

Climate change and the invasion of California by grasses

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Abstract

Over the next century, changes in the global climate are expected to have major consequences for plant communities, possibly including the exacerbation of species invasions. We evaluated this possibility in the grass flora of California, which is economically and ecologically important and heavily invaded. We used a novel, trait-based approach involving two components: identifying differences in trait composition between native and exotic components of the grass flora and evaluating contemporary trait–climate relationships across the state. The combination of trait–climate relationships and trait differences between groups allows us to predict changes in the exotic-native balance under climate change scenarios. Exotic species are more likely to be annual, taller, with larger leaves, larger seeds, higher specific leaf area, and higher leaf N percentage than native species. Across the state, all these traits are associated with regions with higher temperature. Therefore, we predict that increasing temperatures will favor trait states that tend to be possessed by exotic species, increasing the dominance of exotic species. This prediction is corroborated by the current distribution of exotic species richness relative to native richness in California; warmer areas contain higher proportions of exotic species. This pattern was very well captured by a simple model that predicts invasion severity given only the trait–climate relationship for native species and trait differences between native and exotic species. This study provides some of the first evidence for an important interaction between climate change and species invasions across very broad geographic and taxonomic scales.

Keywords: California, climate change, exotic species, functional traits, grass, grassland, height, invasive species, leaf nitrogen, seed mass

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Introduction

Biodiversity is threatened by many aspects of global change, including changing climate, alien species, habitat destruction, and degradation, overexploitation, pollution, and disease (Wilson, 1992; Wilcove *et al.*, 1998; Sala *et al.*, 2000). Interactions between these aspects are likely to be common and important, but relatively few studies have addressed them, particularly over large areas and across many species (Dukes & Mooney, 1999; Sala *et al.*, 2000; Ziska *et al.*, 2005; Thuiller *et al.*, 2007). Climate change may promote the spread of exotic species, but broad empirical support for this idea has been scarce and the underlying mechanisms remain largely unexplored (Beerling & Woodward, 1994; Simberloff, 2000; Chown *et al.*, 2007; Vilá *et al.*, 2007; Peterson *et al.*, 2008; Willis *et al.*, 2010; Verlinden & Nijs, 2010).

Trait-based ecology provides useful tools to assess the importance of this interaction over large spatial and taxonomic scales (Lavorel & Garnier, 2002; McGill *et al.*,

2006; Thuiller *et al.*, 2007). Abiotic conditions can be conceptualized as filters that, by acting on functional traits, determine local community membership (Diaz *et al.*, 1998; Thuiller *et al.*, 2004; Cornwell *et al.*, 2006). By modifying these filters, climate change is expected to alter the composition of plant communities, which will change their trait composition (Suding *et al.*, 2008; Sandel *et al.*, 2010). In some systems, exotic species will possess the traits favored by the new climate regime. As a result, climate change may exacerbate native biodiversity loss due to exotic species in these systems (Dukes & Mooney, 1999; Hobbs & Mooney, 2005; Willis *et al.*, 2010). To assess the likelihood of this outcome within a particular system, it is necessary to understand (i) the differences in trait composition of native and exotic species groups, and (ii) the expected changes in environmental filters resulting from climate change (Fig. 1). Herein, we address these two components in the context of California's heavily invaded grass flora (D'Antonio *et al.*, 2007), and ask whether predicted climate changes will exacerbate or dampen the ongoing invasion of California's grasslands.

In California, temperatures are expected to warm by between 2.2 and 5.8 °C by 2100, depending on the CO₂ emissions scenario and the sensitivity of the climate

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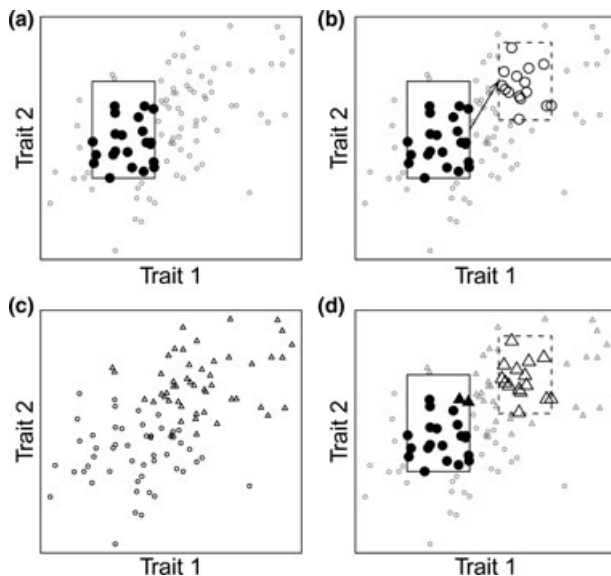


Fig. 1 Trait-based filtering on community membership imposed by climate. Species in a regional species pool (circles) have a certain bivariate distribution of trait values (a). Climatic conditions at a particular site impose a filter (box), restricting local community membership to a subset of the regional species pool with particular trait values (filled circles). Changing climate (b) alters the climatic filter (dashed box, open circles), producing a community with a different trait composition. Within the regional species pool, native species (circles) and exotic species (triangles) may differ in their traits (c). Under these conditions, a climate change may have different effects on native and exotic groups, in this case increasing the proportion of species that are exotic (d).

model (Loarie *et al.*, 2008). Changes in precipitation are less certain, but are likely to include moderate decreases in some areas of the state (Hayhoe *et al.*, 2004; Cayan *et al.*, 2008). With increased mean annual temperature, we should expect to see increased potential evapotranspiration (PET; Holdridge, 1959), increased temperature seasonality (Hayhoe *et al.*, 2004; Cayan *et al.*, 2008) and, in areas without substantial increases in precipitation, increased water deficits. Climate changes are expected to contribute to a substantial statewide expansion of grasslands (Lenihan *et al.*, 2003; Hayhoe *et al.*, 2004).

Large-scale trait–climate relationships can provide the basis for understanding how these changes should alter environmental filters on the grass flora in California (Diaz & Cabido, 1997; Sandel *et al.*, 2010). With increasing temperature, communities typically shift toward species with higher SLA (Niinemets, 2001; Wright *et al.*, 2005), higher leaf N per area (N_{area} ; Wright *et al.*, 2005), lower leaf N per mass (N_{mass} ; Reich & Oleksyn, 2004; Han *et al.*, 2005), larger seed masses (Moles *et al.*, 2007), greater maximum heights (Moles

et al., 2009), and larger leaves (Dolph & Dilcher, 1980). Plant communities receiving high precipitation contain taller species (Moles *et al.*, 2009) and species with lower N_{area} (Wright *et al.*, 2005). For grasses specifically, increasing temperatures can sometimes favor C_3 grasses (Read & Morgan, 1996; Alward *et al.*, 1999), but there is generally an increased abundance of C_4 grasses at the expense of C_3 species with increased temperature over large spatial scales (Teeri & Stowe, 1976; Ehleringer *et al.*, 1997; An *et al.*, 2005).

The relationships between functional traits and climate can be combined with trait differences between native and exotic species to derive predictions for the interactions between climate change and species invasions at a large scale (Fig. 1). We used this approach to assess the likelihood that climate change will alter the course of the invasion of California's grasslands. We address three major questions in this study. First, how is grass diversity currently distributed in California, and how does the proportion of species that are exotic vary across the state? Second, how do the traits of California's grass species relate to climate? Finally, how do exotic species, as a group, differ in their traits from native species, and should these differences favor or disfavor exotic species under climate change scenarios? We also consider the historical pattern of exotic grass invasions into California, including changes in the trait composition of exotic grasses through time.

Materials and methods

Species distributions

We mapped distributions of all grass species within California. These maps were based on a map of California that divides the state into 35 floristically defined subregions (Hickman, 1993). We then divided each of these subregions into 100m elevational bands, using a high-resolution digital elevation map of the state. The combined division of the state into subregions and each subregion into bands yielded 800 discrete zones across the state. This is the same approach used by Kraft *et al.* (2010) and K. Simonin, M. Shuldman, B. Sandel, N. Kraft, E. Waller, K. Krasnow, L. Chiono, D. Christianson, C. Divittorio, G. Goldsmith, K. Peay and D. Ackerly (in review).

We used a flora of California, the Jepson Manual (Hickman, 1993), to determine the zones where each grass species occurs. For each species, the Manual reports the subregions and range of elevations where the species occurs; combining these allowed us to determine the zones occupied by each species. Another example using this approach to studying trait patterns in woody species can be found in K. Simonin, M. Shuldman, B. Sandel, N. Kraft, E. Waller, K. Krasnow, L. Chiono, D. Christianson, C. Divittorio, G. Goldsmith, K. Peay and D. Ackerly (in review).

We used the Jepson Manual to determine whether each species was native or exotic. The Manual excludes casual or

erratic species, so the term exotic herein refers to species that are at least naturalized and may be invasive. We also focused particular attention on those species listed by the USDA as invasive and noxious weeds. Of 107 such species in California, 24 are grasses (USDA PLANTS Database, 2011).

Except where otherwise noted, all analyses were performed in R (R Development Core Team, 2010).

Trait information

We collected information on the traits of grass species in California. These included traits that relate to growth strategy [maximum height and plant lifespan, leaf lifespan (LL)], reproductive strategy (seed mass, month of first flowering, length of flowering period), and light capture strategy [specific leaf area (SLA), leaf length and width, leaf N concentration per mass (N_{mass}) and per area (N_{area}), and photosynthetic pathway]. Trait information came from several sources. Maximum height, leaf width, leaf length, first month of flowering, and length of flowering period were taken from the Jepson Manual species accounts (Hickman, 1993). Species origin (native or exotic) and plant lifespan (annual or perennial) were also determined from these species accounts. We used several published sources of leaf traits, most notably the Glopnet database (Wright *et al.*, 2004), but also the datasets of Tjoelker *et al.* (2005) and Reich & Oleksyn (2004) to obtain information on SLA, LL, N_{mass} and N_{area} . We used genus-level information to determine whether each species utilizes C_3 or C_4 photosynthetic pathways (Hattersley & Watson, 1992). Finally, we obtained mean seed masses for each species from the Kew Gardens seed information database (Liu *et al.*, 2008). In the few cases where multiple trait values were available for a species, we used the mean of all available values. Trait coverage ranged from complete or nearly complete for qualitative and easy-to-measure traits to very incomplete for some more difficult traits (Table 1). We investigated the sensitivity of our results to missing trait data, and found that the results here were generally robust, particularly for traits with measurements for at least 50 species (Appendix S1). We further

assessed the likelihood that trait measurement errors (broadly construed to include sampling errors, instrument errors, database errors, and application of trait values from other regions) could contribute to bias in our results (Appendix S1).

For each of the 800 zones in California, we calculated means for each of these traits across all species present in that zone for which trait data were available (zone mean trait values). Quantitative traits were log-transformed prior to calculation of the zone mean. For qualitative traits, we simply calculated the proportion of the species present in the zone that had a particular trait state (e.g. proportion perennial).

For the exotic species of California, we estimated the time of introduction by querying the records of the California Consortium of Herbaria records (<http://ucjeps.berkeley.edu/consortium/>) to determine the earliest recorded collection of the species within California. This method underestimates the time that a species has existed in California because a species will typically not be collected immediately upon its arrival. We attempted to control for this by also recording the first known record of each native grass species. We calculated the percentage of total native grass richness that was known in each year, and assumed that the same percentage of exotic species was known in that year (in other words, we assumed there was no collection bias favoring either native or exotic species). Specifically, we divided the number of exotic species known in a particular year by the percentage of native species that were known in that year. This allowed us to eliminate the effect of increasing knowledge of the state flora through time, and thereby to estimate the number of exotic grass species in the state through time.

Climate data

PRISM (PRISM Group, 2008) and Daymet (<http://www.daymet.org/climateSummary.jsp>) climate data for California were combined to generate means for each zone in the state for several climate variables. PRISM data are presented at ca. 800 m resolution, and we first resampled it at a 1 km resolution to match the Daymet data. In complex topography and coastal

Table 1 Comparison of trait geometric means (and standard errors) of exotic and native grasses of California

Trait	Native	Exotic	P-value	N
Height (cm)	69.715 (1.044)	79.963 (1.054)	0.0447	427
Leaf length (cm)	13.582 (1.08)	19.28 (1.075)	0.0010	238
Leaf width (mm)	4.215 (1.057)	6.861 (1.072)	0.0000	394
LL (months)	3.139 (1.157)	2.103 (1.069)	0.0907	10
SLA (mm ² mg ⁻¹)	12.878 (1.152)	23.475 (1.078)	0.0018	28
N_{mass} (%)	1.583 (1.116)	2.272 (1.062)	0.0082	45
N_{area} (g m ⁻²)	1.239 (1.174)	0.949 (1.08)	0.1549	28
Seed (mg)	0.667 (1.119)	1.043 (1.144)	0.0111	293
Perennial (%)	78.7	48	0.0000	435
C_4 (%)	26.5	33.5	0.1508	424
Begin flowering (months)	5.49	5.00	0.0629	155
Flowering period (months)	2.27	2.55	0.2798	155

P-values are for *t*-tests or chi-squared tests comparing native and exotic trait means, with a sample size of *N* species. LL, leaf lifespan; SLA, specific leaf area.

areas, PRISM data has generally produced better predictions than Daymet, so we used PRISM data when available (Daly, 2006; Daly *et al.*, 2008). These included monthly maximum and minimum temperatures and monthly precipitation data.

We also estimated PET for each zone, which required combining information from Daymet (monthly solar radiation) with PRISM (monthly maximum and minimum temperatures). PET was estimated using the model of Priestley & Taylor (1972). Applying this equation required us to assume a soil heat flux rate, which was estimated to be 5% of net radiation. Further details can be found in K. Simonin, M. Shuldman, B. Sandel, N. Kraft, E. Waller, K. Krasnow, L. Chiono, D. Christianson, C. Divittorio, G. Goldsmith, K. Peay and D. Ackerly (in review).

The final set of climate variables we obtained for each zone were mean annual temperature, seasonality of temperature (annual maximum minus annual minimum), annual precipitation, PET, water balance (total precipitation minus PET), months of water deficit (number of months of the year with PET > precipitation), and cumulative water deficit (summed water deficit in all months of deficit, expressed as negative numbers).

Human Influence Index

Human impacts on ecosystems may include increasing the rate of species introductions or producing disturbances that favor exotic species. We examined these possibilities using the Human Influence Index (HII), a measure of human impacts that incorporates population density, land cover changes, accessibility, and electrical power infrastructure (Sanderson *et al.*, 2002). We calculated the mean HII value within each zone. HII was treated in the same manner as the climate variables in the analysis.

Analysis

We first asked if native and exotic species differ in their trait states. We tested each trait individually, using a *t*-test to compare native and exotic species in the case of quantitative traits, and a chi-squared test in the case of qualitative traits. To make the three-way comparison of trait values among native, non-weedy exotic, and weedy exotic species we used ANOVAS.

For each zone within California, we calculated the richness of native and exotic species and generated maps of these patterns. We then asked how species richness of each group, as well as the proportion of species in each zone that are exotic, relate to mean annual temperature and mean annual precipitation.

Next, we asked how the traits of the grass flora as a whole relate to climate. To make these comparisons, we plotted climate variables against zone mean trait values across all 800 zones. We calculated correlation coefficients for all pairs of climate variables and traits, transformed to improve the linearity of the relationship where appropriate. We used a locally weighted regression technique, loess regression (Williams & Devlin, 1988), to graphically display the relationship between climate and traits. For each trait, we also examined multiple

regression models relating the trait to all possible linear combinations of climate variables and selected the best model using AIC scores (Appendix S2).

Given trait–climate relationships and trait differences between native and exotic species groups, it is possible to obtain a quantitative prediction for each zone in California for the prevalence of exotic species. This prediction is based on (i) the relationship between temperature and zone mean trait values for native species, and (ii) the relationship between a species' trait value and the probability that species is native (Fig. 2). Here, we used zone mean trait values of only native species to avoid the circularity of predicting the proportion of exotic species from trait means that included exotic species. We first used loess regression to fit a curve to the temperature–trait relationship for native species. Then, we used logistic regression to obtain an estimate of the probability that a species with a given trait value is native. Combining these allow us to start with a temperature, obtain the predicted zone mean trait value of a zone at that temperature, and to convert this into a prediction for the fraction of the community in that zone that is native. We demonstrate this approach using leaf width (see Fig. S1 for other traits). Because zone mean traits are less variable than individual species traits, the range of predictions for proportion native was much smaller than the observed range (Fig. 2d). Thus, the predicted proportion provides an index of relative susceptibility to exotic species, rather than a 1 : 1 prediction for the proportion of native species. This index can be easily rescaled, however, assuming knowledge of the actual proportion of native species in just a few sites. We used a generalized linear model with logit link function and Gaussian error distributions to relate the predicted proportion and actual proportion of native species for five randomly selected sites. We then rescaled all predicted proportions according to the resulting regression coefficients to obtain a properly scaled prediction of the proportion of native species.

Spatial analysis

There is a strong spatial structure in both the climate and species-level data. We addressed two aspects of this structure. First, we separated two distinct sources of climate variation: moving up an elevational gradient within a subregion, and moving across subregions at a constant elevation. Generally, we show relationships calculated across all 800 zones and along elevational gradients within each zone. We also show some relationships across subregions at constant elevation.

In addition, spatial structure in predictor and response variables can alter their perceived relationships (Kissling & Carl, 2008). We accounted for this using simultaneous autoregressive (SAR) models and compared parameter estimates for these models to ordinary least squares (OLS) regression parameters. We also used Dutilleul's (1993) degrees of freedom correction to modify tests of significance of regression parameters. These analyses were performed using the Spatial Analysis in Macroecology software package (Rangel *et al.*, 2006, 2010). Overall, there was very little difference between

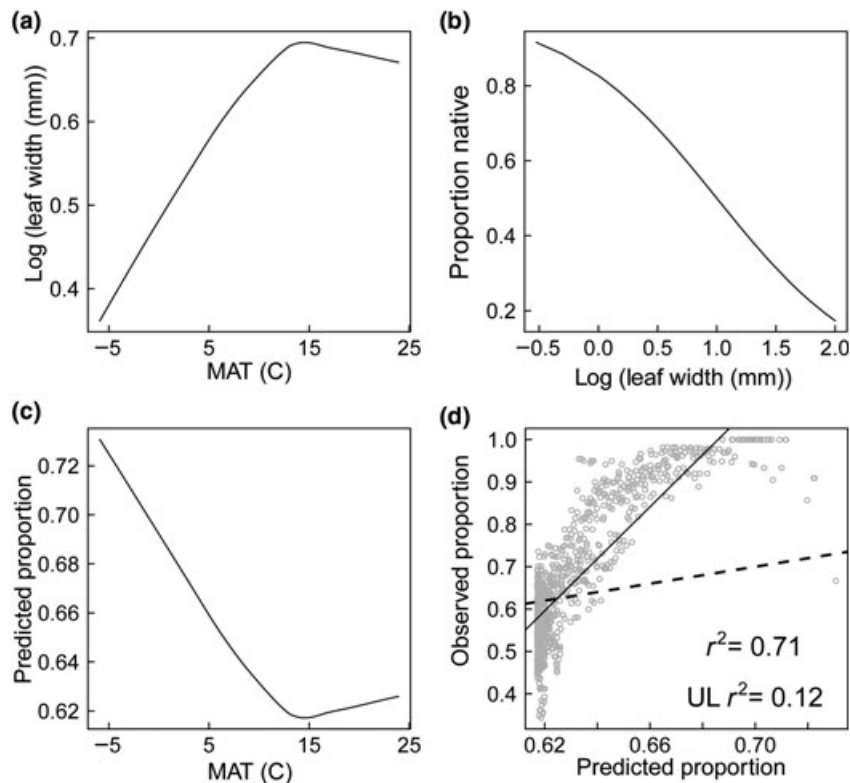


Fig. 2 Predicting exotic richness patterns in California based on species traits, using leaf width as an example. With increasing temperature, leaf width among native species increases, up to a point (a). Native and exotic species pools differ in leaf width (b), with narrow-leaved species more likely to be native. These patterns combine to allow a prediction for the proportion native based on temperature (c), which is strongly correlated with the observed proportion native (d) [but note difference in x and y axis scales and the deviation of the regression (solid line) from the 1 : 1 line (dotted)]. The low value of the unity-line r^2 (UL r^2) relative to the standard r^2 indicates that the predicted and observed data points do not fall along the 1 : 1 line.

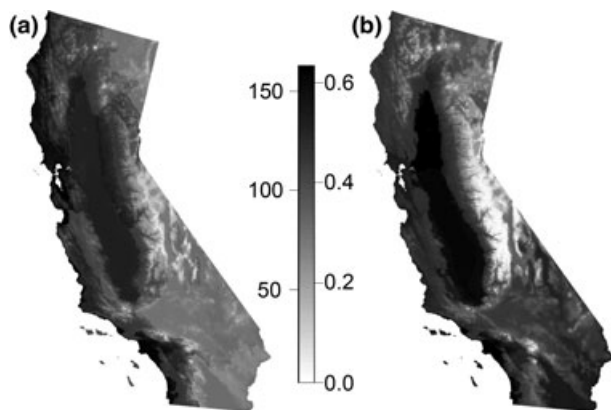


Fig. 3 Patterns of species richness of grass in California. Total species richness (a) is highly variable across the state, and is highest in low elevation areas such as the coast and Central Valley. The proportion of species within a zone that are exotic (b) also varies widely across the state. Near coastal cities and in the Central Valley, the majority of species are exotics, while mountainous regions are almost exclusively occupied by native species.

OLS and SAR parameters, and we present OLS results herein (but see Table S1 for SAR results).

Results

Total grass species richness varied substantially across the state, with a maximum of 163 and minimum of three species in a zone (Fig. 3a). The proportion of grass species within a zone that are exotic also varied widely across the state (range 0–66%; Fig. 3b). Considering the entire dataset, native richness showed a hump-shaped relationship with temperature, but relationships within subregions were generally monotonically increasing. Exotic richness showed a similar pattern, but the proportion of species that are exotic increased strongly with increasing temperature ($r^2 = 0.79$; Fig. 4), as did the proportion of species that are noxious weeds ($r^2 = 0.49$; Fig. S2). Mean annual precipitation was not strongly related to richness or the proportion exotic.

In total, there are 258 native and 177 exotic grass species in California. These two groups of species differ in

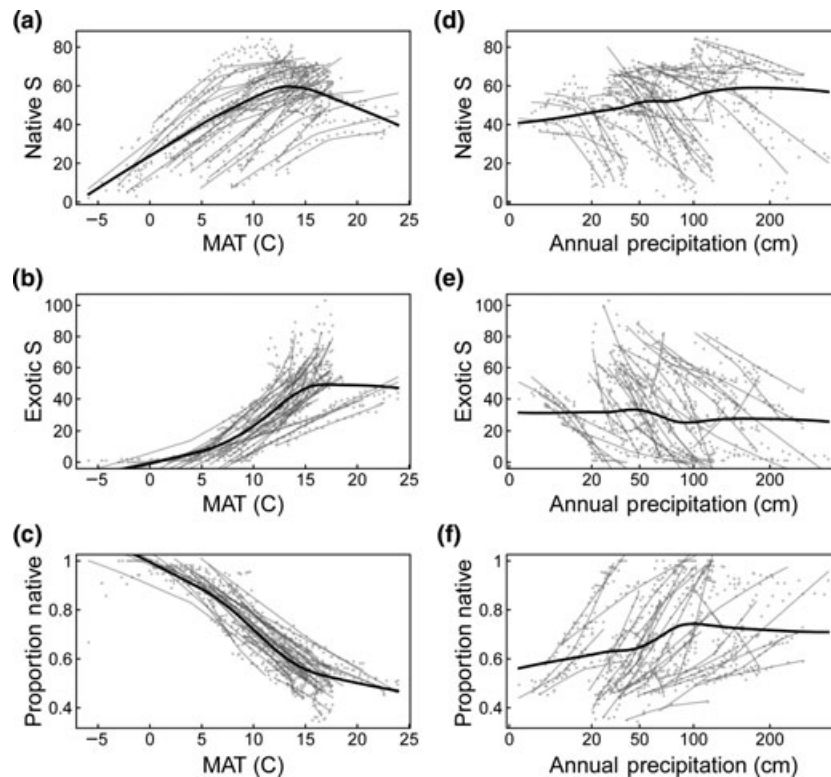


Fig. 4 Relationships of species richness and climate. Each point represents one zone within California, the heavy line shows the loess regression relationship across all zones, and the gray lines show relationships along elevation gradients within each of 35 subregions. Native richness showed a hump-shaped relationship with temperature, although most within-region relationships were monotonically increasing, and almost no relationship with precipitation. Exotic richness increased with temperature monotonically. Mean annual temperature was a very strong predictor of the proportion of species within a zone that are exotic.

their traits, with exotic species being taller ($P = 0.0447$), having longer ($P = 0.0010$) and wider ($P < 0.0001$) leaves, higher SLA ($P = 0.0018$), higher N_{mass} ($P = 0.0082$), higher seed mass ($P = 0.0111$), and being less likely to be perennial ($P < 0.0001$; Table 1). For most of the traits, noxious invasive weeds had the most extreme trait values, while other exotics were intermediate between weeds and native species (Fig. S3). Trait differences between native and exotic species were robust to varying assumptions about the nature of missing trait data and error in our trait data (Appendix S1).

Many of the traits of grasses were strongly related to mean annual temperature in both the bivariate and multivariate approaches (Fig. 5, Table 2, Appendix S2). At warmer sites, species on average were larger (both taller and larger-leaved), with higher SLA, greater N_{mass} , shorter-lived leaves, lower N_{area} , larger seeds, earlier flowering times, and longer flowering seasons. The proportion of species within a zone that are perennial also decreased strongly as a function of mean annual temperature, as did the proportion that are C_4 , though the proportion C_4 was best

explained by cumulative water deficit, a variable that combines information on temperature and precipitation. Relationships between temperature and species traits remained strong even under assumptions of strong bias in trait collection and a poor correlation of true and measured trait values, although confidence was lower for poorly collected traits, including LL, N_{mass} , and N_{area} . In general, knowledge of distribution of the plants of California is quite good, but some poorly collected species may not have well-understood ranges. Well-collected species (at least 100 herbarium records) showed trait–climate correlations very similar to the overall relationships shown herein, while other species (fewer than 100 records) showed weaker relationships to climate (Appendix S1). Thus, there is an indication that incomplete knowledge of some species ranges added noise to this analysis, but well-known species strongly demonstrated the patterns reported herein.

While temperature appeared to provide the dominant control on grass trait variation, other environmental variables also appeared important. With increasing cumulative water deficits, decreasing water balances,

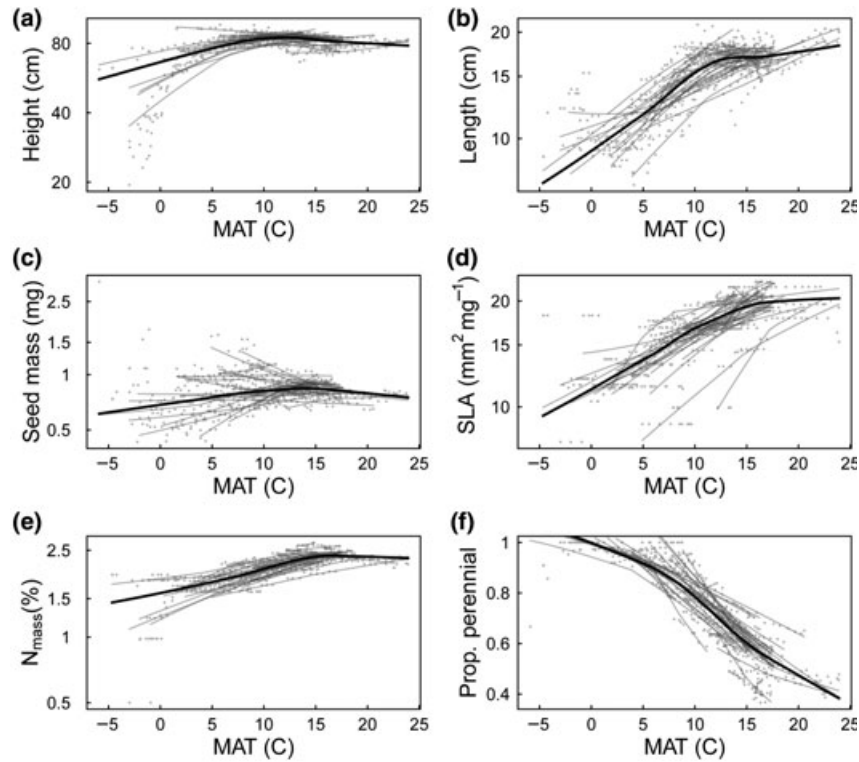


Fig. 5 Relationships of temperature and grass traits. Lines and symbols are as in Fig. 4. As temperature increases, the mean characteristics of the grass assemblage within a zone change significantly. These changes include increased mean height, increased leaf length, increased SLA, increased N_{mass} , and a decreased proportion of perennial species.

Table 2 R values for correlations between several climate variables and zone mean trait values, across all California grasses

Trait	Deficit months	Water balance	Cumulative deficit	PET	Sqrt (precip)	Mean temperature	Temperature seasonality	Sqrt (human influence)
Native	-0.283	0.313	0.381	-0.389	0.276	-0.890	-0.311	-0.515
Perennial	-0.358	0.375	0.453	-0.428	0.356	-0.892	-0.323	-0.463
C_4	0.615	-0.611	-0.716	0.585	-0.646	0.678	0.447	0.140
log(height)	-0.021	-0.052	-0.156	0.294	0.031	0.539	0.251	0.232
log(length)	0.211	-0.262	-0.364	0.427	-0.201	0.801	0.267	0.377
log(width)	0.048	-0.097	-0.198	0.290	-0.034	0.791	0.220	0.489
log(LL)	0.035	0.016	0.000	-0.123	-0.073	-0.484	-0.178	-0.450
log(SLA)	0.195	-0.230	-0.266	0.266	-0.205	0.748	0.289	0.484
log(N_{mass})	0.157	-0.193	-0.263	0.306	-0.146	0.761	0.252	0.402
log(N_{area})	-0.161	0.179	0.177	-0.153	0.173	-0.440	-0.155	-0.319
log(seed mass)	0.102	-0.099	-0.071	0.076	-0.085	0.182	0.120	0.078
Begin flowering	-0.364	0.396	0.492	-0.539	0.332	-0.874	-0.325	-0.371
Flowering length	0.440	-0.483	-0.586	0.601	-0.431	0.889	0.440	0.368

For each trait, the best r value is in bold. For nearly all the traits, zone mean values were most strongly related to mean annual temperature. LL, leaf lifespan; PET, potential evapotranspiration; SLA, specific leaf area.

and increasing months at deficit, grasses became longer-leaved with higher SLA, higher N_{mass} , lower N_{area} , and larger seeds. As human impacts increased,

zones became increasingly exotic-like in their trait composition, possibly reflecting the increased richness of exotic species in heavily used areas. This is likely due

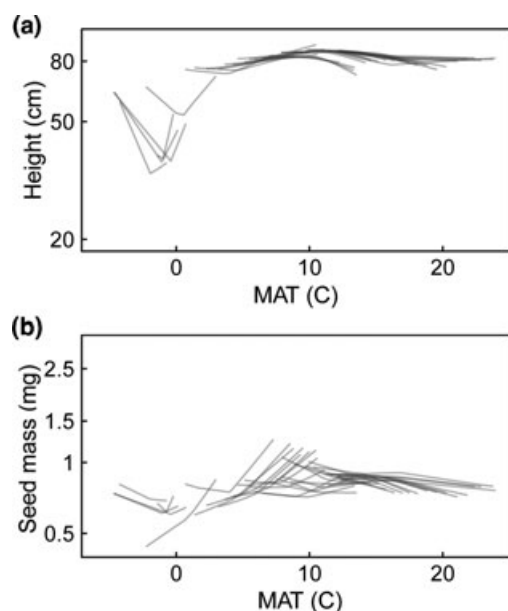


Fig. 6 Relationships between mean annual temperature and two traits (as in Fig. 5). However, in this case, the lines show loess fits to patterns across subregions, holding elevation constant (rather than patterns within subregions, allowing elevation to vary). While plant height was consistently positively correlated with temperature along elevational gradients, little consistent relationship was found among subregions at constant elevation (a). In contrast, the pattern of seed mass along elevational gradients was idiosyncratic. Among subregions, however, a hump-shaped relationship appears (b), with high elevations (cold areas) showing positive temperature–seed mass relationships and low elevations (warm areas) generally showing negative relationships.

to a combination of increased propagule pressure and increased disturbance.

Our analysis of trait–climate relationships across elevational bands within subregions and within elevational bands across subregions revealed some variation around these basic relationships. For example, moving up elevational gradients within subregions consistently led to reductions in mean grass height. However, there was little consistent relationship between height and temperature when elevation was kept constant and multiple regions were compared (Figs 5 and 6). Seed mass showed either positive or negative relationships to temperature within subregions. However, at low elevations, across subregions, seed mass increases with temperature, while at high elevation it decreases (Figs 5 and 6). This produces the ambiguous within-subregion relationship. Generally, clines in traits were stronger along elevational gradients within subregions than across subregions at the same elevation.

We were able to predict the proportion of species in each zone that are native very effectively using only

zone mean annual temperature, trait–temperature relationships for native species, and trait differences between native and exotic species groups. The proportion of native species, predicted from leaf width patterns, was strongly correlated with the observed proportion ($r^2 = 0.71$; Fig. 2d). However, the relationship was nonlinear, and the predicted proportions spanned a much smaller range of values than observed proportions, leading to a poor fit to the 1 : 1 line. Rescaling the predicted proportions based on five randomly sampled sites where the proportion native was assumed to be known largely resolved these problems, leading to quantitative and accurate predictions of the proportion of native species ($r^2 = 0.81$; Fig. 7). We used unity-line r^2 to describe the deviation of the observed–predicted data from the 1 : 1 line (Romdal *et al.*, 2005; Sandel, 2009). Prior to rescaling, the unity-line r^2 was 0.12, while after rescaling it was 0.77, or nearly equal to the standard r^2 . The same approach explained a smaller but still substantial fraction of the variation in the proportion of species that are noxious weeds (Fig. S4; standard $r^2 = 0.52$, unity-line $r^2 = 0.33$). Other traits enabled rather strong predictions for the proportion native, with the notable exception of seed mass (Fig. S1).

Our estimates of exotic richness through time suggest that, prior to 1860, there were ca. 20–30 well-established exotic species in California (Fig. 8a). This number increased sharply through the early 1900s, but exotic richness increased slowly in the second half of the 20th century. The continued arrival of exotic species into California has changed the composition of the exotic flora. Through time, California's exotic flora has become progressively more perennial, more C_4 , and larger-seeded (Fig. 8b–d). The increasing prevalence of C_4 photosynthesis among exotic grasses has resulted in a similar prevalence as native species (Table 1), while mean seed size across exotic species were once smaller than native species but are currently larger. Finally, while the perennial life history is becoming more common among California's exotic species, it is still much less common than it is among native species.

Discussion

On average, exotic grasses are taller, have longer and wider leaves, and have larger SLA, N_{mass} , and seed size than native grasses. The exotic species that have become noxious weeds differed from other exotic species in the same ways. Exotic species are also more likely to be annuals and native species are more likely to be perennials. In general, these results are consistent with previous work on the differences in traits of native, exotic, and invasive species (Pyšek & Richardson, 2007). These patterns alone have interesting impli-

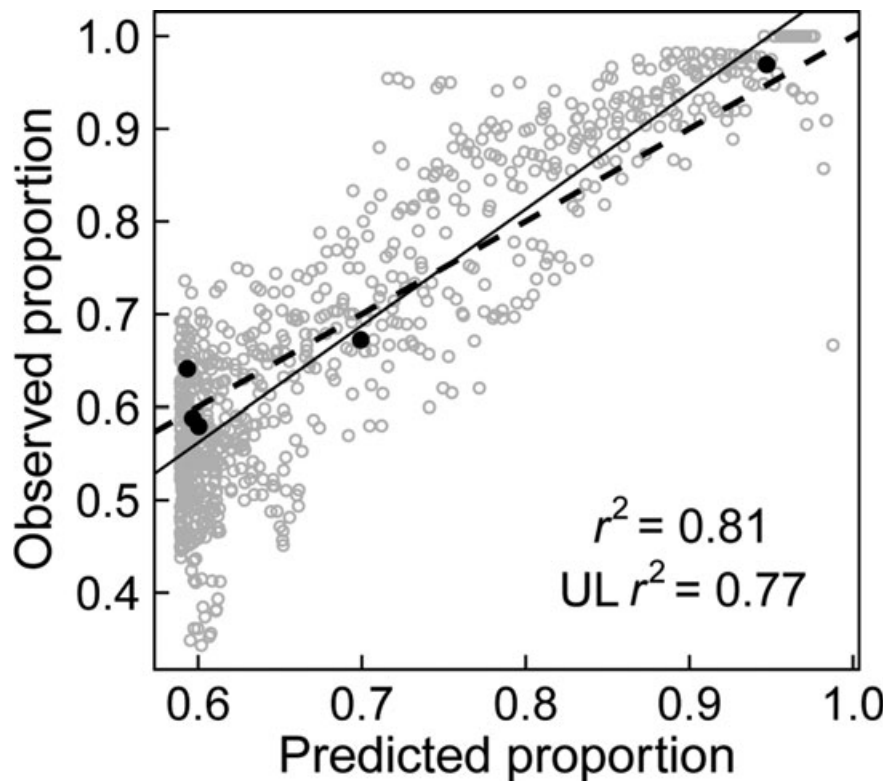


Fig. 7 Prediction for the proportion of species that are native, based on patterns of leaf width among native species and scaled by assuming knowledge of the proportion native in five randomly chosen zones. This rescaling allows a prediction to the remaining 795 zones of California that is both accurate and near the one-to-one line (dashed line, compare with Fig. 2d). The solid line shows the linear regression relationship between predicted and observed data. The five black points represent the five randomly selected zones that were used to rescale the prediction (see text).

cations for the spread of exotic species – exotics that are taller and have more light-capturing ability than native species may outcompete natives for light, and the larger seeds of exotic species could give them a competitive advantage at the seedling stage. Weedy exotic species tend to be particularly extreme in these respects, possibly helping to explain why certain exotic species have become invasive in California. When combined with the climate information, the situation becomes even less favorable for native species. With increasing temperature, the mean traits of a grass assemblage shift: height, leaf length, leaf width, SLA, N_{mass} , and the proportion of annual species all increase. These are all traits for which exotics have higher mean values than natives. Thus, exotic and invasive species are favored at higher temperatures, and currently noninvasive exotics might become invasive with climate change.

This result is supported by the present distribution of grass species richness within California. Based on observed trait differences between native and exotic species and on trait–temperature correlations, we predict that warmer parts of the state should have a higher

proportion of exotic species. In fact, both the proportion of species within a zone that are exotic and the proportion that are noxious weeds are strongly and positively related to mean annual temperature. This was very well captured by our quantitative approach to predicting the severity of invasion across California. Considering only the relationships of width to temperature among native species and the differences in leaf width between native and exotic species produced an index that explained 71% of the variation in the native: total richness ratio in California; scaling this index with data on the true ratio for five randomly selected sites improved this to 81%, with a strong fit to the 1 : 1 line. This strongly validates this trait- and climate-based approach, and shows that native species in warm climates are more ‘exotic-like’ in their traits than native species in cool climates.

Two conditions must be met for climate change to favor one species group (such as exotic species) over another (such as natives). First, changing climate must alter filters that act on traits, leading to communities with altered trait composition. Second, the two groups

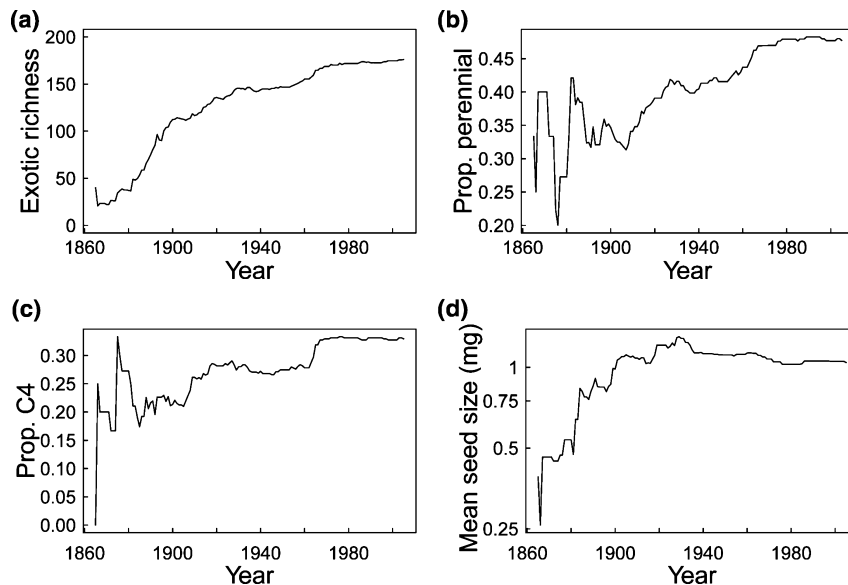


Fig. 8 Changes in the exotic grass flora of California over time. For any year, each exotic species was deemed present in the state if there is an herbarium record of that species before that year, otherwise it was deemed absent. Estimated exotic species richness (a) controls for species nondetection and increased sampling effort through time (see text). The number of exotic species in the state continues to increase into the 21st century (a). Later arrivals in California were more likely to be perennial and C_4 , leading to increasing proportions of these groups within the exotic flora over time (b and c). The earliest detected exotic species in California had small seed sizes. Later introductions increased mean seed size rapidly, until about 1920.

must differ along trait axes. Both of these conditions were clearly met in California, and may be commonly met in other systems as well. Trait–climate relationships are ubiquitous, suggesting that changing climate will typically alter community trait composition (e.g. Reich & Oleksyn, 2004; Wright *et al.*, 2005). And, although generalization has proven challenging, native and exotic species do often differ along at least some trait axes (Rejmanek & Richardson, 1996; Richardson & Rejmanek, 2004; Leishman *et al.*, 2007). Leishman *et al.* (2007) found that invasive exotic plants from a variety of habitats around the world have higher values of leaf traits associated with carbon capture [i.e. foliar nitrogen and phosphorus (N_{mass} and P_{mass}), assimilation rate (A_{mass} and A_{area}), and leaf area ratio (LAR)]. Our results from California grasses support that pattern, although not all the exotic grasses we considered are currently invasive. Exotic species may be better at capturing carbon for short-term benefit and faster growth.

The traits of California's grasses are most strongly associated with temperature. This is somewhat surprising, because some previous work on grass trait relationships with climate have found much stronger effects of precipitation (Oyarzabal *et al.*, 2008). All measures of plant size (height, leaf length, and leaf width) were positively correlated with temperature. This pattern is consistent with broad-scale analyses of plant height (Moles *et al.*, 2009) and leaf size (Dolph & Dilcher, 1980; Simo-

nin *et al.*, in preparation) that have demonstrated increases in plant height and leaf size with increasing temperature. Similarly, as others have found, we identified a positive response of seed mass to temperature (Moles *et al.*, 2007).

Several of the major leaf trait–climate relationships we observed were inconsistent with similar analyses. N_{mass} typically decreases with increased mean annual temperatures, for grasses (Reich & Oleksyn, 2004; Oyarzabal *et al.*, 2008), trees (Swenson & Weiser, 2010), and plants at large (Wright *et al.*, 2005). In contrast, in this study, we found higher community mean N_{mass} values with increasing temperature. Considering all plant species, SLA has been shown to decrease with increasing temperature (Wright *et al.*, 2005; He *et al.*, 2006), while we found an increase in SLA with temperature. These anomalous results could be due to biased sampling of the grass flora for these traits, though the bias would have to be quite severe to reverse the direction of the correlation. Further, though the results might not apply to grasses in general because of low sampling for these traits, they apply perfectly well to the subset of grasses for which trait data were available, and most previous work has also not exhaustively sampled the focal clade.

Increased leaf N concentrations with decreasing temperature may be a means for plants to compensate for reduced photosynthetic reaction rates caused directly

by low temperature (Reich & Oleksyn, 2004). By creating high concentrations of photosynthetic enzymes, plants offset the lower per-enzyme reaction rates caused by low temperature. On the other hand, plants growing in warmer environments are likely to experience higher decomposition rates and greater nutrient availability, leading to an expected positive relationship between temperature and leaf N concentration (Reich & Oleksyn, 2004). Thus, the N concentration of California's grasses may be more strongly controlled by adaptation to nutrient availability, rather than compensation for slowed photosynthetic rates at low temperature.

The shifts we predict in the plant community composition may affect herbivores, causing feedbacks to the plant community (Wookey *et al.*, 2009). Grazing herbivores (e.g. livestock or elk) already negatively affect native plants (Kimball & Schiffman, 2003; Marty *et al.*, 2005), and may reinforce future exotic dominance driven by climate change (HilleRisLambers *et al.*, 2010). Human impacts on the ecosystems of California are expected to intensify over the coming century, which may further promote the spread of exotic species.

Limitations

Large-scale comparative studies based on species traits have great potential to advance our understanding and predictive ability in a wide variety of areas of ecology. However, there are several methodological challenges inherent to such approaches. Species trait measurements are subject to error from a variety of sources, and it is often impossible to obtain trait information for all species. Both these problems may obfuscate patterns and potentially introduce bias.

In this study, we detected widespread trait differences between native and exotic species and along climate gradients. Thus, the problem of missing real patterns because of unavailable or erroneous data does not seem to apply strongly here. Of more concern is the possibility that detected results were the result of bias in measurement or sampling. We performed analyses using Monte Carlo simulations and a range of assumptions about sources of error and missing data (Appendix S1). These analyses showed that bias would have to have been extremely strong in most cases for our detected results to plausibly be due only to bias, particularly for well-sampled traits. Nevertheless, for some traits we have information for only a small number of species, so results for these traits should be considered preliminary.

Imperfect knowledge of the distribution of California's grasses did not seem to be a major source of error. This is perhaps not surprising, given the intensive his-

tory of botanical collections in the state. Trait-climate relationships were somewhat weakened among poorly collected species, suggesting that errors in defining these species ranges may have added some noise to our analysis. Nevertheless, patterns among the many well-collected species of the state strongly support the patterns reported herein.

In general, our analysis of the sensitivity of our results to errors indicated that measurement error, missing data, and errors in species range maps could be sources of noise that would make it difficult to detect existing patterns. However, there was little indication that they could be sources of bias that would spuriously create the detected patterns when, in fact, no such pattern existed.

Conclusion

Temperature appears to provide the dominant control over trait patterns among California's grasses, suggesting that impending changes in temperature will have major impacts on the composition of grass assemblages. Based on trait differences between native and exotic species, these shifts should include increased dominance of exotic species, a prediction corroborated by the current patterns of exotic dominance in the state. Predicting changes in the invasive potential for large numbers of species over large areas with climate change has proven challenging (Peterson *et al.*, 2008); herein, we demonstrate how a comparative trait-based approach can improve such predictions.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Sensitivity analysis

Appendix S2. RLQ analysis

Figure S1. Prediction for the proportion of species that are native based on various traits, and scaled by assuming knowledge of the true proportion native at five randomly selected sites (black dots). For all traits except for seed mass, the modeling approach provides a good prediction for the proportion native [good fit of the regression (solid line) to the one-to-one line (dashed)], with high r^2 and unity-line r^2 values.

Figure S2. Weed species richness and the proportion of species that are weeds increases with increasing mean annual temperature. This relationship is similar to that observed for exotic species in general.

Figure S3. Comparison of trait means for native (N), non-weed exotic (E) and weed (W) species. Different letters indicate significant pairwise differences (*post hoc* Tukey HSD test). For most traits, weeds differed from other exotic species in the same manner as nonweed exotic species differed from native species. This suggests that the trait states possessed by exotic species, expressed in extremes, tend to promote the species becoming invasive.

Figure S4. Prediction for the proportion of species that are invasive weeds based on leaf width. The fit of prediction to observed data is similar to but weaker than that obtained for exotic species in general.

Table S1 OLS and SAR parameter estimate comparison for the relationship between mean annual temperature and the named variable across 800 zones in California.

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