for species that disperse more slowly (i.e., those with long generation times, such as trees; Ellstrand and Scheirenbeck 2000).

Linkages between the distribution of exotic and imperiled species

Even if exotic species are distributed widely, they may not have a strong impact on the native biota (Sax et al. 2002, Davis 2003, Harrison et al. 2006a). At the spatial scale of this study, we do not have direct measures of exotic species' impact, such as changes in relative abundance of native species. However, we can look for associations between the number of exotic species and the number of imperiled species. Given the expectation of a positive correlation in diversity of all groups of species (Stohlgren et al. 2003, Fridley et al. 2004), this test must show the presence of more imperiled species in heavily invaded areas after accounting for the effects of native diversity and the direct effects of human activity. While this result would not demonstrate a causal relationship between exotic invasion and extinction risk, it would demonstrate that similar processes increase invasion and extinction risk and that imperiled species are faced with higher-than-average numbers of exotic species. Diverse assemblages of exotic species have been shown to increase the local abundance and impact of exotic species (Smith and Knapp 2001).

Materials and Methods

We combined two publicly available data sets for this analysis. The first data sets are the lists of vascular plant taxa (species and recognized varieties) in each of 93 regions in California, USA, (CALFLORA; *available online*)[8] as originally compiled by Richerson and Lum (1980), and more recently analyzed by Seabloom et al. (2002). The species lists include extirpated species, so our analyses are not biased by recent, human-induced extinctions. These regions are loosely based on counties that are subdivided at biologically meaningful boundaries (e.g., the crest of the Sierra Nevada Mountains). The second data source is the Jepson Herbaria at the University of California–Berkeley (*available online*).[9] It lists species' occurrences within the floristic provinces as described in Hickman (1993). We intersected these two data sets to construct a new data set that listed species occurrences in 234 regions (area = 1754 ± 1859 km^2; mean ± SD); this beta version database is described in Harrison et al. (2000), was analyzed in Williams et al. (2005), and received a full treatment in Viers et al. (2006). Due to unresolved taxonomic questions, the distributional data include 5930 of the original 7598 taxa (species and recognized varieties, hereafter referred to as species) listed in the more complete CALFLORA data set. We reran analyses using the full set of species at the coarser scale (93 regions) and found no qualitative effects of the missing species on the results discussed here; neither were there detectable biases when considering patterns of regional endemicity (Harrison et al. 2000).

CALFLORA provides basic taxonomic and life-history information for each species. In this study we consider (1) whether the species is native or exotic, (2) the life-form (annual, herbaceous perennial, shrub, or tree), (3) whether the species has state or federal listing as a noxious weed or is listed by the California Exotic Pest Plant Council as an invasive and damaging wildland weed, and (4) whether the species has state or federal listing as being at risk of extinction. It is important to note that while it is difficult to accurately assess extinction risk, plant species are typically not listed as being at risk of extinction until they are restricted to fewer than five locations or fewer than 100 individuals (Wilcove et al. 1993, Schemske et al. 1994). For this reason, we consider the species that meet our criteria of imperiled plant species to be at severe risk of extinction. By comparison, The Nature Conservancy lists more than twice as many species as being at risk of extinction (1679 species) than meet our criteria (709 species) (Stein et al. 2000, Seabloom et al. 2002).

We compiled a complementary data set containing biophysical data for each of the regions including elevation, distance to coast, net primary production (NPP), total annual precipitation, growing-degree-days (0°C baseline), and soil organic C (Seabloom et al. 2002, Williams et al. 2005). We also compiled data on the intensity of human impact. In this study, we analyzed the proportion of a region dedicated to agricultural or urban land use. The agricultural land use category included pasture, hayfields, row and field crops, orchards, and vineyards (see Davis et al. 1995; metadata *available online*).[10] Seabloom et al. (2002) and Williams et al. (2005) provide more detail on the biophysical and human-impact data. NPP values are annual values estimated by the GLO-PEM terrestrial ecosystem model (Goetz et al. 2000) averaged across all years (1982–1999). Growing-degree-days and total annual precipitation data represent 30-year means (1961–1990) from the National Center for Environmental Prediction Reanalysis Project (NCEP) reanalysis data set (Kistler et al.

[8] ⟨http://www.calflora.org⟩
[9] ⟨http://ucjeps.berkeley.edu⟩

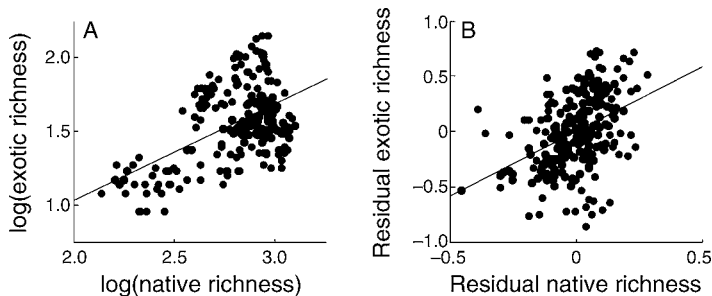[10] ⟨http://www.biogeog.ucsb.edu/projects/gap/data/cnddb/11100.html⟩

FIG. 1. Correlation between exotic and native vascular plant richness in 234 contiguous regions in California, USA, in (A) log plots and (B) residual plots. Diverse native communities have more exotic species ($r = 0.501$, $P < 0.001$), even after controlling for area, environmental factors (annual precipitation, net primary productivity, soil organic carbon, growing degree days, elevation, and distance to coast), environmental heterogeneity (elevation standard deviation), and human impact (percentage cover of urban and agricultural land use) ($r = 0.443$, $P < 0.001$).

2001), resampled to the GLO-PEM 64-km^2 grid with grid points 8 km apart (Bartlein, *personal communication*). NPP and climatic values for each region represent the mean of constituent grid points. Soil organic C is derived from the Shirazi et al. (2001) data set.

All statistical analyses were conducted in SAS version 8.1 (SAS Institute, Cary, North Carolina, USA), except the randomization test that was performed in Matlab version 6.5 (MathWorks, Natick, Massachusetts, USA). Structural equation models were developed using the CALIS procedure in SAS and compared following Li (1975) and McCune and Grace (2002).

RESULTS

Null model: overall correlation between native and exotic species

We found a positive correlation between native and exotic richness in California ($r = 0.501$; Fig. 1A, Table 1). We tested whether this correlation was different from the predictions of the null model of no difference between native and exotic species using a permutation test, in which we randomly reassigned species to the categories of native or exotic species and recalculated the correlation between native and exotic richness. In this way, we maintained the total number of native and exotic species and the distribution of range sizes in the

original data. We repeated this randomization 1000 times and found that the observed correlation between native and exotic richness ($r = 0.501$; Table 1) was significantly lower than the mean correlation ($r = 0.98$) calculated under the assumption of no difference between the native and exotic species ($P < 0.001$).

Environmental constraints on the distribution of exotic species

The differences in the distribution of native and exotic richness are due in part to differences in how native and exotic species respond to environmental and human impact gradients (Fig. 2).

We used Canonical Correlation Analysis to display the multivariate relationships between the number of native, exotic, weedy exotic, and imperiled species, as well as various explanatory factors including area, net primary productivity, annual precipitation, soil organic carbon, elevation, elevation standard deviation, distance to coast, and percentage cover of agriculture and urban land. The correlations between the first richness and environmental axes ($r^2 = 0.748$) and second richness and environmental axes ($r^2 = 0.724$) were significantly greater than zero ($P < 0.001$).

Native richness is highest in cool areas with high rainfall and, to a lesser extent, high productivity. Exotic diversity also increased with productivity but was also

TABLE 1. Distribution of California vascular plant species and the correlation of native and exotic vascular plant richness for five life-forms of increasing generation time: annuals, herbaceous perennials, shrubs and vines, and trees.

Variable	Native	Exotic	Imperiled	Native vs. exotic correlation	P
Percentage annuals	31.3	48.8	36.5	0.710	<0.001
Percentage perennials	52.4	36.0	48.7	0.611	<0.001
Percentage shrubs	13.0	7.6	13.7	0.165	0.012
Percentage trees	3.0	6.1	1.1	−0.087	0.189
Percentage vines	0.3	1.5	0.0		
Total taxa	6774	824	271	0.501	0.001

Notes: Richness is calculated in 234 contiguous regions. Correlations were calculated for log$_{10}$-transformed richness. Vines are included with shrubs when calculating correlations due to the low number of species in each region. All groups differ based on a χ^2 test ($P < 0.0001$), such that exotics have more annual species than do the native or imperiled species.
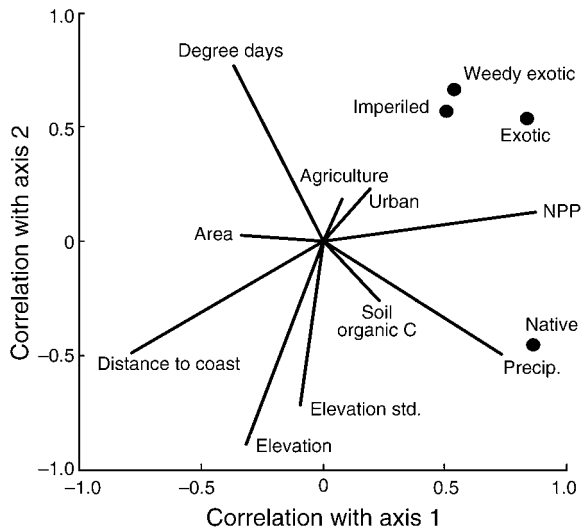
FIG. 2. Canonical correlation between richness of four groups of vascular plants (native species, native species with state or federal listing as being at risk of extinction, exotic species, exotic species with state or federal noxious weed status) in 234 contiguous regions in California, USA. There was a strong correlation between the first canonical richness and biophysical axes ($r^2 = 0.748$, $P < 0.0001$) as well as the second canonical richness and biophysical axes ($r^2 = 0.724$, $P < 0.0001$).

high in low-lying coastal areas with high levels of human impact (Figs. 2 and 3). The distribution of native species and weedy exotics (those species with state or federal listing as noxious weeds or listed as wildland weeds) is more different than between natives and the overall pool of exotic species. The richness of weedy exotic species is remarkably similar to the distribution of imperiled species. Both weedy and imperiled species richness are highest in low-lying coastal areas with high levels of human activity and are uncorrelated with productivity and precipitation (Fig. 2). We have included agricultural and wildland weeds in our analyses (see *Methods*). There are eight species, less than 1% of the total, that are strictly agricultural weeds, species that are listed by state or federal agricultural agencies and not by the California Exotic Pest Plant Council. Inclusion of agricultural weed status does not impact the overall species lists to any significant extent.

The observed positive relationship between native and exotic richness cannot be entirely explained by similar responses to environmental factors. We fit separate linear regression models of native, exotic, and imperiled richness using all human impact and biophysical variables (annual precipitation, net primary productivity, soil organic carbon, growing-degree-days, elevation and distance to coast, environmental heterogeneity, elevation standard deviation, percentage of urban land cover, and percentage of agricultural land cover). The residual native and exotic richness values from these linear regressions are still significantly correlated (Figs. 1B and 2). Thus, areas that have higher native diversity

than predicted by the environmental regression model also have higher-than-expected numbers of exotic species. Potential sources for this residual correlation are nonlinear relationships or latent variables (e.g., road density) not included in the regression model.

Functional and phylogenetic constraints on the distribution of exotic species

The lower-than-expected correlation between native and exotic diversity (based on the permutation test) may stem from underlying functional or phylogenetic differences between the pool of exotic species that have been introduced to California and the resident pool of native species. The exotic species pool is rich in annuals (Table 1); nearly half of the exotic species are annuals, whereas only ~30% of the native species are annual. Controlling for these differences did not uniformly increase the correlation between native and exotic diversity. The within-group correlation of native and exotic herbaceous species (annuals and perennials) is higher than the overall correlation, while the within-group correlation of native and exotic woody species (shrubs and trees) is dramatically lower than the overall correlation (Table 1).

There are also distinct differences in the phylogenetic lineages of the native and exotic species. Of the 170 vascular plant families currently in California, 10% have no native taxa, 45% have no exotic taxa, and 45% have native and exotic taxa. However, within-family correlations between native and exotic richness generally are no stronger than the overall correlations (Table 2), indicating that phylogenetic lineage differences per se are not primarily responsible for the low overall correlation between native and exotic richness.

There is a strong correlation between the number of native and exotic taxa in the 76 families that have both native and exotic taxa ($r = 0.799$, $P < 0.0001$), such that families that are species-rich in natives are also species-rich in exotic species. There are phylogenetic groups in which the native : exotic ratio is strongly biased (Fig. 4). For example, 21.1% of exotics are monocots while only 13.9% of natives are monocots ($P < 0.0001$, based on a χ^2 test). This pattern is driven by the high diversity of exotic grasses; 15.6% of the exotic taxa are grasses, while only 4.5% of the native taxa are grasses ($P < 0.0001$, based on χ^2 test) (Fig. 4). Taxonomic groups over-represented in the exotic flora also have a higher percentage of annual species. For example, 46.6% of the exotic monocots are annual while only 10.4% of the native monocots are annual ($P < 0.0001$, based on χ^2 test). Similarly, 56.9% of the exotic grasses are annual while only 21.1% of the native grasses are annual ($P < 0.0001$, based on χ^2 test).

Dispersal constraints on the distribution of exotic species

It is possible that the current distribution of exotic species may be more constrained by dispersal than the distribution of suitable habitat. We examine three lines
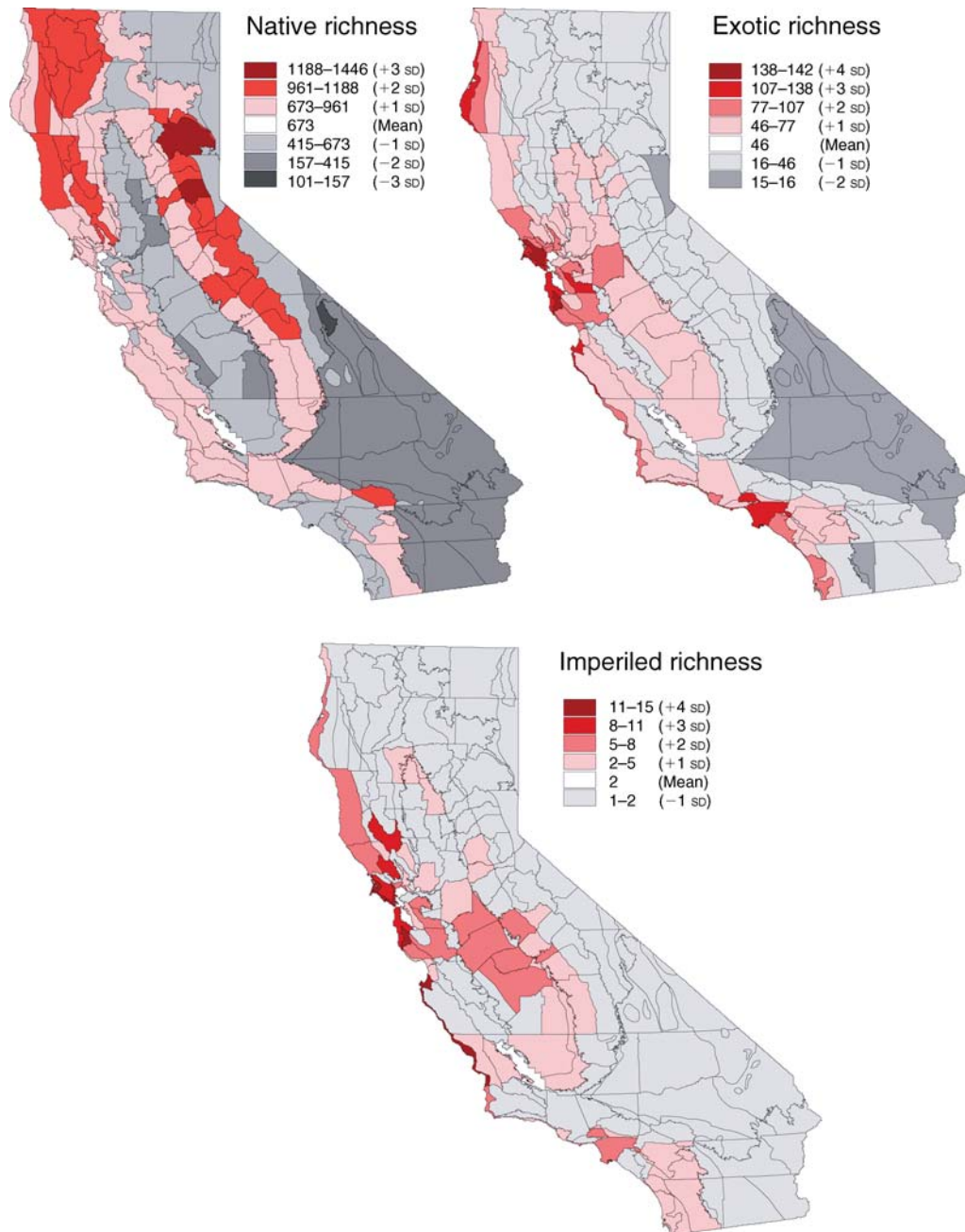
FIG. 3. Diversity of native, exotic, and imperiled species in 234 contiguous regions in California, USA. Imperiled species are defined as native species with state or federal listing as imperiled. Color shading categories are divided into standard-deviation units (e.g., light gray areas are less than 1 SD below the mean, and light pink areas are less than 1 SD above the mean).

of evidence to assess the importance of dispersal limitation. First, dispersal limitation is suggested by the higher density of exotic species in coastal areas (Figs. 2 and 3), areas that presumably have higher rates of introduction of exotic propagules than do remote inland areas. Alternately, exotic species may be constrained to coastal areas for other reasons (e.g., lower climatic variability and seasonal extremes). Second, if the distribution of exotics is limited by their ability to

disperse, the mean range size of an exotic species should be less than that of a functionally similar native. We found that the modal range size of exotic species was 10 times smaller than functionally similar native species (Fig. 5). Third, dispersal limitation should be more severe for longer-lived taxa, which is consistent with our finding that the correlation between native and exotic diversity decreased with plant generation time from annuals ($r = 0.71$) to herbaceous perennials ($r = 0.59$) to

TABLE 2. Correlation of native and exotic richness within the six most speciose vascular plant families in California.

Family	Native richness	Exotic richness	Native vs. exotic		Species richness		Native vs. exotic	
			r	P	Native	Exotic	r	P
Asteraceae	1017	121	0.126	0.227	1017	121	0.126	0.227
Brassicaceae	328	49	0.143	0.170	328	49	0.143	0.170
Fabaceae	472	72	0.513	<0.001	472	72	0.513	<0.001
Poaceae	312	130	0.210	0.042	312	130	0.210	0.042
Polygonaceae	334	22	−0.360	<0.001	334	22	−0.360	<0.001
Scrophulariaceae	387	31	0.326	0.001	387	31	0.326	0.001

Note: Richness is calculated in 234 contiguous regions.

shrubs ($r = 0.15$) to trees ($r = -0.06$). In contrast to our predictions, exotic and native annuals did not have more similar range sizes than longer-lived taxa. Thus, although all exotic species have much smaller ranges than native species, native and exotic species with high dispersal rates (i.e., short generation times) are much more similar in their distribution within their ranges than slow-dispersing species (i.e., those with long generation times).

Distribution of exotic and imperiled species

There is a positive correlation between the number of exotic and imperiled species, and this relationship is strongest for weedy exotic species that are most likely to pose a threat to rare natives (Figs. 2 and 6; Table 1). This positive correlation is potentially confounded by the positive correlation between habitat loss and the number of exotic and imperiled species (Fig. 2). However, the strong positive correlation between the number of exotic and imperiled species persisted even after controlling for the effects of human impact and environmental gradients (Fig. 6) and background patterns of native diversity (Fig. 7). Thus, the relationship between invasibility and extinction risk is distinctive from, and stronger than, the positive correlation between native and exotic diversity.
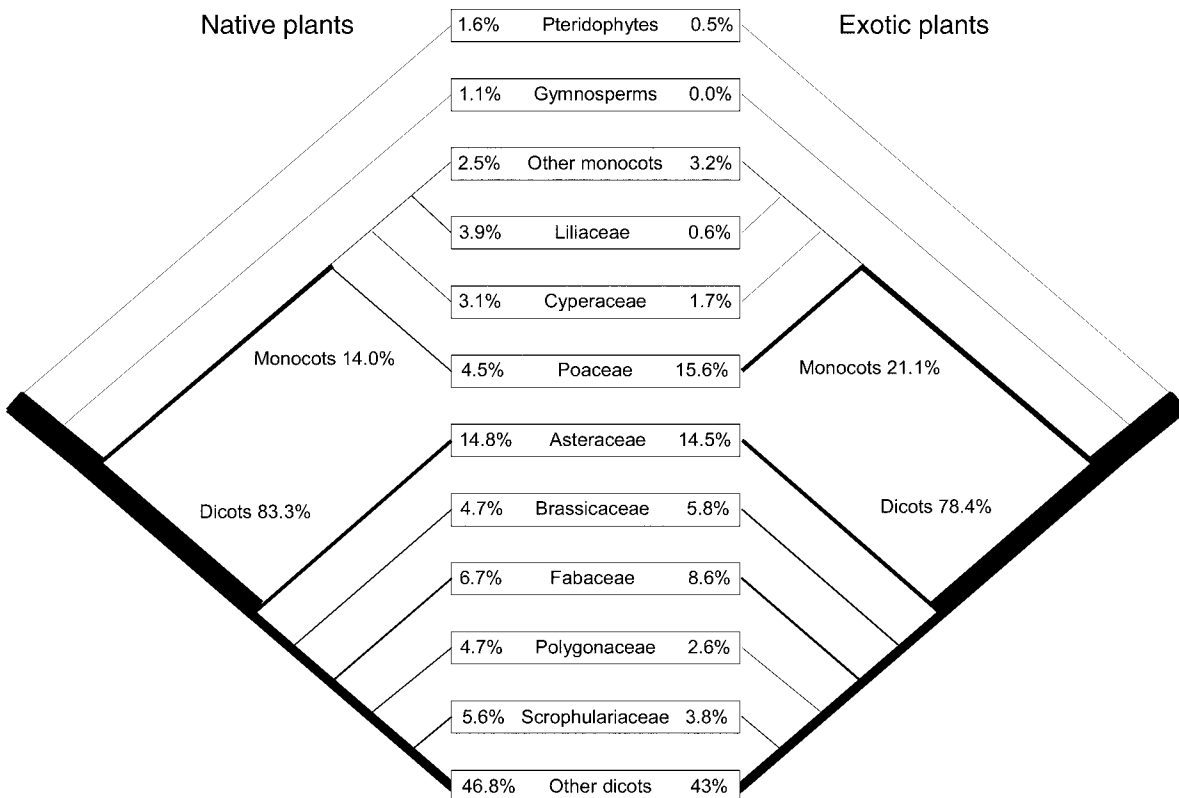

FIG. 4. Comparison of the phylogenetic structure of the native and exotic pool of species in California, USA. Species-level diversity is shown for the eight most species-rich angiosperm families. The weighting of the branches represents the percentage of species in each group within the native and exotic species pool. The exotic species pool is dominated by annual grasses and other monocots.
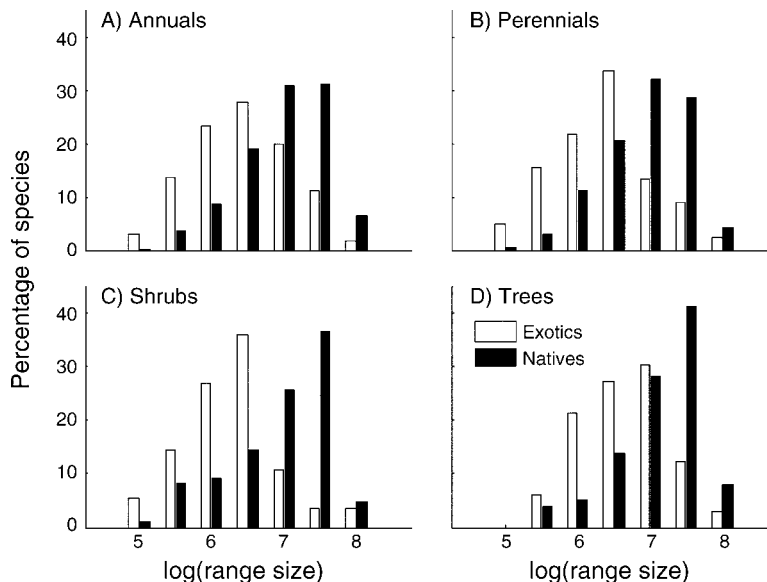
FIG. 5. Log-transformed range size (originally measured in hectares) of native and exotic vascular plants in California, USA, for groups of species with increasingly long generation times (A–D; annuals < herbaceous perennials < shrubs < trees). Exotic species have smaller ranges than native species of similar generation times. The number of taxa in each category are as follows: annuals (1519 native and 343 exotic), perennials (2506 native and 258 exotic), shrubs (525 native and 59 exotic), and trees (162 native and 38 exotic).

Synthesis of diversity, invasion, and human impact

We used structural equation modeling (SEM) to examine the complex interplay existing among the environmental factors, human impact, native diversity, invasion, and extinction risk. Due to the strong correlation between productivity and precipitation ($r = 0.65$), models with both productivity and annual precipitation are difficult to fit, but give similar results. Here we present the model that has productivity as the only bio-environmental variable: it incorporates a range of abiotic factors that are critical to plant growth (e.g., precipitation, temperature, and soil fertility). Note that this analysis does not test for nonlinear relationships among the variables.

Environmental factors strongly impact rates of habitat conversion (percentage cover of urban or agricultural land use). More land has been converted in low-lying, productive, coastal areas. Invasion (exotic richness) was strongly related to the environment, native diversity, and intensity of human impact (habitat conversion). The effects of species–area relationships were addressed using two alternate methods: (1) the inclusion of "area" as a descriptive variable and (2) converting "species richness" to "species density" (species per square kilometer). There were no qualitative differences between either of these approaches or the SEM model without any explicit treatment of area. Here we present the models of species richness because these models provided a better fit to the observed covariance matrix than the species density models (Fig. 7). Area was not a significant factor in any of the models and is not discussed further.
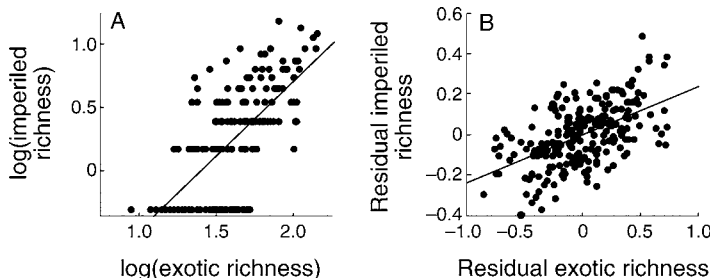

FIG. 6. Correlation between imperiled (those species with state or federal listing as being at risk of extinction) and exotic vascular plant richness in 234 contiguous regions in California, USA, in (A) log plots and (B) residual plots. Highly invaded communities have more imperiled species ($r = 0.739$, $P < 0.001$), even after controlling for gradients of environmental factors (annual precipitation, net primary productivity, soil organic carbon, growing degree days, elevation, and distance to coast) and human impact (percentage cover of urban and agricultural land use) ($r = 0.501$, $P < 0.001$).
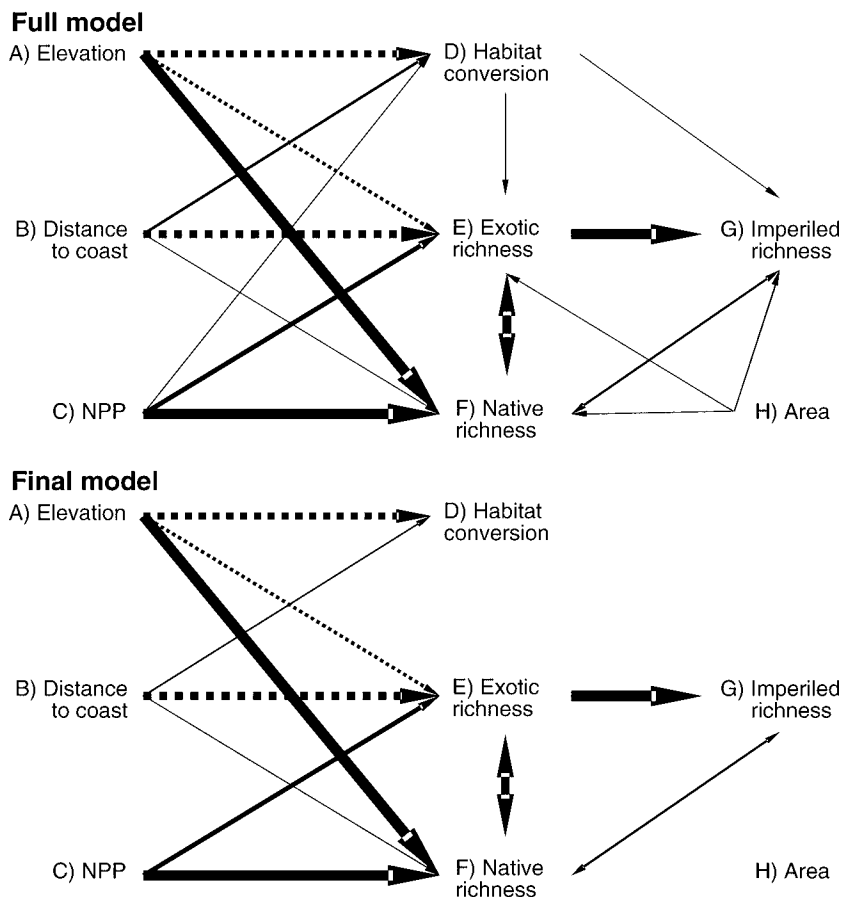
Full model

Final model

Fig. 7. Structural equation modeling of factors controlling the richness of imperiled (rare) species in California, USA. Line thickness represents the strength of the partial correlation between each factor (standardized path coefficient). Positive relationships are shown as solid arrows, and negative relationships are shown as dashed arrows. The final model contains only links that cannot be removed without lowering the overall model fit relative to the full model. Environmental factors have strong impacts on native and exotic richness of vascular plants in California, and richness of imperiled species is primarily a function of the diversity of exotics, rather than conversion of native habitat to agricultural or urban land use.

The significance of connections within the overall model (Fig. 7, top) can be tested by determining whether there is a significant increase in the χ^2 value as a result of removing specific links in the model. The direct link between habitat conversion and exotic richness (D→E) can be removed without significantly lowering the predictive power of the model ($P = 0.519$). The direct links between imperiled richness and habitat conversion (D→G, $p = 0.827$) can also be removed without reducing the model fit. However, removing the link between exotic richness and imperiled richness (E→G) dramatically lowers the model fit ($P < 0.001$). The fit of the final model does not differ from the full model ($P = 0.295$). The covariance structure predicted by the final model (Fig. 7, bottom) does not differ from the true covariance structure of the original data ($P = 0.073$), and accounts for a large portion of the variance in native richness ($r^2 = 0.64$), exotic richness ($r^2 = 0.76$), and imperiled species richness ($r^2 = 0.44$).

In our final model, exotic richness is a function of productivity and covaries with native richness; the number of imperiled species is most strongly correlated solely with the number of exotic species. This strongly implies that exotic species are able to spread into areas with low human impact and large numbers of imperiled species. The correlative nature of the data does not allow us to determine whether the large number of invasive species in some areas has caused more species to become imperiled, but it is clear that hotspots of threatened species are exposed to an inordinately high number of exotic species. We stress that there is a positive correlation between habitat conversion and the number of imperiled species, as shown by the canonical correlation analysis (Fig. 2) and the full structural equation model (Fig. 7, top). However, this direct correlation between habit conversion and imperiled species is much weaker than the direct correlation between exotic and imperiled species, and so is not

present in the more parsimonious structural equation model (Fig. 7, bottom).

Discussion

In our analyses, we examine the distribution of more than 800 exotic plant taxa currently established in California, USA. These species are phylogenetically and functionally distinct from the native flora. Annual species and grasses are overrepresented in the exotic species pool. While our analyses do not address the interesting question of why certain groups of taxa are overrepresented in the exotic flora, grasses have been shown to be overrepresented as agricultural weeds and natural-area invaders worldwide (Daehler 1998). The distribution of these exotic species suggests that their current ranges may represent a small fraction of their potential distributions; exotic species ranges are ~10 times smaller than functionally similar native species. It is unlikely that the current restricted distribution of exotic plants represents an equilibrial state in which exotic species are dependent on continued human activity. Exotic diversity is only loosely correlated with human activity. Rather, these data suggest that exotic species are spreading into the landscape ahead of the wave of human habitat conversion, as has been seen to be the historical pattern in California. For example, *Erodium cicutarium* spread throughout California grassland habitats in advance of the extensive grazing of Spanish livestock in the 18th century (Mensing and Byrne 1998).

Although hotspots of exotic invasion are often located in coastal areas or transportation corridors that have high levels of propagule introduction (Rejmanek and Randall 1994, Mack and Erneberg 2002, Gelbard and Harrison 2003, Levine and D'Antonio 2003, Mack 2003), many undeveloped areas of high native diversity have also been highly invaded by exotic species, as illustrated by the positive correlation between native and exotic diversity and the mapped patterns in Fig. 3. Furthermore, the correlation between native and exotic diversity is highest for species with short generation times, those that would be expected to spread most rapidly through the landscape. However, native and exotic annuals did not have more similar range sizes than native and exotic trees, contrary to our expectations. Thus, although exotic species generally have much smaller range sizes than native species, similar processes govern the distribution of native and exotic species with short generation times (and associated higher dispersal rates), leading to a strong positive correlation between the diversity of native and exotic annual plants. In contrast, the diversity of long-lived native and exotic trees and shrubs appears to be governed by distinct processes, resulting in low correlation between native and exotic diversity.

Other studies have found that herbaceous exotic species equilibrate more rapidly with the environment than longer-lived species (Forcella 1985, Forcella and Harvey 1988, Ellstrand and Schierenbeck 2000). For example, in an examination based on herbaria records of 40 exotic species in the northwestern United States, Forcella (1985) found that annual species had faster rates of spread than did perennial species and that the primary pattern of weed spread was from coastal to inland areas. Similarly, the spread of two species of invasive, exotic grasses (*Cortaderia selloana* and *C. jubata*) through California originated from introduction points in coastal cities and spread into more undisturbed habitat (Lambrinos 2001). These patterns are in accordance with our inference that annual species are less limited by dispersal in California than are longer-lived species, and that high diversity of exotics in coastal California may reflect the higher introduction rates in coastal ports.

There are exceptions to these general observations, however. Ultramafic substrates in California are particularly notable due to their relatively high levels of endemic plants adapted to their nutrient-poor soils. It has been observed that both natural (e.g., fire) and anthropogenic disturbance (e.g., roads, grazing, etc.) have little effect on the composition and richness of serpentine endemic plant species (Harrison et al. 2006*b*). Furthermore, Harrison et al. (2006*a*) suggest that there are a host of direct and indirect relationships among native, endemic, and rare plant species affected by exotics when examined at multiple scales, but they conclude that native herbs on serpentine plant species do not show a detectable direct impact from exotic cover, in part due to inhospitable edaphic conditions. That being said, the restricted set of considered species (i.e., those found on ultramafic substrates) and strong statewide geographic patterns of serpentine show only one facet of the flora examined in the current analyses.

If exotic species are not at equilibrium, we are faced with an "invasion debt," such that exotic plant ranges and impact will continue to expand even in the absence of continued introductions. Ultimately, the ranges of exotic species may closely mirror those of functionally similar native species: a 10-fold increase. The presence of an invasion debt raises this question: how long will it take for species to expand throughout a new habitat? In California, well-established exotic species continue to spread for many years (Rejmanek and Randall 1994). For example, *Cortaderia* continued to spread for at least 100 years (Lambrinos 2001). Similarly, the 40 species of exotic plants studied by Forcella (1985) required an average of 37 ± 12 years to spread across 50% of their eventual range (Forcella 1985). A study of six invasive wetland plants in Quebec, Canada found similar variability in dispersal rates; some species could reach their maximum range in a few decades, while others have continued to expand for over 120 years (Delisle et al. 2003). In their review, Ellstrand and Shierenbeck (2000) found that lag times for herbaceous species were on the order of decades while most trees and shrubs required at least 150 years before they began to invade.

An examination of plant community responses to abrupt paleo-environmental changes can provide further insight into plant dispersal abilities. Davis and Shaw (2001) found that trees disperse through the landscape at rates of 20–40 km per century (rare cases reach 100–150 km per century) in response to climate change. Similarly, Williams et al. (2002) found that local plant communities require 100–200 years to adjust to abrupt climatic shifts.

Thus, although it is unlikely that we will experience the full impact of the current suite of exotic species for decades to centuries, we may well face an exponential expansion phase over the next several decades and associated increases in economic and ecological costs. In addition to the impact of the spread of the current suite of exotic plants in California, introductions probably will continue to increase over time. The United States currently has only ~30% of the 6741 recognized weed species worldwide (Westbrooks 1998). Given the continuing potential for intentional and unintentional introductions through trade (Mack and Erneberg 2002, Levine and D'Antonio 2003, Mack 2003), many of these species are likely to become established. Clearly, there is great potential for further introductions and associated impact.

What will be the impact of a dramatic increase in the number of exotic species? In 1994 alone, the economic impact of exotic weeds in the United States was a loss estimated at $13 billion, and the 12 most severe weed species caused $97 billion in economic losses from 1906 to 1991 (Westbrooks 1998). Invasions may also cause extinctions in the native flora. About 57% of the imperiled species in the United States are currently threatened by exotic species (Stein et al. 2000). We found a strong positive correlation between exotic richness and the number of imperiled species in California. Weedy and invasive exotics were even more tightly linked to the distribution of imperiled species than were exotics as a whole (Fig. 2), and these species are likely to pose the largest risk for imperiled native taxa. Furthermore, as Schwartz et al. (2006) point out, there is a strong negative correlation between public land area and human population density, thus limiting our capacity to protect imperiled native taxa.

We stress the correlative nature of our results linking exotic invasions to extinction risk. We cannot definitively establish a causal relationship between extinction risk and invasion. Areas with large numbers of exotic species also have higher-than-average numbers of imperiled species. Experimental data suggest that diverse pools of exotic species will be more effective at invading native communities (Smith and Knapp 2001). While it is a subject of current debate whether direct competition from exotic species is a significant threat to native biota (Davis 2003), exotic invasions can reduce native species abundance, alter disturbance regimes, and lead to increased pathogen loads for native species. Any of these factors can increase the extinction risk of already

imperiled species, especially given that these species are often present in small, restricted populations that can be driven extinct by demographic or environmental stochasticity (Lande 1993, Wilcove et al. 1993, Mills and Smouse 1994, Schemske et al. 1994).

We have emphasized the impact of exotic species on native communities. However, there is a positive correlation between habitat conversion and the number of imperiled species (Figs. 2 and 7). The weakness of this correlation, relative to the direct correlation between the number of exotic and imperiled species, should not be interpreted as evidence that habitat conversion is unimportant. Human development in California is highest in low-lying areas near the coast, whereas native plant diversity in California increases with mean elevation (Richerson and Lum 1980, Dark 2004). As a result, the most species-rich habitats currently have fairly low rates of habitat conversion. The nonrandom nature of human impact in California has probably eased the impact of human habitat conversion on the native flora. In areas where species richness declines with mean elevation, we would expect the most species-rich areas to have the highest human impact (a positive correlation between human impact and species richness). Modeling work suggests that correlations between habitat conversion rates and species diversity only have short-term effects on species extinction rates (Seabloom et al. 2002). Furthermore, the coarse scale of our data also precludes detecting local extinctions that occur within individual regions.

Globally, conversion of natural habitat by human activity has led to numerous species extinctions (Terborgh 1992, Pimm and Askins 1995, Sinclair et al. 1995, Vitousek et al. 1997). In the United States, habitat conversion threatens 87% of all imperiled species (Stein et al. 2000). Furthermore, Marchetti et al. (2004) document that in California, the proportion of a watershed impacted by humans is a significant factor in promoting both the invasion of exotic fish and the extinction of native fish. Habitat loss is particularly important in the tropics, where rates of conversion are increasing, and in low-lying habitats that tend to be underrepresented in protected areas (Sinclair et al. 1995, Scott et al. 2001).

Invasions by exotic species are one of the most severe threats to global biodiversity, and we are becoming increasingly aware of their large impacts on the world's economy. Despite their importance, we still have little ability to make general predictions about the forces that constrain exotic invasion and the potential impact on native communities. Our analysis of the distribution of exotic and imperiled plant species in California suggests that the current distribution of exotic species represents a nonequilibrial state in which the areas of high exotic diversity represent core areas of introductions from which exotic species are spreading through the landscape. In the absence of future introductions, we could still expect a 10-fold increase in cover of exotic plants in

California as these species come into equilibrium with the environment and their range size distribution converges on that of the native community. The species that have the greatest long-term potential for spread are exotic shrubs and trees, species that have a particularly strong impact on the structure and function of ecosystems. The strong correlation between exotic diversity and the number of imperiled taxa suggests that this invasion could result in a dramatic rise in the number of native species threatened with extinction.

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