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LETTER

Anthropogenic impacts upon plant species richness and net primary productivity in California

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Abstract

We assess the importance of anthropogenic land-use, altered productivity, and species invasions for observed productivity–richness relationships in California. To this end, we model net primary productivity (NPP) *c.* 1750 AD and at present (1982–1999) and map native and exotic vascular plant richness for 230 subecoregions. NPP has increased up to 105% in semi-arid areas and decreased up to 48% in coastal urbanized areas. Exotic invasions have increased local species diversity up to 15%. Human activities have reinforced historical gradients in species richness but reduced the spatial heterogeneity of NPP. Structural equation modelling suggests that, prior to European settlement, NPP and richness were primarily controlled by precipitation and other abiotic variables, with NPP mediating richness. Abiotic variables remain the strongest predictors of present NPP and richness, but intermodel comparisons indicate a significant anthropogenic impact upon statewide distributions of NPP and richness. Exotic and native species each positively correlate to NPP after controlling for other variables, which may help explain recent reports of positively associated native and exotic richness.

Keywords

California, human impacts, land cover change, net primary productivity, species richness, structural equation models.

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INTRODUCTION

Human endeavours have had strong impacts on global biodiversity through the intentional and unintentional introduction of species and species extinctions (Vitousek *et al.* 1997; Mack & Erneberg 2002; Sax *et al.* 2002). Similarly, humans have altered ecosystem productivity worldwide through land use and alteration of nutrient cycling (Vitousek *et al.* 1997; Tilman *et al.* 2001). While these impacts are often investigated independently, in most systems species diversity and productivity are linked, with the form and direction of the relationship varying by scale (reviews by Rosenzweig & Abramsky 1993; Rosenzweig 1995; Grace 1999; Waide *et al.* 1999; Loreau *et al.* 2001; Mittelbach *et al.* 2001; Worm & Duffy 2003). Further dependencies between ecosystem productivity and biodiversity arise from a shared dependence upon external abiotic factors (e.g. rainfall, solar energy, or soil fertility). The processes regulating species richness and productivity at regional to global scales can only be addressed with observational data and models, but observational studies are complicated by the need to disentangle various controls on species richness, the difficulty of obtaining direct measures of productivity, and widespread and accelerating alterations of ecological systems by human activities.

At regional to global scales, productivity is believed to positively influence species richness (Pianka 1966; Rohde 1992; Rosenzweig 1995; Hawkins *et al.* 2003). However, debates continue over the relative importance of historical vs. environmental factors (Currie & Paquin 1987; Latham & Ricklefs 1993; Badgley & Fox 2000; Francis & Currie 2003; Hawkins & Porter 2003b) and the importance of energy availability, water availability, and other environmental variables (Wright 1983; Currie & Paquin 1987; Currie 1991; O'Brien 1993, 1998; Wright *et al.* 1993; Hawkins *et al.* 2003). Net primary productivity (NPP), the difference between carbon fixed by photosynthesis and carbon lost to autotrophic respiration, directly measures the energy flowing into an ecosystem. However, most studies of species–energy relationships have used indirect proxies for energy availability, such as actual evapotranspiration or potential evapotranspiration (Richerson & Lum 1980; Currie & Paquin 1987; Currie 1991; O'Brien 1993; Francis & Currie 2003) because of the difficulty of obtaining regional field measurements of NPP. Remotely sensed observations of vegetation greenness, combined with terrestrial ecosystem models, provide direct estimates of NPP (e.g. Paruelo *et al.* 1997; Field *et al.* 1998; Liu *et al.* 2002), but current NPP values are heavily modified by human land-use (DeFries *et al.* 1999; Imhoff *et al.* 2004). The pervasive effects of human activities on both ecosystem function and biodiversity thus complicate analyses of richness–productivity relationships.

California is a hotspot of vascular plant diversity, home to more than 20% of all vascular plant species in the USA, and nearly 30% of its flora consists of endemic species (Stein *et al.* 2000). Humans have lived in California since the late Pleistocene, but exotic species introductions were limited until 1542, when European explorers first arrived. Significant European land-use began in the late 1760s with the establishment of missions and cattle ranchos, and intensified in the late 1860s after the establishment of the transcontinental railroad produced a boom in agricultural exports and increased immigration. Californian plant communities are now highly invaded, with exotics accounting for 10.8% of vascular plant species and 48.9% of annual plant species (E.W. Seabloom *et al.* pers. comm.). The degree and kind of anthropogenic impact varies widely, with human population densities highest in coastal regions and agricultural land-cover greatest in semi-arid interior regions (Seabloom *et al.* 2002). In a now-classic paper, Richerson & Lum (1980) found that climatic indices, such as mean annual precipitation and mean annual temperature, were the strongest predictors of plant species richness in California. They reported no significant independent effect of productivity on richness, but used an indirect index of productivity (growing season length multiplied by total precipitation), did not study exotic species, and did not examine the impact of human activities.

In this paper, we assess the importance of anthropogenic land-use, alteration of ecosystem productivity, and species invasions upon observed productivity–richness relationships in California. Cross-referenced floristic lists from the CalFlora botanical (http://www.calflora.org) and Jepson Herbarium (http://ucjeps.berkeley.edu/active.html) databases provide richness data for 230 subecoregions. We estimate both current and historical NPP values, the latter representing California *c.* 1750, prior to permanent European settlement and land-use. We first test alternate structural equation models (SEMs) of NPP–richness–climate relationships prior to European settlement, then test a second set of SEMs to evaluate whether current NPP–richness relationships have been significantly altered by human land-use. A final analysis evaluates whether the controls on exotic species richness differ from those for native species.

DATA AND METHODS

Species richness

We constructed a spatially resolved data set of vascular plant richness for 5930 taxa (species and named varieties hereafter referred to as species) in California by cross-referencing floristic lists from the CalFlora database (Richerson & Lum 1980) and Jepson Herbarium (Hickman 1993). Both data sources are comprehensive floristic surveys, based upon herbarium specimens collected over the past century, but the data sets differ in spatial organization. The smallest spatial units in the CalFlora data set are subcounties, divided at topographic divides and other biophysically relevant transitions (Richerson & Lum 1980), whereas floristic lists in the Jepson Herbarium are grouped into ecoregional plant communities (Hickman 1993). The intersection of these two data sets results in 230 'subecoregions' after removing slivers (small regions at the margins of intersecting polygons resulting from slight mismatches in intersected GIS layers) less than 100 km^2 (Fig. 1); species are listed as present in a subecoregion only if they are present in both subcounty and ecoregion (Harrison *et al.* 2000, J.H. Viers *et al.*, pers. comm.). The 5930 taxa covered in these analyses represent a sample of the 7721 taxa in the full CalFlora database, because of unresolved taxonomic discrepancies, such as sub-species, variant, and species *nova* naming differences, between the two data sources (CalFlora and Jepson). The results of this analysis are qualitatively similar when run on the full species list at the coarser scale of the CalFlora data set (94 regions).

Species are designated as native or exotic and extinct or extant, based upon designations within the CalFlora database. The native species list may include some early invaders (e.g. *Erodium cicutarium*, Mensing & Byrne 1998), but the number of early invaders should be small relative to the total number of species in California, and are unlikely to alter the results presented here. The 'historical' species list comprises all native species (including extant and extinct

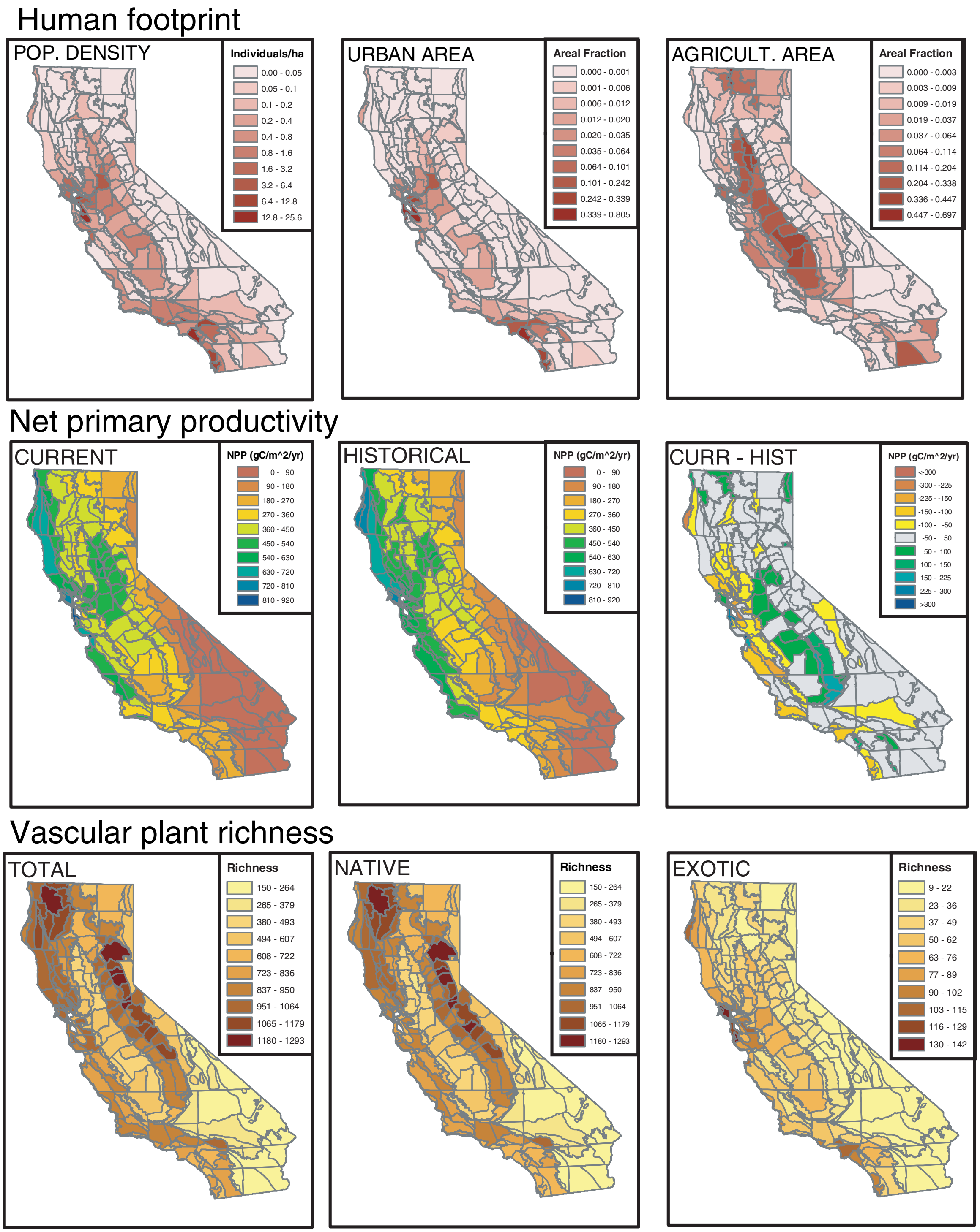


Figure 1 Top Row: Maps of three indices of the intensity of human activities and ecological impacts in California: human population density (individuals/ha) and the fractional area of each 'subecoregion' converted to agricultural or urban use. The subecoregions were created by intersecting Richerson & Lum's (1980) subcounties with Jepson ecoregions (see Methods). Middle Row: Mapped estimates of annual NPP (kgC ha^{-1} year^{-1}) for (left) the present, representing an average of GLO-PEM estimates for 1982–1999 (Goetz *et al.* 2000); (middle) historical NPP values (*c.* 1750); and (right) the difference between the two. Bottom Row: vascular plant richness for (left) the combination of native and exotic species, (middle) native species, and (right) exotic species.

species) in the cross-referenced data set whereas the 'current' species list comprises all extant species (including both native and exotic species). Extinct plant species are few in number (< 0.5% of the data set), are all native species, and do not significantly affect these analyses.

NPP

Current NPP values are represented by 18-year averages (1982–1999) of annual NPP (gC m^{-2} $year^{-1}$) estimated by the terrestrial ecosystem model GLO-PEM. GLO-PEM is a quasi-mechanistic model driven by remotely sensed observations of vegetation greenness and climatic variables including temperature, precipitation, downward longwave and shortwave radiation, specific humidity, wind speed, and atmospheric pressure (Goetz *et al.* 2000). GLO-PEM NPP estimates are consistent with other terrestrial ecosystem models (Cramer *et al.* 1999) and are accurate to within 10–30% of field measurements (Goetz *et al.* 2000). We assigned mean NPP values to subecoregions by averaging all gridded NPP values (8 km resolution) within each subecoregion.

To estimate historical NPP, we selected locations from a network of reserve areas compiled by the Gap Analysis Program (Stoms & Hargrove 2000). Although these systems are not pristine, current NPP in these areas is most likely to approximate historical values. For these sites, we constructed a stepwise Gaussian general linear model (GLM function in R v1.8.1) that predicted NPP as a function of bioclimatic and edaphic variables (Table 1). Variables and variable transformations were selected by mixed stepwise regression; the allowed transformations were untransformed, log, and squared transformations. The decision to omit or retain variables was based upon the model Akaike Information Criterion (AIC) at each step; this criterion resulted in retaining predictor variables of marginal significance (Table 1). We opted to retain these marginally significant variables because our goal was to build a model with the greatest predictive power, not to assess the significance of individual variables. We selected 80% of the resultant 1172 8-km grid cells to parameterize the model and reserved the remaining 20% to test model accuracy. The model explained 83.7% of NPP variance in the test data set. After statistical testing, model parameters were applied to all 8-km grid cells in California to predict historical NPP and subsequent values were spatially averaged by subecoregion (Fig. 1). This approach predicts NPP in the absence of major European land-use, but omits the effects of historical climatic variations upon NPP.

Climatic, edaphic, and anthropogenic variables

The selected bioclimatic variables (Table 1) represent important climatic regulators of ecophysiological processes and species distributions (Woodward 1987). All bioclimatic variables are calculated from a global climate data set for 1961–1990 with a 10-min spatial resolution (New *et al.* 2002) and interpolated to the GLO-PEM 8-km grid (P. Bartlein and S. Shafer, pers. comm.). By using recent climates to model historical NPP, we assume that climate variations over the past 200 years have not significantly altered NPP distributions in California. Edaphic variables are from the Shirazi *et al.* (2001) data set of derived soil properties for the conterminous USA, a subcounty-scale data set based upon the State Soil Geographic Database. This data set includes textural properties, water-holding capacity, and organic carbon content, but does not include information on nitrogen or phosphorus concentrations. Human population densities are 1990 census values; 1990 data are used because these correspond to the middle of the date range for the modelled current NPP and the date of the species data from

Table 1 Bioclimatic and edaphic predictors of historical NPP

Variable	Description	*F*-value	*P*-value
AET	Actual evapotranpiration (mm)	2.757	0.097
ANNP*	Total annual precipitation (mm)	2183.486	< 0.0001
AWC	Available water capacity (cm cm^{-1})	40.165	< 0.0001
CEC	Cation exchange capacity (cmol kg^{-1})	na	
ELEV	Mean elevation above sea level (m)	548.748	< 0.0001
GDD_5*	Growing degree-days above 5 °C	3.102	0.078
MTCO	Mean temperature of coldest month (°C)	na	
MTWA	Mean temperature of warmest month (°C)	241.726	< 0.0001
ORGC*	Organic matter (% by weight)	na	
PJANPANN	Fraction of annual precipitation in January	15.379	< 0.0001
PJULPANN	Fraction of annual precipitation in July	0.497	0.481
WTD	Depth to water table (m)	na	
PET	Potential evapotranspiration (mm)	92.160	< 0.0001

na, not applicable: these variables were discarded during stepwise regression.
*These variables also used in structural equation models.

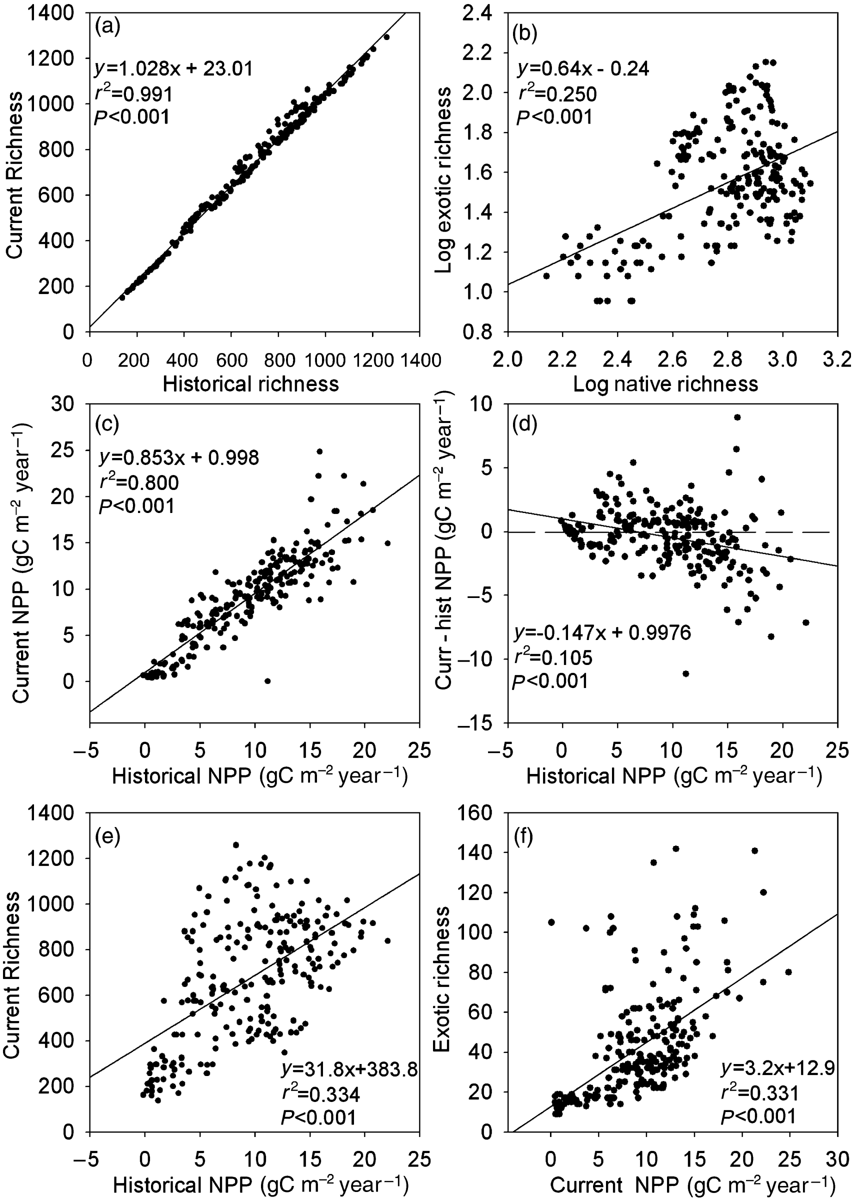


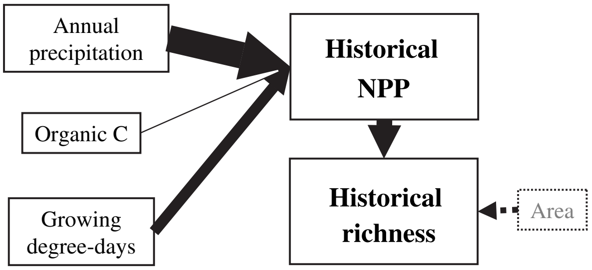
Figure 2 Scatter plots of (a) historical species richness vs. current species richness, (b) native species richness vs. exotic species richness, (c) historical NPP vs. current NPP, and (d) historical NPP vs. the difference between current and historical NPP. The dashed line in 3d indicates the position of the zero line (current–historical NPP = 0).

the Jepson Flora. Fractional area converted to urban and agricultural use are estimated from the DISCover global 1-km land cover map, version 2 (http://edcdaac.usgs.gov/glcc/globdoc2_0.asp, Loveland *et al.* 2000), using the International Geosphere-Biosphere Programme (IGBP) classification scheme.

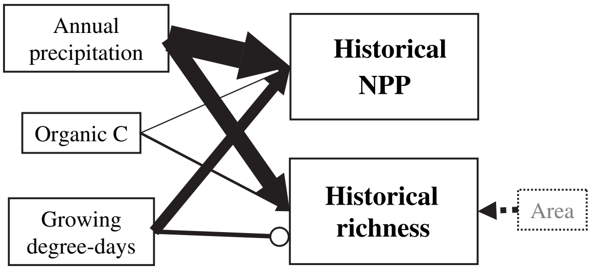
Statistical analyses of NPP–richness relationships

We separately analysed NPP–richness relationships for the historical and current system states, employing SEMs to disentangle the relative importance of environmental and anthropogenic influences on NPP and plant species richness (Li 1975; McCune & Grace 2002). We constructed three alternate models for the period prior to European settlement (Fig. 3): (1) plant richness was directly controlled by NPP, with abiotic variables exerting only indirect effects on richness (mediational model); (2) plant richness and NPP were not directly linked but separately controlled by ambient energy, hydrological regime, and soil resources (abiotic model); and (3) plant richness was affected by both abiotic variables and NPP (combined model). The combined model is similar to the abiotic model, but, to preserve a degree of freedom, one path was dropped to accommodate the addition of the NPP–richness pathway; we chose the path with the lowest

(a) Mediational model



(b) Abiotic model



(c) Combined model

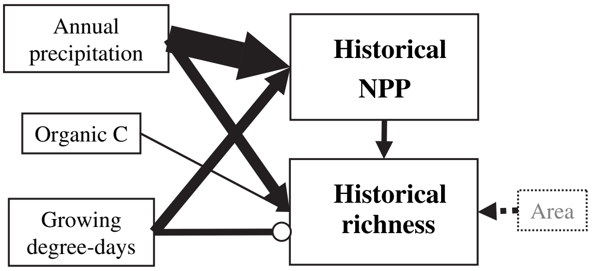
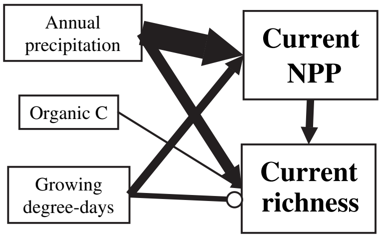
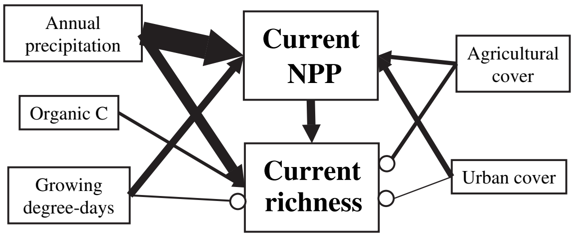


Figure 3 Path diagrams for three alternate structural equation models of historical NPP–richness–environment relationships. The width of each line is proportional to its path coefficient (see Table 3). Positive relationships are represented by arrows and negative relationships by circles.

(a) Combined model, current system



(b) Anthropogenic model



(c) Anthropogenic model, exotic species

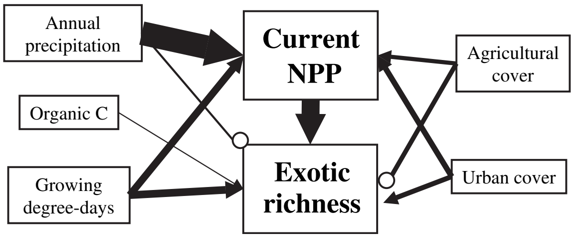


Figure 4 Path diagrams for structural equation models of the relationship between current or exotic species richness, NPP, and abiotic and anthropogenic variables. See Fig. 3 for information about figure conventions.

contribution to the chi-squared statistic for the abiotic model. The manifest variables chosen to represent abiotic factors – growing degree days on a 5 °C base (GDD_5), annual precipitation (ANNP), and soil organic carbon (ORGC) (Table 1) – represent different dimensions of environmental space. They are not strongly collinear (highest pairwise $r^2 = 0.43$, for GDD_5 and ANNP) and, after square-root transformation (ANNP, GDD_5) or log-transformation (ORGC), passed tests for normality. The chi-squared statistic was used to check for significantly poor fits of the models to the data and the AIC was used to compare among models. Low AIC values correspond to high goodness-of-fits relative to the number of model parameters (Hilborn & Mangel 1997). All SEM analyses were run using procedure CALIS in SAS (v8.01). A parallel series of experiments tested whether adding subecoregional area and a path between area and richness improved model fit (Fig. 3).

We then evaluated whether anthropogenic land-use had significantly altered the relationships among NPP, richness, and environmental variables by selecting the model with the best fit to the historical data, rerunning it for the current system (combined model, current system), and comparing this model to an alternate model that included indices of post-settlement land-use intensity (anthropogenic model) (Fig. 4). Land-use intensity is represented by the percent agricultural and urban area per subecoregion. We conducted an additional experiment in which exotic species richness was substituted for current species richness, to explore whether exotic species in California follow or differ from the relationships observed for the total species pool (anthropogenic model, exotic species).

RESULTS

Spatial patterns of richness and NPP in California: historical vs. current

Native richness in California increases with mean elevation (Seabloom *et al.* 2002) and is highest in the Klamath Ranges, North Coast Ranges, and Sierra Nevada Mountains (dark brown areas in northern and eastern California in Fig. 1). Native richness is lowest in the arid south-eastern corner of the state. This reverse latitudinal gradient in species richness is also observed in native specialists, such as serpentine endemics (Harrison *et al.* 2000). Because native species compose 90% of species in our data set, historical and current species richness closely correlate ($r = 0.995$, $P < 0.0001$; Figs 1 and 2a). The distribution of exotic species, however, markedly differs, being highest in urbanized coastal areas and moderately elevated in the Central Valley, where native richness is relatively low (Fig. 1). This pattern likely results from the long history of European settlement in coastal cities that hence serve as gateways for exotic species (Mensing & Byrne 1998; Seabloom *et al.* 2002; Levine & D'Antonio 2003; Mack 2003). Exotic richness is highest in areas with high native species richness (Fig. 2b) ($r = 0.50$, $P < 0.0001$).

Current and historical NPP are highest in northern California and coastal areas and lowest in arid regions (Fig. 1). The linear correlation between current and historical NPP (Fig. 2c) is strong ($r = 0.89$, $P < 0.0001$) but weaker than the relationship for current and historical richness. Post-settlement increases in NPP occur mainly in semi-arid areas converted to agricultural use, particularly in the southern half of the Sacramento and San Joaquin Valleys in central California, where increases in NPP can exceed 100%. In these areas, irrigation and fertilization have increased NPP beyond the limits imposed by environmental constraints. Conversely, decreases in NPP are less common and tend to occur in coastal regions with high population densities (Fig. 1). The largest absolute decreases in NPP occur in small coastal subecoregions (e.g. the Lost Coast in north-western California, Marin County north of San Francisco), but these must be interpreted with caution, because they may include as few as one 8-km gridcell and individual gridcells may overlap the land/sea interface. The largest percent decrease in NPP relative to historical values is in the South Coast ecoregion of San Diego County, where NPP has decreased by nearly 50%. Overall, there is a negative relationship between historical NPP and post-settlement changes in NPP ($r = 0.32$, $P < 0.0001$; Fig. 2d), suggesting that human land-use has reduced the spatial heterogeneity of NPP.

Abiotic, biotic, and anthropogenic influences on species richness

Among the three models for the relationship between historical richness, NPP, and abiotic variables (Fig. 3, Table 2) the mediational model most poorly fit the observed data (AIC = 124.2), the abiotic model had an intermediate fit (AIC = 7.239), and the combined model best fit the data (AIC = −0.198). The mediational model failed because covariances between historical species richness and abiotic variables were too high to be explained as an indirect linkage through NPP. Conversely, the abiotic model underpredicts the strength of the correlation between NPP and richness. The rank order of path coefficient size is similar among models (Fig. 3, Table 3). In all models, annual precipitation is the strongest predictor of NPP and (in the abiotic and combined models) richness, consistent with prior analyses of Californian plant diversity (Richerson & Lum 1980). Growing season length and strength (represented by GDD_5) exert a weaker influence upon NPP and a negative influence on plant richness, reflecting the reduced plant diversity in south-eastern California. Soil organic carbon exerted the weakest effects upon NPP and richness. Adding area as a predictor of species richness resulted in worsened model fits (mediational model: AIC = 130.31; abiotic model: AIC = 12.83; combined model: AIC = 2.71), suggesting that areal extent was not an important determinant of subecoregional richness. NPP positively correlated with plant richness (Figs 2e and 3, Table 3), even after consideration of direct abiotic effects upon richness.

Application of the combined and anthropogenic models to the current system suggests that human land-use has

Table 2 Summary statistics for SEMs

	Historical system (Fig. 3)			Current system (Fig. 4)		
	Mediation	Abiotic	Combined	Combined	Anthropogenic	Exotic
χ^2	130.2	9.24	1.80	1.65	0.128	0.128
d.f.	3	1	1	1	1	1
P-value	< 0.0001	0.002	0.180	0.199	0.721	0.721
AIC	124.2	7.239	−0.198	−0.347	−1.872	−1.872
r^2 NPP	0.644	0.644	0.641	0.568	0.626	0.626
r^2 Rich	0.350	0.623	0.637	0.645	0.663	0.461

Table 3 Path coefficients for SEMs

		Historical (Fig. 3)			Current (Fig. 4)		
From	To	Mediation	Abiotic	Combined	Combined	Anthropogenic	Exotic
ANNP	NPP	0.995	0.995	1.007	0.924	0.886	0.886
GDD_5	NPP	0.416	0.416	0.403	0.310	0.268	0.268
ORGC	NPP	0.057	0.057	–	–	–	–
AGRIC	NPP	–	–	–	–	0.159	0.159
URBAN	NPP	–	–	–	–	0.210	0.210
ANNP	Rich	–	0.629	0.427	0.415	0.395	−0.076
GDD_5	Rich	–	−0.166	−0.251	−0.200	−0.182	0.288
ORGC	Rich	–	0.095	0.084	0.077	0.123	0.045
AGRIC	Rich	–	–	–	–	−0.145	−0.175
URBAN	Rich	–	–	–	–	−0.009	0.185
NPP	Rich	0.591	–	0.204	0.276	0.315	0.674

affected the distribution of NPP and plant richness in California (Fig. 4). The combined model (AIC = −0.347) had a somewhat poorer fit to the data than the anthropogenic model (AIC = −1.872; Table 2). The sign and relative strength of the path coefficients for the abiotic variables were similar between the combined and anthropogenic models, and between the applications of the combined model to the current and historic data (Table 3). Habitat conversion tended to exert a positive effect on NPP and a negative effect on richness (Fig. 4, Table 3). NPP remained an important predictor of richness.

The controls on exotic species distributions appear to differ in several important respects from the controls for the total species pool (Fig. 4, Table 3). Environmental controls on species richness were diminished in importance or reversed in directionality. Annual precipitation exerted only a very weak influence on exotic species, and is slightly negative. Growing degree-days had a positive effect upon exotic richness, in contrast with its negative effect upon current species richness. Exotic species richness tended to be higher in highly urbanized subecoregions. The negative effect of agricultural land-cover conversion upon exotic species richness is surprising, given that invasive species tend to be most common in disturbed areas (Jenkins & Pimm 2003). Agricultural area, however, exerted a positive indirect effect upon exotic species richness through its positive effect on NPP. Strikingly, NPP emerged as the strongest predictor of exotic species richness (Figs 2f and 3, Table 3).

DISCUSSION

Our analyses of post-European-settlement changes in species richness and NPP support prior reports that the impacts of human activities upon biodiversity and ecosystem function in California are pervasive, locally intensive, and non-random in their distribution (Vitousek *et al.* 1997; Tilman *et al.* 2001; Seabloom *et al.* 2002). Within individual subecoregions, the percent land area converted to anthropogenic use exceeds 80% (South Coast ecoregion, San Diego County) and exotic species compose up to 14.5% of the subecoregional flora (Central Coast ecoregion, Marin County; Southern Coast ecoregion, Los Angeles County). Approximately 1000 vascular plant species have become established in California since European colonization (Rejmanek & Randall 1994; Rejmanek 2003; Stohlgren *et al.* 2003). Although statewide extinctions have been rare (Stein *et al.* 2000), many areas are now dominated by exotic species. For example, more than 9 million ha of native perennial grassland is currently dominated by exotic annual grasses introduced from Europe (Heady 1977). Exotic invasions have tended to reinforce the existing patterns of diversity in California, because exotic invasions are highest in high diversity areas.

Conversely, human impacts have tended to reduce the spatial heterogeneity of NPP, because of increases in NPP in semi-arid areas through irrigation and decreases in NPP in historically productive coastal areas (Figs 1 and 2d). Urbanization effects on NPP are less extensive and are spatially variable, depending in part upon the severity of pre-urbanization resource limitation (Imhoff *et al.* 2004).

The statewide spatial patterns of NPP and species richness are still primarily arrayed along environmental gradients. Annual precipitation emerges as the dominant control of both historical and present NPP and species richness in California, with growing-season ambient energy (GDD_5) a weaker control. The observed pre-eminence of annual precipitation replicates the results of Richerson & Lum (1980) and supports the hypothesis that water availability is the primary driver of plant richness in mid- and lower-latitudes (Hawkins *et al.* 2003).

Within this environmental context, human land-use is a significant predictor of plant richness and NPP. A model that included indices of urban and agricultural land-cover conversion better fit the data than a model that lacked these predictor variables (Fig. 4, Table 2). Thus, these indices of anthropogenic impact explain variance in the current distribution of NPP and species richness not explained by bioclimatic variables. The effect of human activities is small relative to environmental constraints in part because the human footprint is still fairly small, with 7.8–17.5% of California converted to urban and agricultural use (Davis *et al.* 1998; Loveland *et al.* 2000; Vogelman *et al.* 2001; US Geological Survey 2004) and exotic species composing 10% of the Californian flora. As human population levels and resource use continue to grow, the effects of anthropogenic activities upon the statewide distribution of species richness and NPP are likely to increase.

For both the historical and current system states, NPP is a significant predictor of vascular plant richness, even after controlling for other environmental factors. NPP directly measures the energy entering an ecosystem – both for plants to allocate to growth, reproduction, herbivory defence, and other processes, and for consumption by other organisms. Thus, the inclusion of the NPP–richness pathway in the SEM models supports the hypothesis that species richness is in part maintained by energy availability (Wright 1983). However, the importance of energy availability for plant species richness in California appears to be secondary to the importance of water availability. The pre-eminence of water availability is probably not universal: recent studies suggest that energy availability is a better predictor of richness in high latitudes and water availability is more critical for low- to mid-latitude ecosystems and regions with pronounced moisture gradients such as California or South Africa (O'Brien 1998; Hawkins *et al.* 2003). Furthermore, the form and mechanisms governing NPP–richness relationships are scale-dependent (Waide *et al.* 1999; Mittelbach *et al.* 2001), so that the interpretive domain of this paper is limited to regional to global scales.

The shared positive coupling between native and exotic species richness and NPP may in part explain the tendency for native and exotic species richness to be positively correlated at multiple scales (Levine 2000; Deutschewitz *et al.* 2003; Stohlgren *et al.* 2003). Exotic species in California appear to preferentially invade areas of high productivity, where native species richness is already high. The alignment of exotic and native richness along productivity and environmental gradients (Levine & D'Antonio 1999) thus appears to supercede local-scale resistance of communities to invasion through niche filling and competitive exclusion (Grime 1973; Tilman 1999). The tendency of humans to settle in highly productive areas may further increase rates of invasion in these areas by increasing rates of introduction (Seabloom *et al.* 2002; Rejmanek 2003). The controls of native and exotic species are not, however, identical, as shown by differences between the SEMs for exotic and current species richness (Fig. 4). Environmental variables exert a reduced influence on exotic species richness, and exotic species richness, unlike native species richness, is positively coupled to percent urban area (Fig. 4).

The lack of any clear effect of area upon floristic richness is consistent with prior analyses of floristic richness in California (Richerson & Lum 1980; E.W. Seabloom *et al.*, pers. comm.), but remains a puzzling feature of the data, given the generality of species–area relationships. This absence of a relationship is likely in part because subecoregion sizes are non-randomly distributed in California (Fig. 1). Subecoregions tend to be smaller in more species-rich coastal areas and larger in the arid and species-poor south-eastern corner of the state (Fig. 1).

Two important sources of uncertainty in our analyses are the modelled NPP values and the assumption of climatic stability since *c.* 1750. Because there is no *a priori* reason to expect that the 10–30% error of the GLO-PEM NPP estimates correlates with other terms in the SEMs, there is no reason to expect this uncertainty to bias the SEMs. Instead, the primary consequence should be to weaken the apparent correlation between NPP and other variables. Global mean temperature has increased by *c.* 0.5 °C since 1750 (Mann *et al.* 1998), and regional climates in California have experienced both natural climatic variability (Cook *et al.* 1999) and land-cover feedbacks such as urban heat trapping and shifts in the partitioning between latent and sensible heat fluxes in irrigated regions (Pielke *et al.* 1998). This variability is unlikely to drastically affect the statewide patterns of energy–water relationships and species distributions in California. Nevertheless this paper may overestimate the stability of NPP–richness relationships, and one avenue for further research would be to explicitly model the effects of post-European-settlement climate change upon ecosystem productivity and diversity.

These results are unlikely to be sensitive to spatial autocorrelation. Although exotic plant species richnesses in California are spatially autocorrelated, ordinary least squares and spatial autoregressive models identified similar suites of predictor environmental variables (Dark 2004), and SEM analyses of butterfly and plant species richness in California found no evidence for autoregression after NPP was included in the model (Hawkins & Porter 2003a). To check, we regressed current richness against NPP with and without an autoregressive term. We fitted three types of autoregression models to the spatial variance (spherical, exponential, and Gaussian) with and without nuggets (local variance > 0). NPP remained a significant predictor of richness in the spatial models.

The impacts of humans in California on ecosystem functioning (NPP) and biodiversity (species richness) are mediated by the strong constraints exerted by the abiotic environment on the distribution of human impacts, productivity, native diversity, and invasion. This regional case study demonstrates that these feedbacks must be considered when attempting to understand, and eventually predict, the effects of humans on global ecosystems. Nevertheless, human activities are clearly an important and growing influence on NPP and species richness in California. The areal extent of agricultural and urban land is a significant predictor of species richness and NPP, although the percent land-cover conversion in California (7.8–17%) is lower than the average for the conterminous USA (32%, Imhoff *et al.* 2004). Moreover, anthropogenic impacts are spatially variable and non-random in their distribution, which may increase the rates of future species losses (Seabloom *et al.* 2002) and loss of productive lands to urbanization (Nizeyimana *et al.* 2001; Imhoff *et al.* 2004). As human population levels and resource requirements continue to grow, NPP and species richness distributions in California are likely to be increasingly affected by anthropogenic land-use.

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