Effects of a directional abiotic gradient on plant community dynamics and invasion in a coastal dune system

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Summary

1 Local abiotic factors are likely to play a crucial role in modifying the relative abundance of native and exotic species in plant communities. Natural gradients provide an ideal opportunity to test this hypothesis.

2 In a coastal dune system in northern California, we used comparative and experimental studies to evaluate how a wind and soil texture gradient influences the relative abundance of native and exotic plant species in this community.

3 We detected small-scale spatial variation in soil texture along a 200-m gradient from relatively sheltered to more exposed. Sand coarseness significantly increased with exposure while soil nitrate levels significantly decreased. The more extreme end of the gradient was also subject to greater wind speeds and less soil moisture.

4 The plant community consistently responded to this gradient in the 7 years censused. Species richness decreased with exposure, cover of natives decreased and cover of exotics increased at the more extreme end of the gradient.

5 A single-season wind-shelter experiment similarly shifted the balance between native and exotic species. Shelters decreased the relative density of exotic species and increased the relative density of natives regardless of position on the gradient.

6 These comparative and manipulative findings both suggest that a single factor, wind, at least partially explains the success of exotic species in a coastal dune plant community. This supports the hypothesis that local abiotic conditions can explain differences in invasibility within a plant community.

Key-words: abiotic factors, coastal dunes, gradients, nitrogen availability, plant community composition, plant invasions, soil particle size, wind.

Introduction

Worldwide, many plant communities are becoming increasingly dominated by non-native/exotic plant species (Mooney & Drake 1986; Drake *et al.* 1989; Cronk & Fuller 1995; Vitousek *et al.* 1996; Lonsdale 1999; Mack *et al.* 2000; Mooney & Hobbs 2000; Pimentel *et al.* 2000). A growing number of studies have documented that these exotic species are having adverse effects on native plant communities and altering ecosystem-level processes (Braithwaite & Lonsdale 1987; Vitousek *et al.* 1987; Braithwaite *et al.* 1989; Vitousek & Walker 1989; D'Antonio & Vitousek 1992; Alvarez & Cushman 2002).

This unfortunate reality has stimulated a wealth of research, much of it focusing on the factors that promote plant invasion, including disturbance (Hobbs & Huenneke 1992; Sher & Hyatt 1999; Cushman *et al.* 2004), nutrients and water (Huenneke *et al.* 1990; Maron & Connors 1996; Hamilton *et al.* 1999; Davis *et al.* 2000; Carino & Daehler 2002; Holway *et al.* 2002; Hoopes & Hall 2002), diversity (Crawley *et al.* 1999; Levine & D'Antonio 1999; Levine 2000; Naeem *et al.* 2000; Kennedy *et al.* 2002) and herbivory (D'Antonio 1993; Maron & Vila 2001). We suspect that one of the most important keys to understanding invasibility of a community is how invasion processes vary along biotic and abiotic gradients within a local environment. However, investigators often neglect to identify the underlying suite of abiotic factors, or concomitant changes in multiple factors, that may promote invasion within a local environment. Hence, a comprehensive understanding of invasibility may be

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achieved through explicit identification and manipulation of environmental variation along gradients.

Gradients have been successfully used to understand many aspects of plant ecology as they provide an ideal opportunity to study natural variation in abiotic factors that may drive community change (Grime 1977, 1979; Tilman 1988; Goldberg 1990; Bertness & Callaway 1994; Callaway 1995, 1997). However, relative to the large number of studies on invasion, natural gradients have not been used extensively to predict the relative abundance of native and exotic species in plant communities (D'Antonio 1993; Holway *et al*. 2002; Hoopes & Hall 2002; Jurjavcic *et al*. 2002; Kolb *et al*. 2002; Von Holle 2005; MacDougall *et al*. 2006). Gradients can be used at many scales but are particularly informative when interrelated changes in abiotic factors can be quantified. Furthermore, if we can predict how native and exotic species respond simultaneously to regular changes in abiotic factors along a gradient, this may provide insight into key factors that influence the relative balance between natives and exotics within an invaded system.

Using both comparative and experimental approaches in a dune system on the coast of northern California, we have tested the importance of an abiotic gradient in determining the relative abundance of native and exotic plant species in this community. We specifically test three questions: (i) do wind and soil characteristics effectively constitute a small-scale directional gradient; (ii) does the plant community respond to this gradient and concomitantly is there a shift in the relative balance between native and exotic plant species; and (iii) does direct manipulation of wind affect the plant community and the relative native/exotic balance?

Methods

STUDY SYSTEM

The study site was a coastal hind-dune system located on Bodega Head, a small peninsula in Sonoma County, California (38°19′N, 123°3′W). The 100 × 210 m study area was located within Sonoma Coast State Beaches and consisted of two adjacent dune ridges and the associated trough between them. The north end of the ridges and trough was closest to the open ocean (but not exposed to direct salt spray) and the south end was adjacent to the sheltered Bodega Bay. This area is characterized by a Mediterranean-type climate, with 90% of the annual precipitation occurring between October and April (Barbour *et al*. 1973). The sandy top soils of this dune system generally contain very little organic matter and are fast-draining and nitrogen-poor (Barbour *et al*. 1973). Unlike many dune systems in northern California, this site is not dominated by *Ammophila arenaria* (Poaceae; European beachgrass), and still has a relatively diverse native flora. The two most abundant shrub species in this system are *Lupinus chamissonis* (Fabacaeae) and *Ericameria ericoides* (Asteraceae), with 15% and 20%

cover, respectively (J.H. Cushman, unpublished data). The plant community is also composed of annual and perennial herbs, forbs and grasses, both near the shrubs and in the interstices. This study focused only on the dynamics between the herbs, forbs and grasses found in the interstices.

ABIOTIC ATTRIBUTES OF DUNE GRADIENT

In 1997, at the establishment of the long-term monitoring project, soil characteristics were recorded at 12 plots distributed along a 210-m stretch of coastal hind dune. One end of this linear array of plots was located 100 m from Bodega Bay, while the other end was situated 1 km from the Pacific Ocean (hereafter referred to as sheltered and exposed, respectively). Plots were 6 × 6 m in size and arranged at the following 12 distances on the flat dune trough moving from sheltered to exposed: 3, 15, 41, 53, 79, 91, 117, 129, 155, 167, 193 and 205 m. In late February 1997, three 40-g soil samples were collected at a depth of 0–15 cm from each of these 12 locations. These samples were analysed for ammonium (NH_4^+) and nitrate (NO_3^-) content using standard KCl procedures (Page *et al*. 1982; Wheatley *et al*. 1989), and values were expressed per g of dry mass of soil. In early May 1997, soil samples were collected from the same locations to determine how sand particle size and soil moisture varied along the 210-m gradient. Each 40-g sample was first sifted through a 2-mm mesh sieve to remove large organic matter. Soil samples were then sifted through a nested set of four sieves (1167 μm, 590 μm, 250 μm and 53 μm) (Gee & Bauder 1986). We determined the proportional mass of all four particle size classes and calculated a sand coarseness index for each sample (see Statistical analyses). Moisture content of each sample was determined gravimetrically.

In 2002, particle coarseness of the sand and soil moisture were measured at much greater replication at the extremes of the dune where manipulative experiments were performed (see Wind-amelioration experiment). Soil cores were collected on eight different days throughout the season and included four wet days (rained that day) and four dry days (3 days after a precipitation event), with 12 replicates for each extreme of the dune. Wet and dry collection days were tested separately to determine if soil moisture differences were ephemeral. In addition to the percentage water content per sample (g H_2O/g sand), we also calculated the percentage of maximum field capacity (% water content in sample/max % water content that field samples could hold). Particle coarseness was measured as before (Gee & Bauder 1986).

Wind speed was measured in 2002 at the two extremes of the dune (bay and ocean) using a Kestrel® hand-held digital anemometer at 1.2 m and 5 cm above the soil surface (11 different randomly selected days sampled, $n = 8$ per dune location per height). We sampled wind speed at two heights to quantify crude differences that may influence plants directly near the soil surface or indirectly above plants.

PLANT COMMUNITY COMPOSITION AND STRUCTURE

Using the 12 plots, species-specific percentage cover of all plant taxa was recorded from 1996 to 2002 at the end of each growing season (typically in May or early June, depending on the seasonal phenology). The point-intercept method was used to estimate cover for each species (Floyd & Anderson 1987) with 126 points sampled per 6×6 m plot. Six transects within each plot were demarcated along an axis of the plot using a stratified-random approach. Points were regularly sampled every 20 cm along each of these transects. These data were used to calculate species richness, heterogeneity of species measured by the reciprocal of Simpson's D, and evenness of species occurrences across samples by E_{var} (Smith & Wilson 1996). Each species was also classified as either annual/perennial and native/exotic, and the relative cover of these groupings was additionally calculated.

To provide a crude estimate of above-ground biomass production along the dune, we harvested one 20-cm-diameter circle of vegetation in each 6×6 m plot in 2002. The circular plots were randomly placed in the interstices between shrubs within the plots to avoid possible shrub effects. The total plant density in each circle was also recorded prior to harvest, and all above-ground biomass was harvested in March 2002, dried for 48 h at 60 °C and weighed.

WIND-AMELIORATION EXPERIMENT

In October 2001, prior to the beginning of the growing season, eight three-sided $0.5 \times 0.5 \times 0.5$ m square wind shelters made of UV-permeable Perspex® were erected, with four pairs of plots at each extreme of the gradient. One plot within each pair was randomly assigned to either shelter or ambient wind conditions. The cold, desiccating winds of this area typically blow from the ocean in the north (Barbour *et al.* 1973), so plots were erected with the open end facing the bay. This design, three-sided and open at the top and back, was selected to maximize wind reduction and minimize temperature increases due to a greenhouse effect. Temperature and wind speed were measured in a subset of the final plots used here (three pairs in the bay habitat) using a hand-held digital anemometer and Hobo® data loggers. Temperature probes were placed in the middle of the plots at the soil surface, and wind speed was measured immediately behind the north-facing Perspex sheet (5 cm away) and the centre of the plots.

The vegetation in a 40×40 cm area was censused within the plots (a 10-cm buffer was left to avoid edge effects) at the start of the growing season in December 2001 and at the end of the growing season in April 2002. The density of each species present was recorded in three locations within the plots: 10 cm from the north-facing sheet, the centre of the plot and 10 cm from the open end of the plots (three 10×10 cm cells were used at each location to count density and were pooled for analysis). At the end of the growing season, vegetation was harvested, dried for 48 h at 60 °C and weighed.

STATISTICAL ANALYSES

Regression analyses were used to test for a relationship between soil characteristics measured in 1997 (coarseness, nitrate and ammonium concentrations, pH and water content) and distance along the gradient. In 2002, full-factorial repeated-measures ANOVAS were used to test for an effect of dune position (sheltered or exposed), census date (8 days) and condition (wet or dry day) on the percentage water content and the percentage maximum field capacity of the samples. In these analyses, we modelled census as a random effect and condition and position on dune as fixed effects. To assess the soil coarseness data (2002), we conducted a principal component analysis to reduce the five measures of coarseness (percentage mass in each sieve class) to a single measure (Manly 1994). We then tested for a relationship between soil coarseness and soil moisture with regression analysis. Differences in wind speed on the dune in 2002 were tested by census date (11 days between January and April), dune position (sheltered or exposed) and height above dune (5 cm and 1.2 m) with a full-factorial repeated-measures ANOVA. ANOVA and regression analyses were done in JMP 5.1.1 (SAS 2004) and multivariate analyses in Canoco version 4.54 with Winkyst 1.0 module and Canodraw (ter Braak & Smilauer 2006).

General interannual plant community-level patterns were assessed with a repeated-measures MANOVA with appropriate interaction effects such as year × factor to initially identify significant effects. Following this, independent repeated-measures ANOVAS were applied to each measure including richness, cover, evenness, relative cover by native/exotic, and species richness by native/exotic classifications. Census was modelled as a random effect in all analyses, and Tukey's HSD *post-hoc* contrasts were applied to test for directional temporal patterns in measures.

Separate repeated-measures MANOVAS were also used to screen for effects of census (7 years) and gradient position (12 locations) on the plant community responses including richness, evenness and relative cover of species. Repeated-measures ANOVAS with contrast analyses were then applied to each response variable with significant year–distance interaction terms (Scheiner & Gurevitch 2001) followed by regression analyses. Annual vs. perennial and native vs. exotic species classifications were also tested as factors. As an external check on possible inflated Type II error, a community-level response to the gradient without classifications was also tested (i) by non-metric multidimensional scaling (NMDS) to assess dimensionality of the species cover matrices (calculated using Bray–Curtis similarities) and (ii) by testing for vectors of maximum correlation between the significant ordination axes describing the plant community and actual linear gradient position

including concomitant environmental variables (McCune & Grace 2002). Rare species (fewer than three occurrences in 24 plots) were excluded, data were arcsine square-root transformed and Sorensen (Bray–Curtis) distance measures were used. Back-transformed values are, however, presented in all figures. Current ordination conventions were used including multiple random starts to seek a global, stable solution, multiple runs with the real data, and reporting of stress and number of iterations used in the final solution (McCune & Grace 2002).

In the wind-amelioration experiment, we first evaluated the efficacy of our manipulations using a repeated-measures ANOVA with wind treatment (+ or – wind), dune position (sheltered/exposed), location within the plots (north end, centre, open end) and census (11 separate days) as main effects. In the subset of plots for which we recorded temperature, a one-way repeated-measures ANOVA (+ or – wind) was used to test for differences. Two separate MANOVAS were used to evaluate vegetation data in this experiment, with wind treatment (+ or – wind), dune position (sheltered or exposed) and microsite location within the plots (north end, centre, open end) nested within wind treatment as the main factors. The response variables were richness, evenness and mean plant size in the first model, and the relative abundance and richness of native and exotic plants in the second. Significant interaction terms ($P < 0.05$) were then tested individually with ANOVAs and *post-hoc* contrast analyses. Using the entire matrix of relative species abundances without arbitrary classifications, community-level responses to wind treatment by dune position were also tested with a blocked multiresponse permutation procedure (MRBP) using treatment and position on dune to determine if the communities were significantly different (McCune & Grace 2002).

In both the gradient survey and the wind reduction experiment, potential interference between natives and exotics in richness and cover in the former and density in the latter were tested via regression analyses of natives vs. exotics.

Results

VARIATION IN SOIL CHARACTERISTICS AND WIND

In 1997, the first eigenvector (PC1) in the principal component analysis accounted for 65.5% of the variation in the four particle size classes tested and was thus used in subsequent statistical analyses as a composite

measure of soil coarseness (Table 1). Distance along the dune from sheltered to exposed predicted variation in soil coarseness in 1997, with samples near the extreme end of the gradient composed of increasingly coarse particles (Fig. 1a; $F_{1,2} = 64.63$, $r^2 = 0.96$, $P = 0.0001$). Concomitantly, soil nitrate concentrations significantly decreased with proximity to the more extreme end of the gradient (Fig. 1c; $F_{1,2} = 31.53$, $r^2 = 0.61$, $P = 0.0001$). No other soil measures such as ammonium concentration or pH were related to distance on the gradient (regression analyses, all $P > 0.10$ and $r^2 < 0.08$, not plotted). In 1997, distance on the gradient did not predict soil water content (Fig. 1e; $F_{1,2} = 0.18$, $r^2 = 0.07$, $P = 0.67$).

In 2002, more detailed measurements of soil coarseness and moisture were performed at the extremes of the dune gradient. Coarseness measures in 2002 corresponded with 1997; PC1 of the principal component analysis described 77.6% of the variation in particle size (Table 1), and the soil was also significantly more coarse near the exposed end of the gradient (ANOVA, $F_{1,175} = 820$, $P < 0.0001$). However, there were differences in water content in 2002, with significantly greater available soil moisture at the sheltered end of the dune, but only on wet days immediately after precipitation (Fig. 1d; ANOVA, $F_{1,175} = 18.18$, $P = 0.0001$). Additional analyses in 2002 to test for soil moisture differences using percentage of maximum field capacity also demonstrated the same trends, with higher capacities at the sheltered end of the gradient (ANOVA, $F_{1,94} = 9.22$, $P = 0.003$). Mean maximum field capacity at the sheltered end of the gradient was 33% (± 4%, 1 SE) and the exposed end 18.5% (± 2%). The coarseness of the sand did not directly predict water content in a given sample in either year (additional regression analyses, all $P > 0.10$ and $r^2 < 0.05$). As expected, the exposed end of the dune was subject to significantly greater wind speeds throughout the winter in 2002 at both 1.2 m and 5 cm above the surface of the dune (Fig. 1f; ANOVA, $F_{1,308} = 29.87$, $P = 0.0001$ with no significant interaction effects). In all years, the cover of bare ground also significantly increased with proximity to the exposed extreme of the gradient [repeated-measures (RM) ANOVA, $F_{1,154} = 7.5$, $P = 0.007$].

VARIATION IN PLANT COMMUNITY COMPOSITION AND STRUCTURE

Description of community-level patterns over time

Total mean plant species richness varied significantly in this coastal dune community from approximately 9 to

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Table 1 Principal component analyses for soil coarseness. Coarseness for each particle size category was calculated as the percentage mass present in each sieve size relative to total sample mass ($n = 96$). The eigenvector loadings are shown for each of the four particle size classes tested

Year	Eigenvalue 1	Cum. per cent	Coarse	Medium	Fine	Silt
1997	2.62	65.5	0.75	0.35	0.56	−0.02
2002	3.88	77.6	0.21	0.71	0.35	0.57
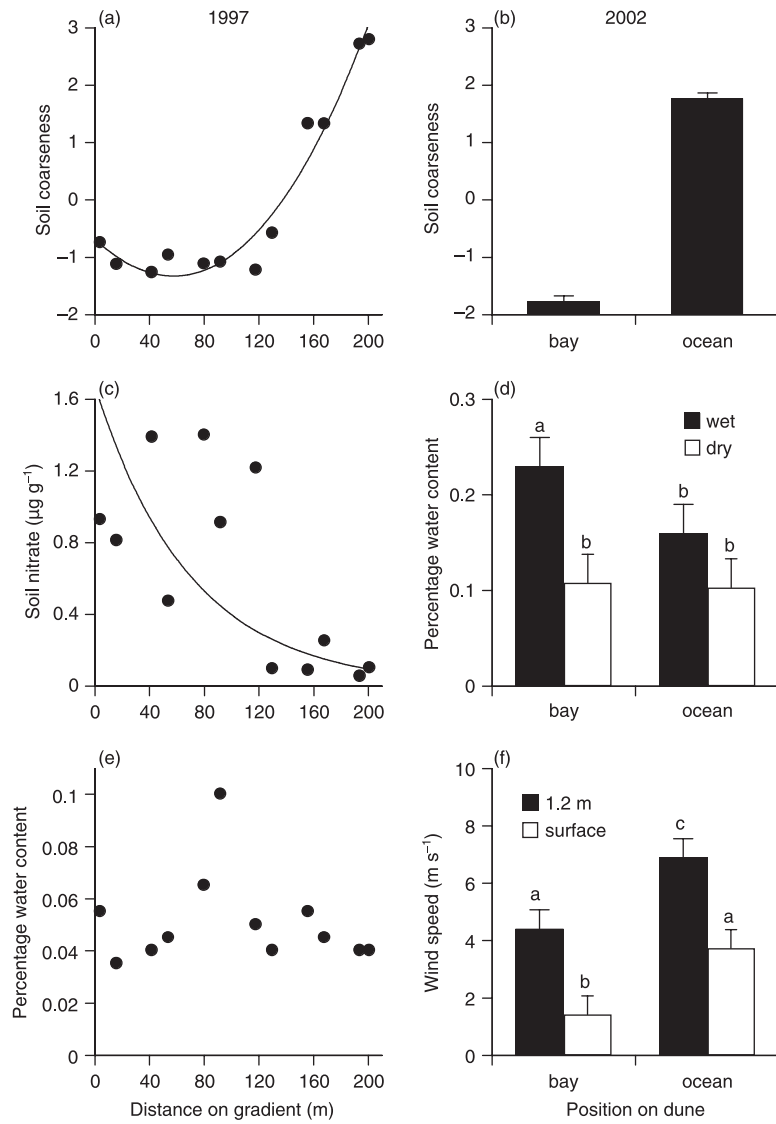
Fig. 1 Variation in abiotic factors on a coastal hind dune at Bodega Bay. In 1997, the abiotic factors were measured along the length of the dune at regular intervals and in 2002 only at the extremes. Lower distances on the dune are near the more sheltered bay and greater distances near the more exposed ocean end of the gradient (about 1 km from the ocean). Different letters denote significance in contrast analyses at $P < 0.05$, and error bars are 1 SE. Fitted lines are significant at $P < 0.05$ and non-linear curves were applied when r^2 was much greater than a linear fit, i.e. greater than a 10% increase. Equations for fitted curves include the following: (a) $f(x) = 1.2E\text{-}7*x^3 + 1.8E\text{-}4*x^2 + -2.2E\text{-}2*x + -6.9E\text{-}1$, and (c) $f(x) = 1.7 * \exp(-1.4E\text{-}2*x)$.

18 species per plot over the 7-year period censused (RM ANOVA, $F_{6,70} = 29.3$, $P < 0.0001$; Fig. 2a). Although more recent years tended to have greater numbers of species, particularly annuals (RM ANOVA, year × lifeform: $F_{6,1} = 34$, $P < 0.0001$), there was no consistent evidence for direct increases with time (Tukey's HSD linear *post-hoc* comparisons, $P > 0.05$). This interannual variation is not surprising given that the plant community is predominantly composed of annual species comprising approximately 60–80% of the total species present in a given plot (Fig. 2a), and that interannual climatic variation is significant in coastal California (Barbour *et al*. 1973). Relative cover of species similarly varied, with significant year to year variation (RM ANOVA, $F_{6,147} = 11.1$, $P < 0.0001$; Fig. 2b). Annuals exhibit both the greatest variation in cover among years (RM ANOVA, year × lifeform: $F_{6,1} = 14.5$, $P < 0.0001$; Fig. 2b) and also comprise the

majority of the total cover of the vegetation (~60–80%). Evenness of species significantly varied from year to year, but not linearly with time (RM ANOVA, $F_{6,70} = 3.1$, $P < 0.006$ with Tukey's HSD contrasts; Fig. 2c). In general, the open interstices of this dune community were consistently composed of the following dominant species in terms of rank order abundance by relative cover: *Bromus diandrus* (exotic), *Vulpia myuros* (exotic), *Chorizanthe cuspidata* (native), *Hypochaeris glabra* (exotic) and *Claytonia perfoliata* (native). The majority of the species cover in this community over a long-term average were thus exotic annual species (RM ANOVA, year × cover type: $F_{6,1} = 11.97$, $P < 0.0001$; Fig. 2d; exotics ~55% and natives ~43% over the 7 years censused). However, the number of native species present (albeit less cover) was consistently higher than the number of exotic species from year to year (RM ANOVA,
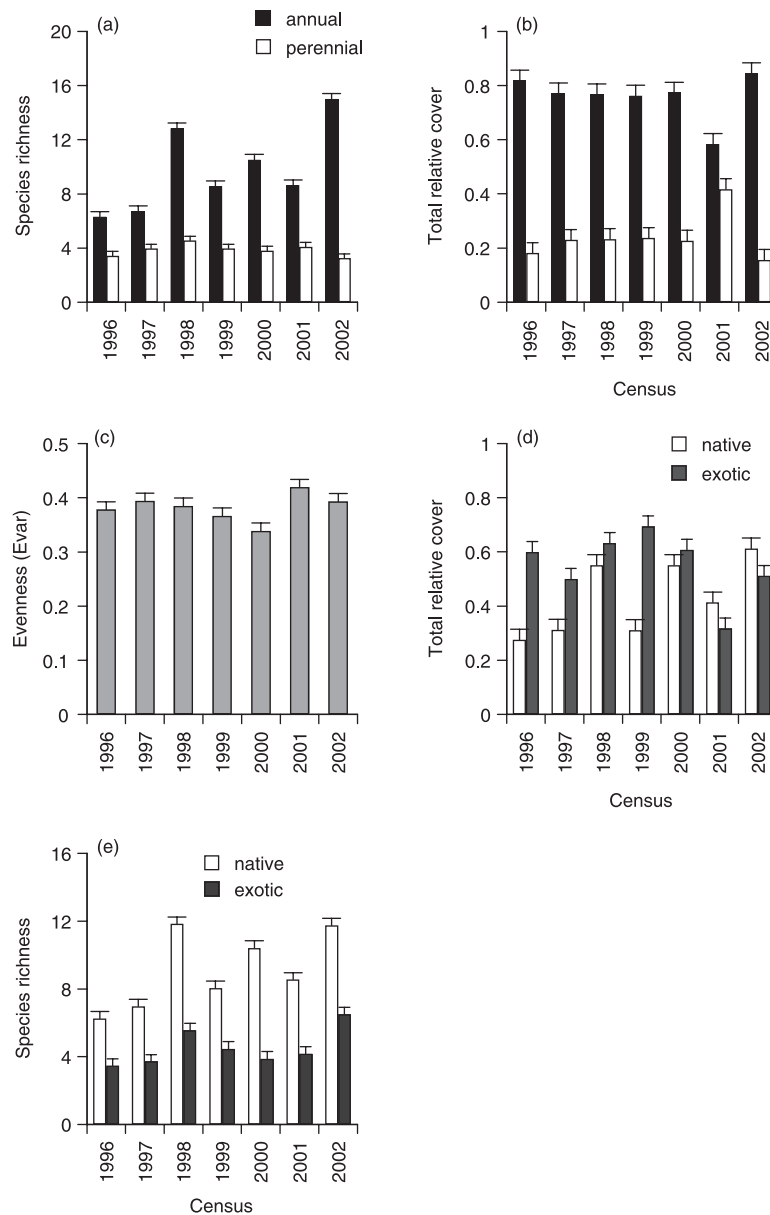
Fig. 2 A description of the community-level trends interannually independent of dune position. Richness is the number of species and evenness calculated using Evar (Smith & Wilson 1996). Error bars denote 1 SE.

year × cover type: $F_{6,1} = 6.24$, $P < 0.0001$; Fig. 2e; exotics ~33% and natives ~ 67% over the 7 years censused) and was significantly less variable (ANOVA comparing the pooled long-term coefficients of variation for mean richness of native vs. exotic species, $F_1 = 28.67$, $P = 0.0002$). This effect was driven by the occurrence of many different rare native species from year to year and not from single dominant natives; nonetheless, the numerically most common natives included *Chorizanthe cuspidata* and *Camissonia strigulosa*. Several exotic species were numerically dominant on the dune including *Vulpia myuros* and *Bromus diandrus*.

Gradient effects on the plant community

Although plant community composition varied seasonally, the general effect of the 200-m gradient was consistent (Table 2). No significant year × distance or higher order interaction effects (i.e. year × factor × distance) were detected in any subsequent statistical tests (i.e. homogeneity of slopes, Table 2). Furthermore, there was no evidence of linear increases or decreases in any response variables with time (*post-hoc* contrasts). As such, gradient effects discussed hereafter are summed across all census years. Total mean species richness decreased with increasing proximity to the more exposed extreme of the gradient (Fig. 3a; $r^2 = 0.53$, $P = 0.0067$) while mean evenness was unrelated to position on the gradient (Fig. 3b; $r^2 = 0.12$, $P = 0.26$). The mean proportion of annual species significantly increased with increasing proximity to the exposed extreme (Fig. 3c; $r^2 = 0.46$, $P = 0.016$) and concordantly log biomass per plant significantly decreased (2002 data, Fig. 3d; $r^2 = 0.44$, $P = 0.019$). Total mean species cover was not

Table 2 Summary of RM ANOVAs for the plant community responses to the gradient over time. Census refers to the 7 years tested, 1996–2002, position to the location on the 200-m gradient (12 locations), and appropriate interaction effects. Large MANOVAs were initially used to screen related response variables and to reduce Type II error

Measure	Effect	d.f.	SS	F ratio	P
Total richness	Census	6	411.8	31.87	0.0001
	Dune position	1	204.9	27.8	0.0001
	Census × Dune position	6	0.24	18.9	0.86
Evenness	Census	6	0.045	2.66	0.022
	Dune position	1	0.011	4.16	0.045
	Census × Dune position	6	0.028	1.64	0.15
Proportion of annuals	Census	6	0.31	12.05	0.0001
	Dune position	1	0.92	21.4	0.0001
	Census × Dune position	6	0.28	1.1	0.37
Total cover	Census	6	0.01	7.4	0.0001
	Dune position	1	0.003	11.31	0.0012
	Census × Dune position	6	0.002	1.2	0.32
Proportion annual cover	Census	6	0.74	10.33	0.0001
	Dune position	1	0.013	1.08	0.3
	Census × Dune position	6	0.08	1.12	0.36
Proportion exotic richness	Census	6	0.07	2.6	0.024
	Dune position	1	0.14	30.42	0.0001
	Census × Dune position	6	0.03	1.24	0.3
Proportion exotic cover	Census	6	0.53	13.7	0.0001
	Dune position	1	0.07	10.97	0.0015
	Census × Dune position	6	0.05	1.23	0.3

Table 3 Environmental factors for the 12 sites located on a coastal dune in California. Only significant factors are reported ($P < 0.05$) from the maximum correlations with the primary axis of the NMDS ordination solution. Means are reported ± 1 SD

Factor	Mean	R_{max}	P
Distance	104 ± 64.2	−0.93	0.0001
NH$_4$	1.15 ± 0.36	−0.82	0.0011
Water content	0.06 ± 0.02	−0.74	0.006

Table 4 Rank-ordered correlations for species significantly correlated with linear distance on the dune ($P < 0.05$). Nomenclature follows Hickman (1996)

Species	Origin	R
Bromus diandrus	exotic	−0.8841
Eriogonum latifolium	native	−0.8393
Phacelia distans	native	−0.7983
Bromus carinatus	native	−0.7961
Leymus pacificus	native	−0.7662
Stellaria media	exotic	−0.7538
Amsinckia spectabilis	native	−0.751
Marah fabaceus	native	−0.6937
Cardamine oligosperma	native	−0.6512
Senecio vulgaris	exotic	−0.6052
Vulpia myuros	exotic	0.5263
Hypochaeris glabra	exotic	0.6761
Aphanes occidentalis	native	0.6829
Erodium cicutarium	exotic	0.6863
Hesperevax sparsiflora	native	0.7124
Rumex acetosella	exotic	0.7341
Cardionema ramosissimum	native	0.7536
Camissonia cheiranthifolia	native	0.761
Chorizanthe cuspidata	native	0.8387

related to the gradient (Fig. 3e; $r^2 = 0.2$, $P = 0.09$) or to mean proportion annual cover (Fig. 3f; $r^2 = 0.09$, $P = 0.31$). Using ordination analyses (NMDS), a global solution was reached with two dimensions (50 iterations achieving a minimum stress of 0.02), and the first ordination axis was very strongly correlated with actual linear distance on the dune from sheltered to exposed while several environmental variables were also correlated (Fig. 4 and Table 3, all vectors plotted but only significant vectors reported in the table). The dominant species *Bromus diandrus* (exotic) was most negatively correlated with actual distance on the gradient, while four other exotics were positively correlated (Table 4). Natives were both negatively and positively correlated to distance on the dune (Table 4). Correspondingly, the relative proportion of exotic species significantly increased with increasing distances on the gradient (Fig. 5a; $r^2 = 0.8$, $P = 0.0001$) and the total relative cover of exotic species increased, but less dramatically, with distance (Fig. 5b; $r^2 = 0.3$, $P = 0.05$). This was likely to be due to different responses to the gradient by individual
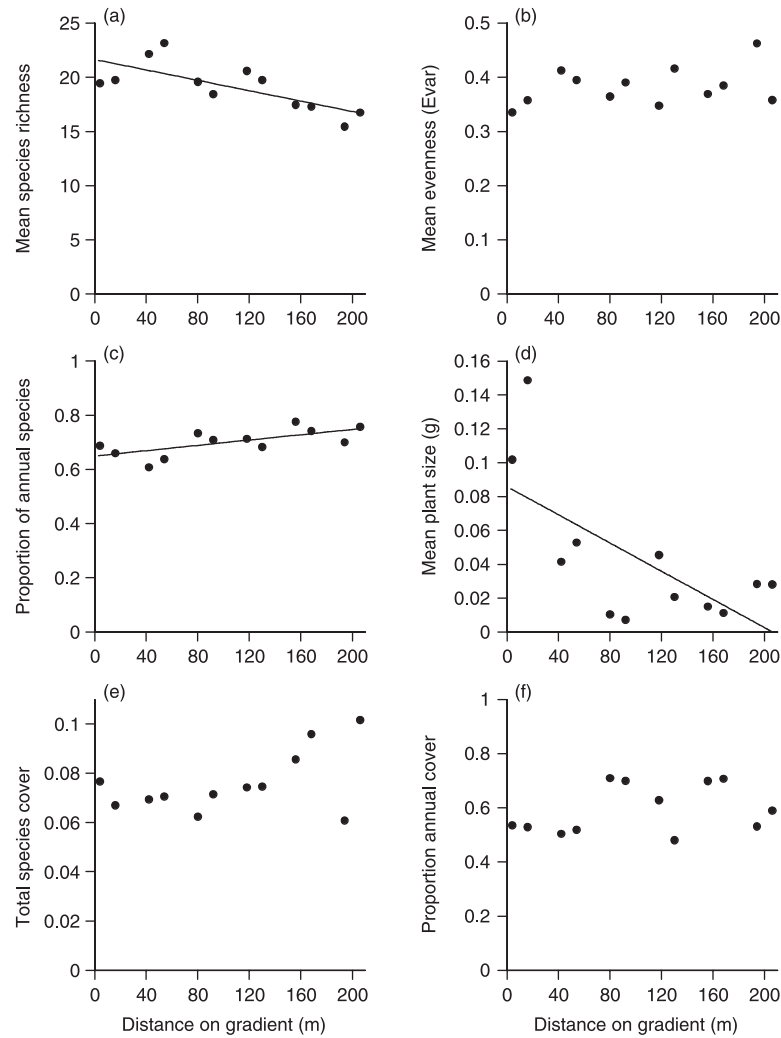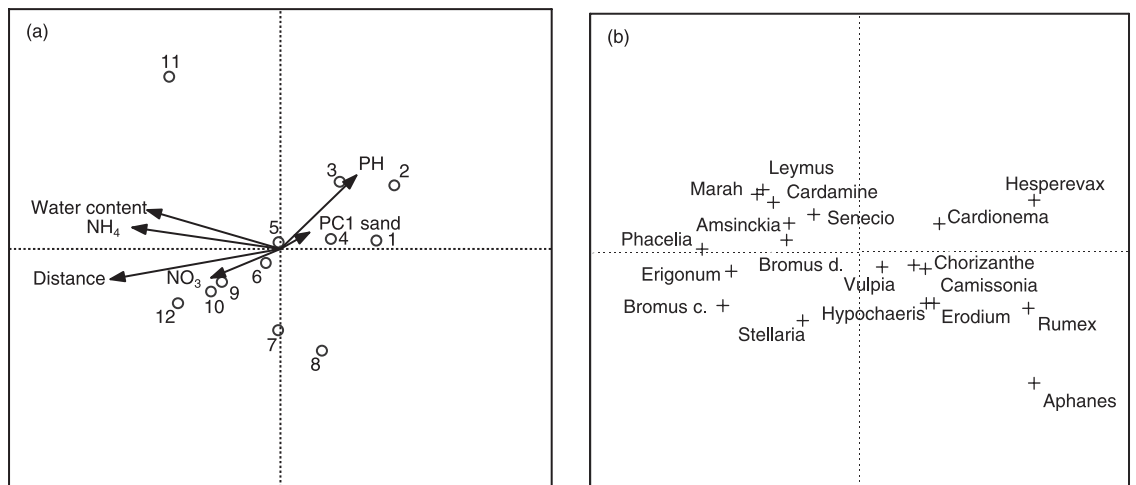
exotic species, i.e changes in *Bromus diandrus* vs. other exotics. Finally, there was no direct relationship between either the number or the cover of native species and that of exotics ($P < 0.5$), suggesting a lack of interference.

Wind-amelioration experiment

The wind shelters were extremely effective at reducing wind speed within the plots ($F_{1,341} = 285.38$, $P = 0.0001$),

Fig. 3 Variation in the plant community by location on the dune. Lower distances on the dune are near the bay and greater distances near the ocean. Richness is the number of species, evenness calculated using Evar (Smith & Wilson 1996), and mean plant size was calculated as total plant density harvested within 10-cm rings/total biomass (irrespective of species). Fitted lines are significant at $P < 0.05$. Equations for fitted curves include the following: (a) $f(x) = -2.4E\text{-}2*x + 2.2E\text{+}1$, (c) $f(x) = 4.9E\text{-}4*x + 6.5E\text{-}1$, and (d) $f(x) = -3.9E\text{-}3*x + -1.2$.

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95, 468–481

Fig. 4 NMDS ordination of plant community cover recorded at 12 sites on a coastal dune system in California (denoted by open circles). Vectors of maximum correlation for the environmental data are fitted to the ordination solution, and the vector labelled 'distance' refers to the actual linear distance on the gradient. PC1 sand refers to axis 1 of the PCA on sand coarseness. Axes range from −1.5 to 1.5 and the plot is centred on 0,0. Species centroid plots for those significantly correlated with linear distance on the dune gradient are shown in (b).
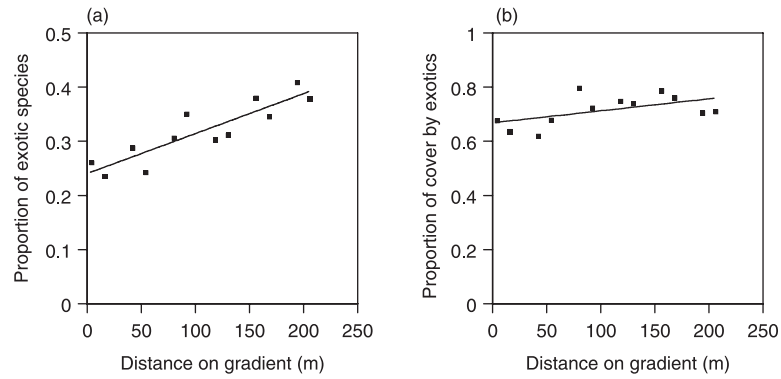
Fig. 5 Regression analyses of the relative response of exotic species to position on the dune gradient. Data shown are pooled from the entire census period. Equations for fitted curves include the following: (a) $f(x) = 7.4\text{E-4}*x + 2.4\text{E-1}$, and (b) $f(x) = 4.4\text{E-4}*x + 6.7\text{E-1}$.
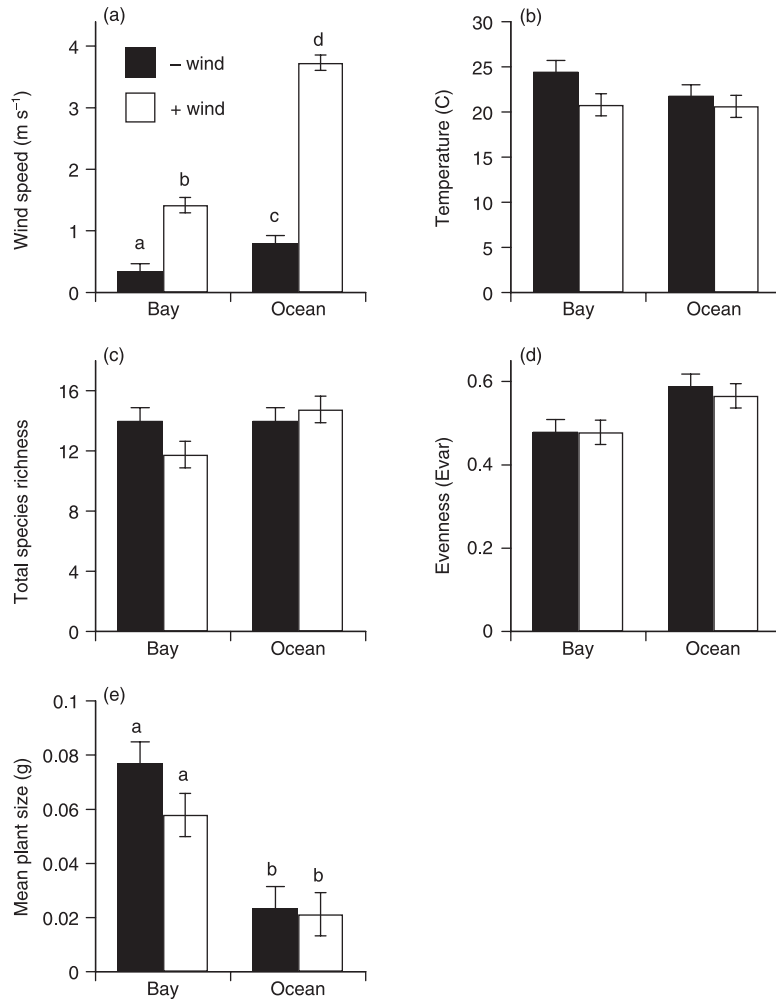

Fig. 6 The effects of a wind reduction experiment on wind speed and temperature, and the generalized response of the plant community. The '– wind' treatment refers to shelters, and the '+ wind' to plots exposed to ambient wind conditions. Different letters denote significance in Tukey's multiple comparison tests at $P < 0.05$; error bars are 1 SE.

particularly near the ocean end of the dune where wind speeds were greater (Fig. 6a; dune position: $F_{1,341} = 136.6$, $P = 0.0001$, and wind reduction × dune position: $F_{1,341} = 60.95$, $P = 0.0001$). Wind speed was not significantly different between the front and centre of the plots $(F_{1,341} = 0.47, P = 0.63)$, and the temperature in the centre of the plots did not significantly differ between sheltered and control plots (Fig. 6b; $F_{1,10} = 0.16$, $P = 0.7$, mean sheltered = 21.8 ± 1.4 °C and control = 21.2 ± 1.4 °C).
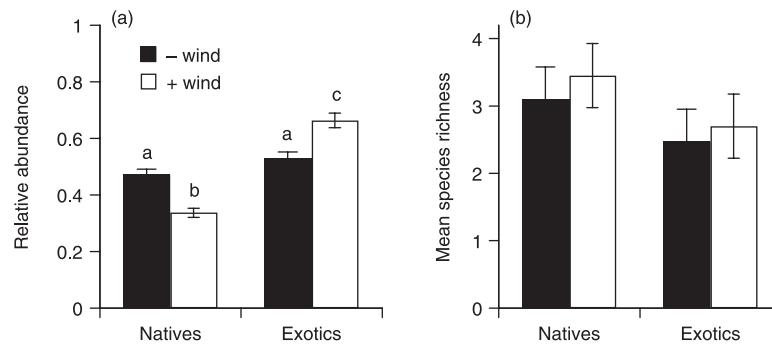
Fig. 7 A comparison of the specific responses of native vs. exotic species to experimental wind reduction. The '– wind' treatment refers to shelters, and the '+ wind' to plots exposed to ambient wind conditions. Different letters denote significance in Tukey's multiple comparison tests at *P* < 0.05; error bars are 1 SE.
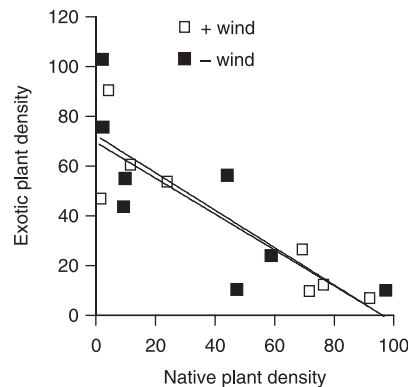
Fig. 8 The relationship between mean native and exotic plant densities in the experimental wind reduction plots. Fitted lines are significant at *P* < 0.05, and relationships were best described by linear curves. Values are pooled for both extremes of the gradient tested (no significant interaction terms; see text). The sheltered treatments were best described by $f(x) = -7.5\text{E-}1*x + 7.2\text{E+}1$, and open plots by the curve $f(x) = -7.2\text{E-}1*x + 7\text{E+}1$.

Experimental wind reduction did not significantly influence general community measures such as total plant species richness or evenness (Fig. 6c,d, MANOVA, wind reduction: $F_{1,12} = 0.08$, $P = 0.34$, wind reduction × dune position: $F_{1,12} = 0.52$, $P = 0.49$), or patterns in whole-community species abundances using a blocked multiresponse permutation procedure on raw density data for all species (MRBP using Euclidean distance measures: $A = 0.17$, $P = 0.16$). While plants were on average larger at the more sheltered extreme of the gradient, i.e. closer to the bay (Fig. 6e; ANOVA with *post-hoc* contrasts, position: $F_1 = 31.5$, $P = 0.0001$), there was no effect of experimental wind reduction on mean plant size (Fig. 6e; ANOVA, treatment: $F_1 = 1.75$, $P = 0.2$). Wind amelioration and dune position significantly and independently affected the relative balance between native and exotic species densities (Fig. 7a; $F_{1,105} = 5.59$, $P = 0.01$, and $F_{1,105} = 78.8$, $P = 0.0001$, respectively; no significant wind × position effects), with wind reduction increasing native plant densities and ambient wind favouring exotics. The mean number of native and exotic species present in

plots was unaffected by wind manipulation (Fig. 7b; anova, treatment: $F_{1,12} = 0.39$, $P = 0.54$). There was a direct negative relationship between native plant density and exotic plant density in both the wind reduction and the open plots (same relations at both dune extremes, Fig. 8; shelter treatment: $r^2 = 0.63$, $P = 0.02$; open plots: $r^2 = 0.81$, $P = 0.002$).

Discussion

In a coastal dune system in northern California, the importance of three aspects of environmental variation were tested in modifying the expression of exotic plant species. First, small-scale variation in abiotic factors effectively constituted a predictable and directional gradient along a 200-m stretch of dune even over a 7-year period. Although many attributes changed along the gradient consistent with predictions, including sand coarseness, nitrate pools and soil moisture, wind was identified as a principal driver of direct and indirect effects. Second, this environmental gradient demonstrated a repeatable influence on plant community composition in spite of significant interannual variation within the community. The more harsh end of the dune consistently favoured dominance by exotic species in both cover and richness. Third, direct manipulation of wind by shelters did not affect general community attributes such as richness, evenness or mean plant size but did significantly shift the balance between native and exotic plant densities within a single season. Wind reduction favoured native species, while ambient high wind conditions favoured exotics. Taken together, these three lines of evidence support the hypothesis that variation in local abiotic conditions can explain differences in invasibility within a plant community. Furthermore, it appears that more harsh conditions were a good predictor of exotic species dominance.

DIRECTIONALITY OF ABIOTIC GRADIENTS

While natural gradients provide an opportunity to test the importance of abiotic factors in determining the outcome of plant interactions in diverse systems, many

factors vary simultaneously and non-independently, thereby limiting our ability to infer invasibility. We chose a dune system that was relatively simple with consistent changes in abiotic factors over a relatively small area. Nonetheless, the abiotic factors we tested were likely to be related and contingent upon specific conditions. For instance, there was a significant difference between soil moisture measurements taken at the bay and ocean ends of the dune, but only on wet, rainy days, while neither coarseness of the sand nor distance on the dune directly predicted soil moisture content. This suggests either that a third factor in the field (likely to be wind in this study) influences soil moisture through desiccation or that variation in the field capacity of the sand influenced its ability to retain moisture (Bamberg & Smith 1968; Gee & Bauder 1986; Sheard & Geale 1988; Michalet *et al*. 2002). This potential temporal or spatial cropping of the true range of variation across a gradient may lead to inaccurate conclusions regarding the relative importance of a specific factor (McCoy 2002). Although it is critical to quantify the variation in individual factors, and often tempting to conclude that a single factor is most important, natural variation along a gradient will be a composite of effects and is best understood by measuring the fullest possible range of conditions in time and space. Hence, conclusions on the relative importance of local variation are best interpreted in light of relatively long-term data sets coupled with experimental manipulations. In this study, additional experiments such as controlled density manipulations or transplant experiments (Von Holle 2005) would have further strengthened our argument on the relative importance of the gradient to invasibility. However, this study does have the scope to suggest that directional changes in a gradient can exist, are consistent, serve as a reliable indicator of 'stress' and can provide a useful predictive context for exotic species.

Another recent study at an adjacent site similarly explored the factors that determine levels of plant invasion within a coastal grassland (Kolb *et al*. 2002). Variation in soil moisture and nitrogen were important predictors of the degree of plant invasion, with higher levels of both favouring exotics, i.e. less harsh sites were more invaded in this study. These relationships were not influenced by 'distance from the ocean'. However, Kolb *et al*. (2002) assessed proximity to ocean differently than in this study; distance referred to direct distance from open ocean, whereas in the current study, distance referred to sheltered or exposed within a hind-dune system not exposed to salt spray or relatively more direct wave effects. Furthermore, Kolb *et al*. (2002) tested the effect of position on a dune, i.e. bottom vs. sides, while we focused on linear changes along an even sand dune surface. Most importantly, relative to dunes, coastal grasslands clearly have unique suites of environmental conditions for both different resident and established exotic plant species. The divergent outcomes of these two studies emphasize the context-dependent nature of biological invasions and suggest that subtle changes in

habitat can influence local invasion dynamics. In this local comparison, changes from a coastal grassland to sandy disturbed dunes provided very different contexts for the expression of exotic species.

PLANT COMMUNITY CHANGES WITH TIME

The composition of this coastal dune plant community varied significantly over time but not linearly. The species assemblage was consistent seasonally in both cover and number of species. Community cover was often dominated by exotic plant species but not richness. This relates to the hypothesis that non-linear environmental heterogeneity can serve as a 'storage effect' for preserving species diversity (Chesson 2000) in space or time, and, in this instance, we propose may potentially maintain native plant diversity within a highly invaded region. A general lack of correspondence between number and cover measures used here is not surprising as there is significant variation in size even among annual plants and as structural measures often relate to both biotic and abiotic interactions locally (Watkins & Wilson 2003). Further research linking seedbanks to dominance of exotics would also be ecologically informative.

PLANT COMMUNITY CHANGES ON ABIOTIC GRADIENTS

In general, few studies have tested the performance of native and exotic species under different environmental conditions or 'stress levels' within a habitat (Nernberg & Dale 1997; Bakker & Wilson 2001; Kolb *et al*. 2002; Von Holle 2005; MacDougall *et al*. 2006). One widely cited hypothesis has been that high levels of environmental 'stress' reduce the invasibility of a habitat (Bakker 1986). However, in this system exotic species generally performed better, or at least were more abundant, at higher levels of 'stress' (increased effects of wind), which suggests that it is possible for exotics to be competitively inferior to natives at low stress but not necessarily at high stress (Alpert *et al*. 2000). Admittedly, stress is often used imprecisely (Körner 2003; Lortie *et al*. 2004), but in this study, both increases in the frequency of annual species and decreases in average mean plant size of species suggest that conditions in the habitat became more limiting at one extreme of the dune relative to the other. Here, regression analyses of native species richness, cover and density against exotics detected a direct negative relationship between increasing natives and decreasing exotics only for plant density. This supports a fundamental tenet of plant ecology that each measure might describe a different attribute of a community and that individual exotic species respond uniquely to both the abiotic gradient and the assemblage of local species. Von Holle (2005) similarly demonstrated that some exotic species can experience either competition or facilitation depending on the level of environmental stress, while a second

recent study concluded that exotic species substitutions can occur along an environmental gradient that was likely to be related to competitive abilities (MacDougall *et al*. 2006). In the present study, the natural gradient effects were consistent and predicted community composition over time. Of course not all exotic species responded in the same manner, i.e. substitutions did occur with different exotics occurring 'naturally' at both ends on the gradient, i.e *Bromus diandrus* decreased towards the ocean whereas *Vulpia myuros* increased, in spite of potential density-dependent interactions with natives. In the wind reduction experiment, however, changes in total exotic plant density occurred through increases in the density of exotic species already present in the plots and not through substitutions. Furthermore, neither total species richness nor evenness responded to the wind treatment, which suggests that the overall composition of the communities under each treatment was similar. As such, it is clear that (i) this system is heavily invaded in terms of cover and density but not relative richness, and (ii) the natural gradient can coarsely predict relative expression of exotic species through two potential pathways, substitutions or changes in relative density, both of which merit investigation.

THE PARTICULAR IMPORTANCE OF WIND ON DUNES

Wind is an important ecological factor that has not attracted a great deal of attention except in ecophysiology (Ennos 1997). Although many abiotic factors changed along the gradient herein, we predicted that wind was a primary driver – both directly and indirectly – of community-level changes. High wind speeds have been shown to reduce plant and whole-community boundary layers and can physically batter individuals (Hadley & Smith 1983; Osmond *et al*. 1987). Blowing sand can also lead to increased rates of desiccation in seedlings through ruptured plant cells that dry out exposed tissues (Fryrear *et al*. 1973). Wind itself can have severe physiological effects on plants (Osmond *et al*. 1987; Ennos 1997), including reduced drought tolerance (Grace & Russell 1977), and has been shown to have profound effects on alpine, subalpine and arctic communities (Marr 1977; Callaghan & Emmanuelson 1985; Carlsson & Callaghan 1991; Shevtsova *et al*. 1995; Baumeister & Callaway 2002; Kammer & Mohl 2002). Prevailing winds off the ocean can also indirectly influence the plant community by altering the coarseness of the sand. This occurs because winds move larger grains of sand shorter distances than finer particles (Barbour *et al*. 1973), which could potentially cause changes in soil moisture and nutrients. It is therefore reasonable to suggest that the particle size gradient was driven by wind, and that the associated variation in soil nitrogen and water availability was an indirect result of increased leaching caused by larger particles. Hence, we would argue that wind has the potential to explain some of the community-level patterns evident along gradients in harsh environments such as coastal habitats, in addition to alpine environments. A more novel extension is that wind can influence invasibility in coastal plant communities through alternative pathways as described above and not simply through seed dispersal. Although we suspect that wind-induced changes in nitrogen and water availability play a role in the patterns we detected, results from the wind-reduction experiment strongly suggest that the direct effects of wind are pronounced in this system. Here, the amelioration of wind modified the relative abundance of native and exotic species within a single season congruent with the vegetation patterns observed over a 7-year period. Windier conditions favoured the exotic species in this system, whereas wind reduction favoured the natives. In a previous wind-shelter experiment at Bodega Bay using shrubs, individual plants of a native species of lupin (*Lupinus arboreus*) positively responded to wind reduction while the exotic individuals (*Lupinus cosentinii*) were unaffected by wind (Gartner 1995). This approach could also be applied to other plant lifeforms to explore whether there are adaptive traits or individual ecotypes associated with the exotic dominants within a system. Nonetheless, we propose that wind can be an important factor with respect to invasions in coastal dune populations or communities.

SYNTHESIS

Gradients have been used extensively in ecology as a primary means to infer plant–plant interactions. Approaches typically associated with gradients, including comparative vegetation analyses, reciprocal transplants, phytometers, abiotic amelioration and detailed mapping of environmental conditions to community dynamics, can be used to contrast the relative importance of hypotheses for invasive species dynamics. In this study, an abiotic gradient was demonstrated, consistent directional effects on a plant community were detected and patterns of exotic species abundance were predicted. Wind acted as a key abiotic driver of exotic species success by shifting the balance towards higher exotic plant densities, but not through changes to other plant community attributes within a single season. Although exotic dominance and general plant community composition was explained by the gradient, exotic species still occurred throughout this dune ecosystem. More encouragingly, however, the persistence of native species richness in this invaded community is relatively high and consistent over a 7-year period, probably due to environmental storage effects.

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