The impact of the invasive alien grass *Cortaderia jubata* (Lemoine) Stapf on an endangered mediterranean-type shrubland in California

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Abstract. Since its introduction in the late 1800s, the perennial tussock grass *Cortaderia jubata* (Lemoine) Stapf has become an increasingly frequent member of coastal plant communities in California and Oregon. In this study, the community changes associated with *C. jubata* invasion into the mediterranean-type vegetation of Vandenberg Air Force Base, California were examined. Pristine plots of maritime chaparral were compared with spatially and topographically matched plots dominated by *C. jubata*. Aerial photographs indicated that the invaded plots had previously been shrubland. *C. jubata* invasion created a structurally less complex perennial grassland that was markedly depauperate in native shrub species. The absence of native shrubs depressed native richness in jubata grassland, but the greater richness of both native and alien herbaceous species made overall richness in jubata grassland indistinguishable from maritime chaparral. Vegetational differences were associated with differences in arthropod and small mammal populations between vegetation types. Arthropod abundance and order diversity were lower in plots dominated by *C. jubata* than in adjacent chaparral. Insect traps in *C. jubata* plots contained a significantly smaller proportion of Hymenoptera and Homoptera and a significantly greater proportion of Aràneae than traps in maritime chaparral. Rodent activity was significantly lower while rabbit activity was significantly greater in jubata grassland compared to maritime chaparral. This study indicates that the presence of *C. jubata* can dramatically alter the mediterranean-type landscape of central California. While it is likely that the initial establishment of *C. jubata* is associated with disturbances that are common in this ecosystem, the ability of *C. jubata* to expand from founding populations and to persist for long periods of time pose a serious threat to the native diversity of these unique systems.

Key words. Biological invasions, chaparral, mediterranean-type ecosystems, shrubland conversion.

INTRODUCTION

Mediterranean-type ecosystems cover less than 5% of the Earth's surface yet contain nearly 20% of the planet's known plant species (Cowling *et al.*, 1996). A number of anthropogenically induced changes threaten this remarkable plant diversity (Rundel, 1998). In particular, the threat posed by introduced non-native species has generated increasing concern (Groves, 1986; Kruger *et al.*, 1989; di Castri *et al.*, 1990; Groves & di Castri, 1991).

Introduced species have the potential to significantly alter population dynamics, community structure and ecosystem level processes (Elton, 1958; Drake, 1988; Macdonald *et al.*, 1989; D'Antonio & Vitousek, 1992). While understanding the precise nature of these changes is critically important for the effective management and conservation of mediterranean-type systems, it is often difficult to quantify the direct community-level effects of introduced species independent of other landscape level disturbances such as habitat fragmentation.

Introduced plants have unquestionably altered the mediterranean-type vegetation of California. Over the last 230 years, more than 1025 plant species have been added to the flora of the state (Rejmánek & Randall, 1994). Entire systems such as the native perennial grassland have been largely replaced by alien plants (Heady, 1977). Additionally, the anthropogenic influences of habitat fragmentation, altered disturbance regimes and the high frequency of new introductions leave the state's remaining mediterranean-type ecosystems highly susceptible to degradation by invasive plants (Mooney & Dunn, 1972; Mooney *et al.*, 1986; Soulé *et al.*, 1992; Alberts *et al.*, 1993). Surprisingly few studies, however, have quantified the changes wrought by these introductions. Moreover, while many introduced species have been identified as serious invasive wildland pests (see Robbins, 1940; McClintock, 1985; Halvorson, 1992), few studies have attempted to quantify how the continued expansion of these invasive species will impact native communities.

One invasive plant with the potential to significantly alter mediterranean-type ecosystems in California is *Cortaderia jubata* (Lemoine) Stapf (jubata grass). *C. jubata* is a large perennial tussock grass native to the Andean regions of Ecuador, Peru and Bolivia. In the later half of the 19th century it was introduced into California, along with the congener *C. selloana* (Schultes) Asch. & Graebner (pampas grass), for use as a landscaping ornamental. Both species have subsequently escaped from cultivation and expanded in coastal habitats along the Pacific coast (Costas-Lippmann, 1976; Lambrinos, 2000). Both species have also become naturalized in New Zealand (Connor, 1965; Edgar *et al.*, 1991), South Africa (Robinson, 1984) and the Hawaiian islands (Chimera, 1997).

Cortaderia jubata has the more restricted distribution of the two species in California, occurring primarily in a narrow band of coastal habitat from central California to southern Oregon (Lambrinos, 2001). This restricted range, however, coincides with some of the region's most diverse and restricted plant communities, and the prevalence of *C. jubata* in these habitats has caused increasing management concern (Cooper, 1967; DiTomaso *et al.*, 1999). Although considerable effort has been expended on the monitoring and control of *C. jubata* populations, no published data exist that describe how these populations threaten the structure of native communities.

In this study, the community level changes caused by the expansion of *C. jubata* in a geographically restricted formation of maritime chaparral along the central coast of California are described. Specifically are examined: (1) how *C. jubata* alters the vegetation structure, plant species composition and plant species diversity of invaded chaparral; (2) how *C. jubata* invasion affects the composition and abundance of insect and small mammal populations.

METHODS

Study area and plot selection

This study was conducted on Vandenberg Airforce Base, Santa Barbara County, CA, U.S.A. (34°41′N, 120°36′W). The base contains most of the remaining stands of Burton Mesa chaparral, a regionally endemic variant of maritime chaparral. This unique shrub community contains four endemic shrub species as well as other narrowly restricted plant species. Less than 40% of the original Burton Mesa chaparral cover still exists, and the remaining acreage continues to be threatened by development and the invasion of non-native species such as *C. jubata* (Davis *et al.*, 1988).

Stands of Burton Mesa chaparral are restricted to the Burton Mesa, a low elevation (30 m) coastal terrace composed of thin sandy soils derived from Orcutt sandstone underlain by a shale or clay hardpan (Shipman, 1972). The climate is mediterranean-type and strongly maritime. The average rainfall is less than 40 cm per year, almost all of this precipitation falling between October and April. *C. jubata* was first recorded on the Burton Mesa in the mid-1970s (Davis *et al.*, 1988), but aerial photographs taken during the 1970s and 1980s indicated that large populations of *C. jubata* did not develop until the mid-1980s. The initial establishment of these large infestations seems to have been associated with large disturbances that occurred during the extension of an aircraft runway and the construction of several buildings (Chris Gillespie, personal communication).

From these initial ruderal populations, however, *C. jubata* has since expanded into the surrounding relatively undisturbed chaparral. Using the aerial photographs, five locations were identified that were currently invaded by *C. jubata* but that had been uninvaded shrubland (Fig. 1). In these five
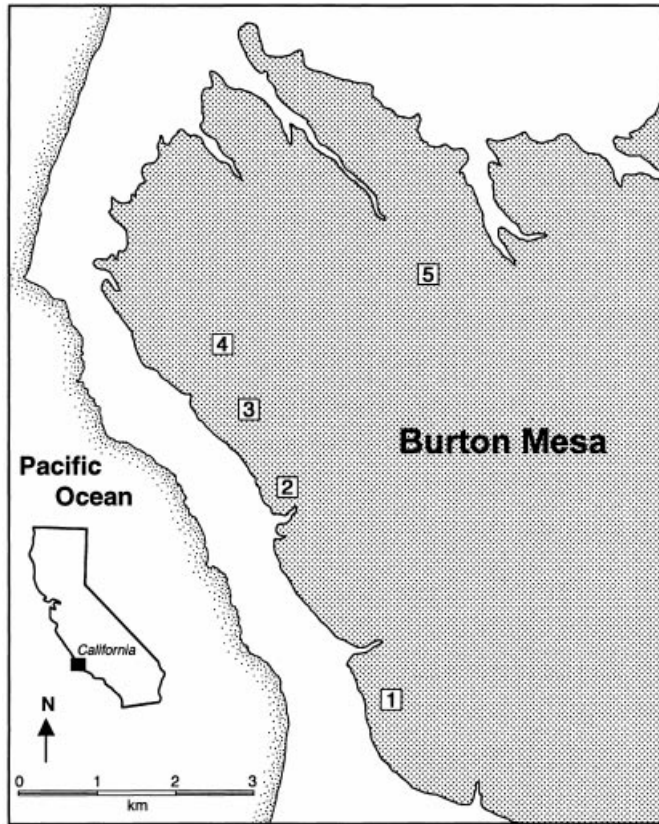
Fig. 1 Location of study plots on the Burton Mesa, Vandenberg Air Force Base, CA (34°41′N, 120°36′W).

locations paired 50 m × 50 m plots were established in stands dominated by *C. jubata* and in immediately adjacent stands of pristine maritime chaparral.

The *C. jubata*-invaded portions of many of the sites were associated with relatively small scale disturbances: one site was bordered by an eroding stream channel, three sites were bordered by dirt roads, while one site was located approximately 100 m from a paved road. The only visible signs of disturbance within stands were narrow paths created by mule deer (*Odocoileus hemionus*) that crossed both invaded and uninvaded stands at three of the five sites.

The cover of dead shrub skeletons was significantly greater in invaded stands than in uninvaded stands (Table 1), consistent with the postulate that the currently invaded stands had greater shrub

cover at the time of invasion. The *C. jubata* individuals composing invaded stands had a distribution of sizes skewed slightly toward the smallest size classes ($g_1 = 0.85$, $SE_{g_1} = 0.34$), although both small and large tussocks (0.002 m^3–4.08 m^3) were present within stands. A similarly skewed distribution of sizes was observed for *C. jubata* individuals currently invading relatively pristine stands of maritime chaparral ($g_1 = 0.86$, $SE_{g_1} = 0.40$; range: 0.002 m^3–3.85 m^3). This similarity, as well as the presence of both large and small size classes, suggested that *C. jubata* individuals were actively recruiting in both invaded and in relatively pristine stands. Stands did not differ significantly in substrate, relief, aspect or elevation.

The age structure of shrubs and fire records indicated that the stands had not burned in over 50 years. The natural fire interval in Burton Mesa

Table 1 Summary of vegetation parameters for maritime chaparral plots and *C. jubata* plots. Values are the overall plot means (*n* = 5). Significance values are for paired *t*-tests with 4 degrees of freedom

Vegetation parameter	Maritime chaparral plots		*Cortaderia* plots		t	P
	$\bar{\mathrm{X}}$	SE	$\bar{\mathrm{X}}$	SE		
Vegetation height (m)	1.81	0.10	1.48	0.07	3.06	0.04
Total percentage vegetative cover	132.21	21.08	103.46	4.81	1.35	0.25
Foliage height diversity	1.33	0.07	1.01	0.03	4.43	0.011
% Bare ground	12.64	1.71	11.70	2.15	0.28	0.79
% Dead shrub cover	7.60	1.00	15.90	1.30	8.14	0.001
Canopy litter depth (cm)	4.30	0.67	19.90	0.81	11.24	0.001
Open litter depth (cm)	1.92	0.29	1.99	0.21	0.30	0.78

chaparral is long, perhaps more than 100 years, but the current fire interval has increased to 20–30 years as a result of controlled and accidental human-caused wildfires (Hickson, 1988). Frequent burning of Burton Mesa chaparral can lead to invasion by the invasive succulent *Carpobrotus edulis*, but *C. jubata* invasion does not appear to be associated with fire (Davis *et al.*, 1988; Hickson, 1988).

Vegetation sampling

Vegetation sampling was conducted in the spring of 1997. At 10 randomly positioned points within each plot vegetation height and the horizontal vegetational densities were recorded at 0 m, 0.5 m, 1.0 m, 1.5 m and 2.0 m above the ground. Horizontal vegetation densities were computed as the reciprocal of the horizontal distance at which a 0.25-m × 0 25-m board would be 50% obscured by vegetation. Vegetation profiles were constructed for each plot by plotting the mean horizontal vegetation density against vegetation height, and the area under each vegetation profile was divided into four equally spaced layers: 0–0.5 m, 0.5–1 m, 1–1.5 m and 1.5–2 m. The foliage height diversity (FHD) was calculated for each vegetation profile as:

$$\mathrm{FHD} = -\Sigma\, p_i \ln p_i \qquad (1)$$

where p_i is the proportion of the total foliage which lies in the ith layer of the vegetation profile (MacArthur & MacArthur, 1961). FHD is an index of the structural complexity of the vegetation.

Litter depth was measured at 5-m intervals along four 25-m transects. Two measurements were taken: litter depth at the nearest point underneath the canopy and litter depth at the nearest point in the open spaces in canopy openings.

The cover of all plant species was estimated in each plot using four 25-m line transects orientated parallel to the coast and spaced 10 m from each other. The cover values for each of the four transects were pooled to provide a plot mean for each species encountered. The presence of any additional plant species not encountered along the transects, but found within the plot, were recorded.

Plant species were grouped into four functional groups for analysis: shrubs, subshrubs, perennial herbs and annual herbs.

For each habitat mean species accumulation curves were computed for all species and for native species only. Mean curves are based on 1000 randomization runs. For each habitat jackknife estimates were calculated of total and native species richness using:

$$S_{\mathrm{jack1}} = S_{\mathrm{obs}} + Q_1\left(\frac{m-1}{m}\right) \qquad (2)$$

where S_{jack1} is the first order jackknife estimate of species richness, S_{obs} is the total species observed in the 20 samples (transects), Q_1 is the number of species found in only one sample, m is the total number of samples (Heltshe & Forrester, 1983).

Mean accumulation curves and jackknife estimates were computed using EstimateS vs. 5 (R.K. Colwell, HTTP://viceroy.eeb.uconn.edu/estimates).

Animal sampling

The relative activity of small mammals was estimated in each plot using scat counts. Counts were conducted in the spring of 1997. In each plot the number of mammalian scat were counted within 1-m^2 quadrats placed every 2 m along each of the four 25-m line transects. Three categories of scat were used for analysis: rabbits (*Lepus californicus*, *Sylvilagus bachmani* and *S. audubonii*), woodrats (*Neotoma fuscipes*) and other rodents (*Dipodomys agilis*, *Peromyscus* spp., *Perognathus californicus*, *Reithrodontomys megalotis*). Unidentifiable scat and scat belonging to species outside the three categories made up less than 5% of the total scat sampled and were not included in the analysis.

Relative insect productivity was estimated in each plot using sticky board traps made of 10-cm × 10-cm white polystyrene boards covered with a thin layer of Tanglefoot®. Ten traps in each plot were hung from the vegetation at a height of 0.5 m above the ground. Traps were set in May 1997, September 1997, January 1998 and May 1998. Traps were sampled one week after being set. Insects were identified to order.

Statistical software

All statistical analyses were performed using SYSTAT® vs. 8.0 (SPSS Inc., Chicago, IL, U.S.A.).

RESULTS

Impact on vegetation

The vegetation structure of stands invaded with *C. jubata* was drastically different than the adjacent maritime chaparral. The vegetation in plots dominated by *C. jubata* was slightly shorter than the adjacent maritime chaparral (Table 1). In addition, plots dominated by *C. jubata* were structurally less complex. *C. jubata* plots were characterized by a single dominant herbaceous layer. In contrast, there was a distinct transition (albeit highly truncated) between canopy and understorey vegetation layers in maritime chaparral (Fig. 2). Foliage height diversity was greater in maritime chaparral plots than in *C. jubata* plots (Table 1). Despite the differences in vegetation structure, the amount of bare mineral soil and total percentage vegetative cover was indistinguishable between
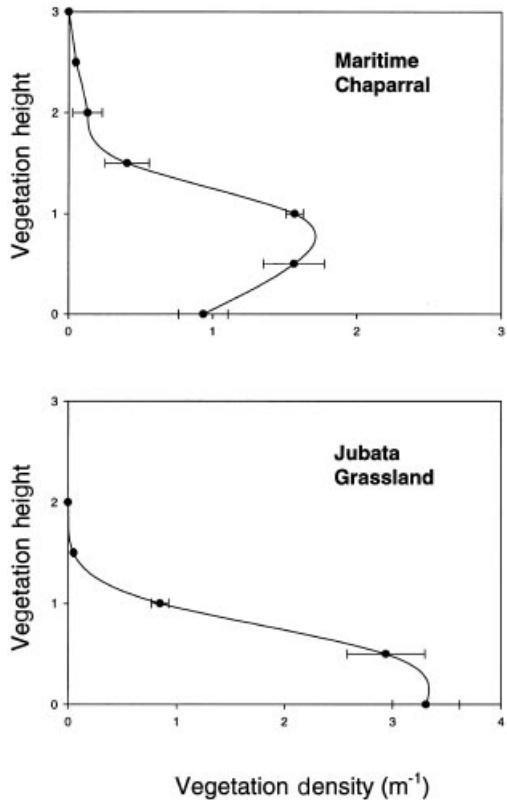

Fig. 2 Vegetation profiles of maritime chaparral and jubata grassland. Points are means (*n* = 5 plots) ±1 SE. See text for definition of vegetation density.

the maritime chaparral plots and *C. jubata* plots (Table 1). Litter depth under the canopy layer was significantly greater in *C. jubata* plots than in maritime chaparral plots. There was no difference, however, in litter depth measured in the openings between the canopy layer (Table 1).

Total species richness was nearly identical in the maritime chaparral plots and *C. jubata* plots (Fig. 3). The jackknife estimates of total species richness in the two habitats were similar (maritime chaparral = 47.20 ± 3.26 SD, jubata grassland = 49.15 ± 3.16 SD). Contrastingly, significantly more native species were found in maritime chaparral plots than in *C. jubata* plots (Fig. 3). The jackknife estimate of native species richness was greater for maritime chaparral than jubata grassland (maritime chaparral = 44.2 ± 3.26 SD, jubata grassland = 32.45 ± 2.16 SD). Species composition was also
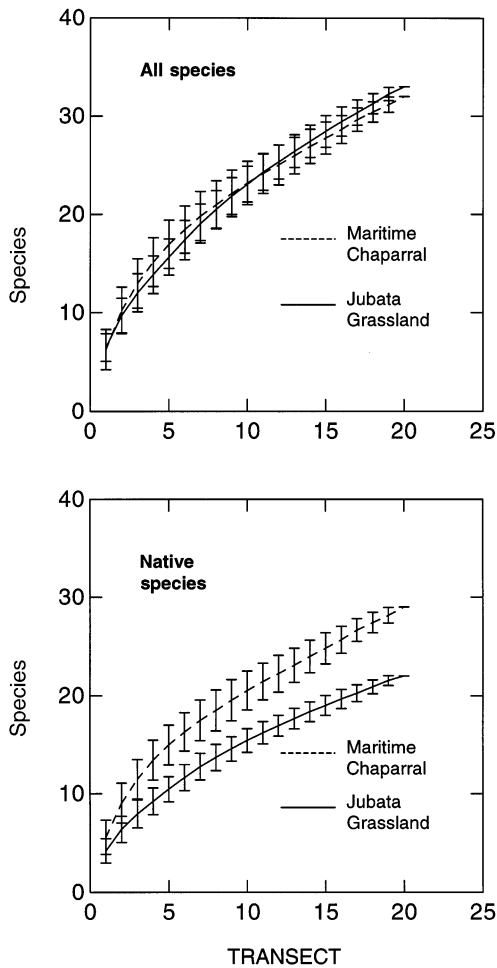
Fig. 3 Species accumulation curves in maritime chaparral and jubata grassland for all species and native species only. Error bars are ±1 SD.

Fig. 4 Distribution of growth forms in maritime chaparral and jubata grassland. Values exclude *C. jubata*. A percentage relative cover; B species richness. S = shrubs; SS = subshrubs; PH = perennial herbs; AH = annual herbs. Values are means ($n = 5$ plots) ±1 SE. Asterisks indicate a significant difference ($P < 0.05$) between invaded and uninvaded plots using a paired *t*-test with 4 degrees of freedom. % Relative cover was arcsine transformed for significance test.

markedly different. Mean shrub cover and mean shrub richness were lower in *C. jubata*-invaded plots (Fig. 4). Overall, six of the nine shrub species (67%) and three of the seven subshrub species (43%) present in the five maritime chaparral plots were absent from plots dominated by *C. jubata* (Table 2). Perennial herb cover, although not richness, was higher in invaded than in uninvaded stands (Fig. 4). Four perennial herb species present in pristine plots were absent from invaded plots: three geophytes in the Amaryllidaceae and Liliaceae; one hemicryptophyte in the Convolvulaceae (Table 3).
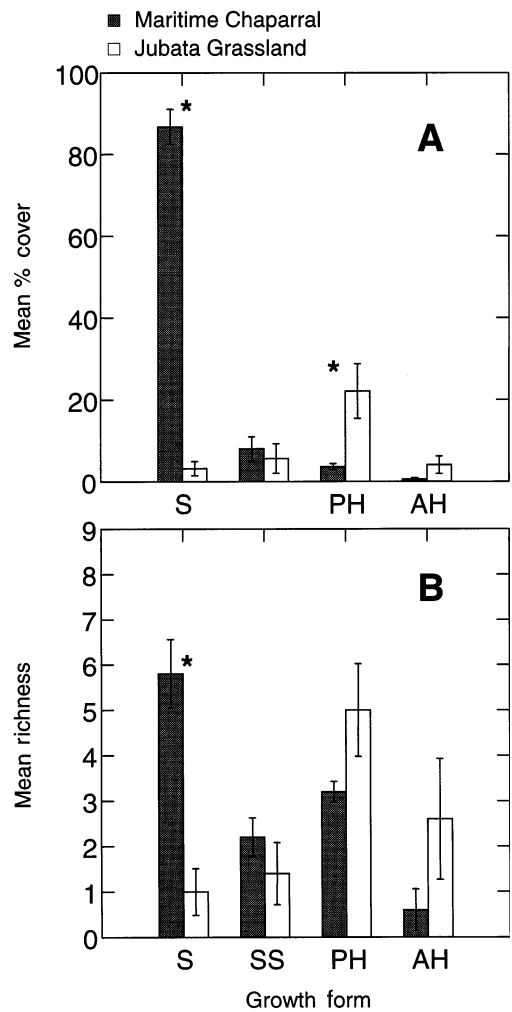
Although mean annual herb richness was indistinguishable between the paired plots, there was greater plot to plot turnover of annual species among the *C. jubata* plots; overall, the *C. jubata* plots contained 10 annual species not found in plots of maritime chaparral (Fig. 4; Table 3). While

Table 2 Relative percentage cover of shrubs and subshrubs in plots of pristine maritime chaparral and plots invaded by *Cortaderia jubata* (*n* = 5)

Species	Family	Maritime chaparral plots		*Cortaderia* plots	
		$\bar{X}$	SD	$\bar{X}$	SD
Shrubs					
Adenostoma fasciculatum	Rosaceae	11.93	6.22	—	—
Arctostaphylos purissima	Ericaceae	47.99	4.44	P	—
Arctostaphylos rudis	Ericaceae	5.56	3.07	—	—
Baccharis pilularis	Asteraceae	3.73	2.07	1.37	0.84
Ceanothus impressus	Rhamnaceae	4.06	2.69	1.20	0.87
Ceanothus cuneatus var. *fascicularis*	Rhamnaceae	11.01	4.97	—	—
Ericameria ericoides	Asteraceae	2.16	1.19	—	—
Eriogonum cinereum	Polygonaceae	P	—	—	—
Salvia mellifera	Lamiaceae	2.81	1.43	—	—
Sub-shrubs					
Carpobrotus chilensis	Aizoaceae	P	—	P	—
Carpobrotus edulis	Aizoaceae	5.51	2.26	2.08	1.12
Croton californicus	Euphorbiaceae	P	—	P	—
Eriophyllum confertiflorum	Asteraceae	P	—	—	—
Helianthemum scoparium	Cistaceae	P	—	—	—
Lotus procumbens	Fabaceae	P	—	—	—
Lotus scoparius	Fabaceae	P	—	3.07	1.99

P < 1% cover. Species in bold type are non-native.

the three annual herb species found in the maritime chaparral plots were native, five of the 12 annual herbs present in the *C. jubata* plots were alien. Only one annual species (*Apiastrum angustifolium*) was present in the maritime chaparral plots but absent from *C. jubata* plots (Table 3).

Impact on animal communities

The density of arthropods captured on sticky board traps was significantly greater in maritime chaparral than in jubata grassland. This difference was consistent despite seasonal changes in insect abundance (Fig. 5; Table 4). The composition of arthropod communities was also different. Hymenopterans and Homopterans made up a significantly greater proportion while Arans made up a significantly smaller proportion of the total arthropods trapped in the maritime chaparral plots compared to the *C. jubata* plots (Fig. 6). Four arthropod orders trapped in maritime chaparral were absent from jubata grassland traps: Hemiptera, Odonata, Opiliones and Orthoptera.

Scat densities suggested differences in small mammal activity between pristine and invaded maritime chaparral. Woodrat and mouse scat was significantly more common while rabbit scat was significantly less common in maritime chaparral compared to jubata grassland (Fig. 7).

DISCUSSION

Shrubland conversion

The results of this study demonstrate that *C. jubata* has the potential to convert shrublands into perennial grasslands in California. Given the poor vegetational record of the sites in this study, it is possible that factors independent of the invasion of *C. jubata*, such as large disturbances, may be responsible for the observed vegetational differences. However, the higher frequency of dead shrub cover in invaded stands compared with uninvaded stands suggests that their current low shrub cover is at least partly a result of *in situ* shrub death, not shrub removal by disturbance. It

Table 3 Relative percentage cover of perennial and annual herbs in plots of pristine maritime chaparral and plots invaded by *Cortaderia jubata* (*n* = 5)

Species	Family	Maritime chaparral plots		*Cortaderia* plots	
		X̄	SD	X̄	SD
Perennial herbs					
Achillea millefolium	Asteraceae	—	—	P	—
Calystegia macrostegia	Convolvulaceae	P	—	—	—
Cortaderia jubata	Poaceae	1.8	1.25	62.1	0.69
Dichelostemma capitatum	Amaryllidaceae	P	—	—	—
Dudleya sp.	Crassulaceae	P	—	P	—
Horkelia cuneata	Rosaceae	1.76	0.86	5.67	1.64
Juncus phaeocephalus	Juncaceae	P	—	P	—
Koeleria macrantha	Poaceae	—	—	P	—
Lotus junceus	Fabaceae	P	—	P	—
Nasella pulchra	Poaceae	P	—	1.28	1.28
Bloomeria crocea	Amaryllidaceae	P	—	—	—
Rumex acetosella	Polygonaceae	—	—	1.2	0.78
Silene laciniata ssp. *major*	Caryophyllaceae	P	—	—	—
Sisyrinchium bellum	Iridaceae	P	—	4.05	2.39
Solidago spathulata	Asteraceae	P	—	7.9	0.86
Zigadenus fremontii	Liliaceae	P	—	—	—
Annual herbs					
Anagalis arvensis	Primulaceae	—	—	P	—
Apiastrum angustifolium	Apiaceae	P	—	—	—
Camissonia micrantha	Onagraceae	P	—	P	—
Chorizanthe diffusa	Polygonaceae	—	—	P	—
Daucus pusillus	Apiaceae	—	—	P	—
Erodium cicutarium	Geraniaceae	—	—	P	—
Filago gallica	Asteraceae	—	—	P	—
Gnaphalium californicum	Asteraceae	—	—	P	—
Gnaphalium purpureum	Asteraceae	P	—	P	—
Hypochaeris glabra	Asteraceae	—	—	P	—
Navarretia sp.	Polemoniaceae	—	—	P	—
Plantago coronopus	Plantaginaceae	—	—	P	—
Vulpia octoflora	Poaceae	—	—	P	—

P < 1% cover. Species in bold type are non-native.

is still possible that the invaded stands contained a less dense shrubland prior to their infestation than the adjacent uninvaded stands. Although aerial photographs indicate that the sites were predominately shrubland, all the sites are located on the edge of the Burton Mesa near the beginning of a transitional zone with the more xeric dune scrub vegetation type (Fig. 1). Less dense shrub cover or differences in species composition near the edges of the range of Burton Mesa chaparral, coupled with the relatively small disturbances

(dirt roads, stream bank) found adjacent to each site may be why the invaded plots where more susceptible to invasion than the neighbouring uninvaded plots.

Although a direct link between *C. jubata* invasion and chaparral decline cannot be established definitively, this study demonstrates that the presence of *C. jubata* does dramatically, and perhaps permanently, alter the landscape of the Burton Mesa. The presence of both small and large *C. jubata* size classes within invaded stands indicates that
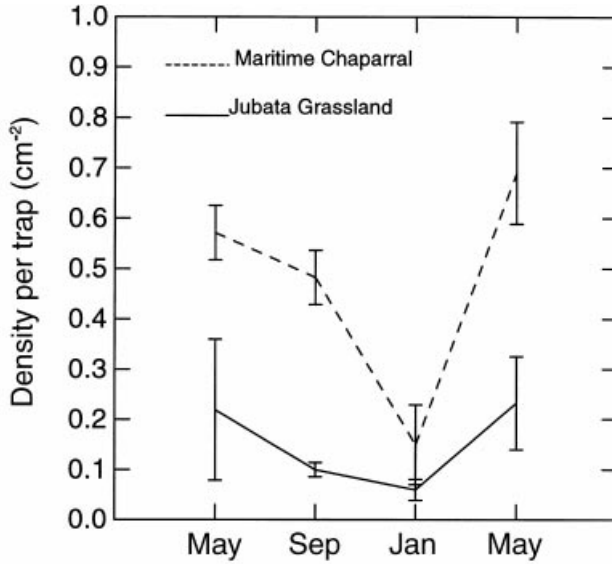
Fig. 5 Insect density captured on sticky board traps in maritime chaparral and jubata grassland. Values are means ±1 SE.

Table 4 ANOVA results for the effects of vegetation type and trapping date on sticky board insect density. Insect density was $\log_{10}$ transformed for analysis

Source of variation	ss	d.f.	F	P
Vegetation type	2.94	1	22.33	<0.001
Month	3.50	3	8.84	<0.001
Vegetation type × month	0.27	3	0.69	0.57
Error	4.22	32		

these populations are not simply the transient result of an acute disturbance. Shrub recruitment within stands of *C. jubata* appears to be very low; the few shrubs found within stands were large, mature individuals. Also, at each of the five sites, populations of *C. jubata* are continuing to expand into the adjacent maritime chaparral. When *C. jubata* individuals were found growing within intact chaparral stands they were often associated with small scale soil disturbances such as water run-off channels. Once established, individuals can persist for long periods of time, and individuals can produce billions of seeds over the course of their reproductive lives (Costas-Lippmann, 1976). During the period of *C. jubata* seed dispersal
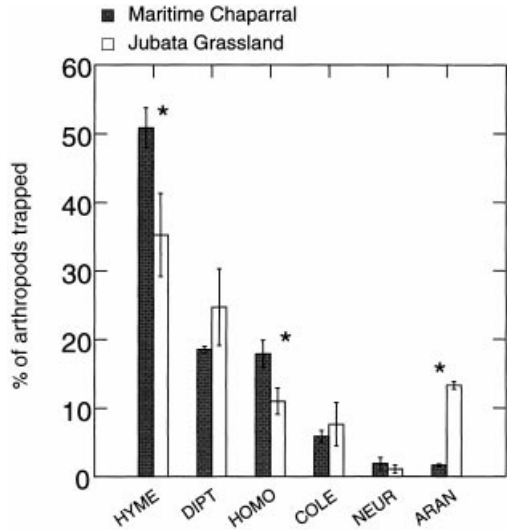

Fig. 6 Relative distribution of the six most common arthropod orders trapped on sticky board traps in maritime chaparral and jubata grassland. Values are the percentage of the total arthropods sampled in each habitat. Asterisks indicate significant differences ($P < 0.02$) using paired *t*-tests with 4 degrees of freedom on arcsine transformed data. HYME = Hymenoptera; DIPT = Diptera; HOMO = Homoptera; COLE = Coleoptera; Neur = Neuroptera; ARAN = Aràneae.
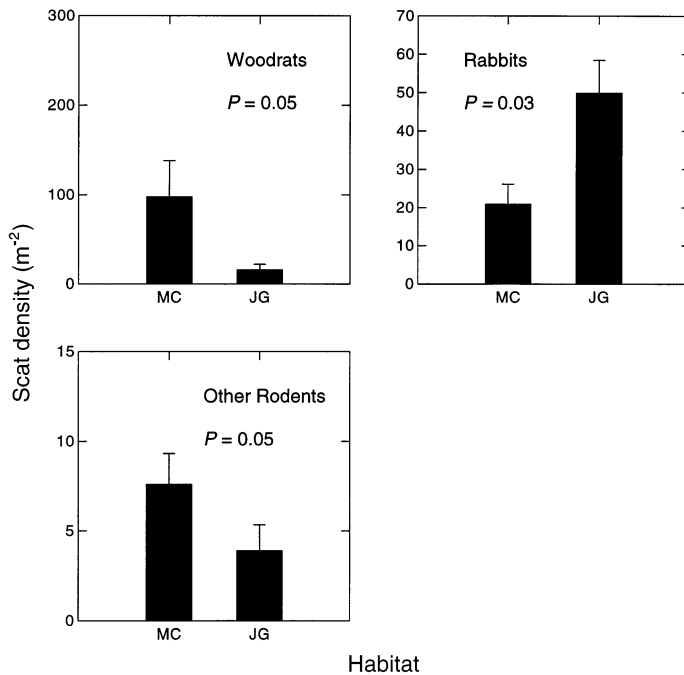
Fig. 7 Small mammal scat density in maritime chaparral and jubata grassland. (Woodrats = *Neotoma fuscipes*; rabbits = *Lepus californicus*, *Sylvilagus bachmani*, and *S. audubonii*; other rodents = *Dipodomys agilis*, *Peromyscus* spp., *Perognathus californicus*, *Reithrodontomys megalotis*). Values are means ($n = 5$ plots) ±1 SE. Means are compared with paired *t*-tests with 4 degrees of freedom.

in early fall, the Burton Mesa is inundated with a prodigious seed rain that in places can reach a density of 3×10^7 seeds/m^2 (Lambrinos, unpublished data). In addition, *C. jubata* is resilient to fire. Although they lack protective burls, the large tussocks of *C. jubata* effectively insulate the growing meristem during a fire. Individuals have been observed re-sprouting only a few weeks following a fire and before the onset of winter rains (Lambrinos, unpublished data).

Such a dramatic and apparently stable replacement of native shrublands by an alien grass has not been documented previously in California. European annual grasses can compete with seedlings of native California shrubs: the growth of *Baccharis pilularis* and *Artemesia californica* seedlings is significantly reduced by competition with annual grasses (Da Silva & Bartolome, 1984; Davis & Mooney, 1985; Eliason, 1995), while Shultz *et al.* (1955) demonstrated a direct relationship between chaparral shrub seedling survival and alien annual

grass density. Despite this, California shrublands have been notably resistant to invasion and displacement by alien grasses. Zedler *et al.* (1983) did show that *Lolium multiflorum* (annual ryegrass) and other alien annuals planted as erosion control following fires can significantly increase the fire frequency in chaparral (especially during wet years), and this can dramatically alter the composition of regenerating stands. In the absence of repeated fire, however, herbaceous aliens do not retard normal successional development by native shrubs (Westman, 1976; Keeley *et al.*, 1981).

Reviewing the literature, D'Antonio & Vitousek (1992) concluded that alien grasses can alter the composition or dominance of shrublands by increasing fire frequency, by altering rates of resource supply, or by competing directly with native shrubs. While there is no evidence that the presence of *C. jubata* has appreciably altered the fire regime or rates of shrub resource supply on the Burton Mesa, some evidence suggests that *C. jubata*

can compete with native shrubs for space and soil resources. *Cortaderia jubata* individuals grow to sizes comparable to many maritime chaparral shrubs (Lambrinos, unpublished data), and *C. jubata* individuals were observed growing through the crowns of mature shrubs or through the skeletal remains of dead shrubs, in many instances completely engulfing the resident shrub.

D'Antonio & Mahall (1991) demonstrated that the invasive perennial *Carpobrotus edulis* can directly compete with native coastal California shrub species for soil resources. *Carpobrotus edulis*, *Ericameria ericoides* and *Isocoma menziesii* all have shallow root systems that overlap when plants grow adjacent to each other. *C. jubata* has similarly shallow fibrous roots, which occupy the same soil layer as shallow rooted chaparral shrubs. Deeper-rooted chaparral shrubs such as *Arctostaphylos* and *Ceanothus* may also be affected by the presence of *C. jubata*. Knoop & Walker (1985) demonstrated that grasses can reduce water availability even at deeper soil depths (20–130 cm). In addition, soils on the Burton Mesa have low fertility and are underlain by a shallow hardpan 1–4 m deep (Shipman, 1972). Shrubs with extensive primary roots on more typical chaparral soils are severely restricted on the shallow soils of the Burton Mesa. Access to shallow soil water available from winter rains or summer fog drip may be more critical for these shrubs than for congeners found in more typical chaparral formations.

In addition to dramatically reducing native shrub diversity, *C. jubata* invasion also alters herbaceous community diversity patterns. While native geophyte and hemi-cryptophyte richness declines, overall herbaceous species cover and richness is higher in *C. jubata* grassland than in uninvaded chaparral. Many of these herbaceous species are common in nearby annual grassland vegetation, and it is not known to what extent these species were present in stands prior to *C. jubata* invasion. However, subtle changes in resource supply rates following the invasion of *C. jubata* (such as changes in litter nutrient content or decomposition rates) could have promoted herbaceous species establishment. Also, the slightly shorter and more uniform vegetation structure of *C. jubata* stands may provide greater or more uniform light penetration for low growing herbaceous species.

The increase in native annuals in *C. jubata* stands does not compensate fully for the loss of native perennials. Alien grasses have been associated with reduced native plant diversity in other mediterranean-type shrublands. Campbell *et al.* (1980) and Vlok (1988) demonstrated a negative association between the density of invading alien annual grasses and forbs and the density and species richness of native annuals and geophytes in fynbos vegetation. Bridgewater & Backshall (1981) showed that alien grasses can reduce diversity in the shrublands of south-western Australia. The diversity of sand dune species along the Pacific coast is negatively correlated with the presence of the perennial grass *Ammophila arenaria* (Barbour *et al.*, 1976). Direct effects of alien grasses on the diversity of mediterranean-type shrublands are difficult to document, however, because alien grass invasion and reductions in native diversity are often both correlated with other landscape changes such as habitat fragmentation, grazing or altered fire regimes. Although this study does not completely isolate these confounding factors, it suggests that once established, long-lived perennial alien grasses can reduce native diversity over extended periods of time even in the absence of large-scale disturbances.

Impact on animal communities

This study demonstrates that the invasion of *C. jubata* can impact animal communities. Arthropod abundance is consistently lower in plots dominated by *C. jubata* than in the control (uninvaded) plots. Similarly depressed arthropod abundance has been documented on California coastal dunes invaded by the invasive dune grass *Ammophila arenaria* (Slobodchikoff & Doyen, 1977), and a number of other invasive grasses have been shown to affect native arthropod communities (D'Antonio & Vitousek, 1992). A large proportion of phytophagous insects are host plant specialists (Price, 1983; Bernays & Grahm, 1988). Consequently, native phytophagous insects often fail to colonize introduced hosts (Crawley, 1987). Andow & Imura (1994) demonstrated that herbivore arthropod assemblages on crop plants in Japan become more specialized the longer the plant species has been in Japan. The reduction in arthropod abundance in jubata grassland may be because *C. jubata* is a relatively inhospitable host for herbivorous arthropods. Consistent with this is the fact that homopterans are significantly less frequent in *C. jubata* plots than in maritime chaparral plots,

and members of the Hemiptera and Orthoptera are absent altogether.

C. jubata may affect arthropod communities indirectly by changing the resource base. Many studies have demonstrated a positive correlation between plant diversity and productivity and arthropod diversity (Murdoch *et al.*, 1972; Southwood *et al.*, 1979; Siemann, 1998). Total plant cover and plant species richness, however, is nearly identical in maritime chaparral and jubata grassland, and they cannot explain differences in arthropod abundance or diversity. Instead the changes in arthropod populations probably reflect the drastic changes in plant community composition. While overall plant richness is not altered by *C. jubata* invasion, native species richness is significantly reduced. Additionally, the replacement of native shrubs and geophytes, most of which have large nectar-rich flowers, by the wind-pollinated *C. jubata* drastically reduces the abundance and diversity of pollen and nectar resources, and this is probably responsible for the reduced frequency of hymenoptera in jubata grassland. Woody perennials also provide a greater diversity of feeding sites for phytophagous insects than do forbs, and this may be another reason for the decline of homopteran, hemipteran and orthopteran species in jubata grassland.

The results of this study also suggest that *C. jubata* invasion can alter small mammal distribution and activity patterns. The lowered woodrat activity in jubata grassland is not surprising given the almost complete lack of woody vegetation in jubata grassland. More surprising is the higher activity of rabbits in jubata grassland compared to maritime chaparral. In mediterranean-type vegetation in California, rabbits rarely venture more than a few metres from protective shrub cover to forage on herbaceous annuals. This activity pattern results in bare zones of heavily grazed vegetation around shrubs along the shrubland–grassland ecotone (Bartholomew, 1970; Halligan, 1974). The high activity of rabbits in jubata grassland may be explained by its unique structure. Compared to native perennial grassland or annual grassland, jubata grassland provides cover that is nearly comparable to maritime chaparral. The mean vegetation height is only slightly shorter than that of chaparral, and large amounts of camouflaging litter accumulate around the base of *C. jubata* tussocks. In addition, the greater abundance and diversity of herbaceous species in jubata grassland compared to maritime chaparral may provide a tempting resource for rabbits.

Implications for conservation and management

The conservation threat posed by *C. jubata* on the Burton Mesa is clear. The presence of *C. jubata* reorganizes the basal trophic levels of the Burton Mesa. A diverse and unique shrub community is replaced by a perennial-dominated grassland. While this grassland contains many native forbs, overall native richness is reduced as a consequence. These drastic changes in the plant community affect arthropod and small mammal communities.

Unfortunately, *C. jubata* is not restricted to the Burton Mesa. *C. jubata* is currently invading a number of locations along the central and northern California coast. While the drier chaparral and coastal sage scrub formations of southern California appear resistant to *C. jubata* invasion, *C. jubata* still threatens some of the state's most diverse and unique shrub communities. These communities are also threatened by human disturbances that lead to habitat destruction and fragmentation. In this study, populations of *C. jubata* apparently established within stands of maritime chaparral at sites of local and relatively minor reduced shrub cover, such as along an eroding stream bank or near the edge of an ecotone. Such sites are increasingly common as remnant stands of shrubland become smaller and more isolated. Unlike many ruderal weeds, however, once established *C. jubata* persists and pre-empts resources on a scale comparable to native shrubs. In addition, the large amount of seeds produced by *C. jubata* populations create a strong and persistent propagule pressure that significantly increases the probability of further expansion into adjacent shrubland. One important management strategy should be to eliminate founding populations before they can grow to the unmanageable sizes currently seen on the Burton Mesa.

Conserving and restoring biodiversity and ecosystem function is hampered by our incomplete understanding of the relationship between the two. Unambiguously separating the effects of species composition and species diversity on ecosystem function have proved difficult (Diamond, 1990; Chapin *et al.*, 1998). Overall plant cover and plant species

diversity on the Burton Mesa are essentially unchanged by the invasion of *C. jubata*, but the changes in animal communities suggest that invaded stands are not the same functionally. Additional work is needed to understand how these changes may alter critical ecosystem services such as soil erosion patterns or ground water cycling.

This study provides quantitative documentation of how an introduced plant alters the structure of a mediterranean-type shrubland. Despite the diversity and abundance of alien plants in the mediterranean-type ecosystems of California, relatively few studies have actually quantified their impact on native communities. Studies that quantify both the community and ecosystem impacts that invasive plants inflict on mediterranean-type ecosystems are urgently required to manage and conserve these highly threatened systems effectively.

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