VARIABLE EFFECTS OF FERAL PIG DISTURBANCES ON NATIVE AND EXOTIC PLANTS IN A CALIFORNIA GRASSLAND

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Abstract. Biological invasions are a global phenomenon that can accelerate disturbance regimes and facilitate colonization by other nonnative species. In a coastal grassland in northern California, we conducted a four-year exclosure experiment to assess the effects of soil disturbances by feral pigs (*Sus scrofa*) on plant community composition and soil nitrogen availability. Our results indicate that pig disturbances had substantial effects on the community, although many responses varied with plant functional group, geographic origin (native vs. exotic), and grassland type. (''Short patches'' were dominated by annual grasses and forbs, whereas ''tall patches'' were dominated by perennial bunchgrasses.) Soil disturbances by pigs increased the richness of exotic plant species by 29% and native taxa by 24%. Although native perennial grasses were unaffected, disturbances reduced the biomass of exotic perennial grasses by 52% in tall patches and had no effect in short patches. Pig disturbances led to a 69% decrease in biomass of exotic annual grasses in tall patches but caused a 62% increase in short patches. Native, nongrass monocots exhibited the opposite biomass pattern as those seen for exotic annual grasses, with disturbance causing an 80% increase in tall patches and a 56% decrease in short patches. Native forbs were unaffected by disturbance, whereas the biomass of exotic forbs increased by 79% with disturbance in tall patches and showed no response in short patches. In contrast to these vegetation results, we found no evidence that pig disturbances affected nitrogen mineralization rates or soil moisture availability. Thus, we hypothesize that the observed vegetation changes were due to space clearing by pigs that provided greater opportunities for colonization and reduced intensity of competition, rather than changes in soil characteristics. In summary, although responses were variable, disturbances by feral pigs generally promoted the continued invasion of this coastal grassland by exotic plant taxa.

Key words: coastal grasslands; community-level effects; feral pigs; functional groups; invasive species; nitrogen mineralization rates; soil disturbances; Sus scrofa; *variable effects.*

INTRODUCTION

Throughout the world, ecological systems are becoming increasingly dominated by nonnative species (Mooney and Drake 1986, Drake et al. 1989, Luken and Thieret 1997, Mack et al. 2000, Mooney and Hobbs 2000). Through their activities as pathogens, predators, herbivores, and disturbance agents, these invaders can profoundly alter systems at the population, community, and ecosystem level (Williamson 1996, Parker et al. 1999, Mack et al. 2000). The severity of this problem has become so great that biological invasions are now recognized as one of the most pressing forms of global change (Vitousek et al. 1996), with pronounced ecological and economic costs (Pimentel et al. 2000).

Biological invasions are unavoidably linked to disturbance in two ways. First, both natural and human-caused disturbances are widely recognized to be key factors promoting the invasion of nonnative species into novel landscapes (Elton 1958, Hobbs 1989, Rejmanek 1989, Hobbs and Huenneke 1992, D'Antonio et al. 1999). Second, although less widely appreciated,

biological invaders can themselves alter the disturbance regimes that characterize their new environments (D'Antonio and Vitousek 1992, Mack and D'Antonio 1998). Exotic taxa can introduce new forms of disturbance or can enhance or suppress existing disturbance regimes. Thus, although disturbance can play critical roles in promoting species diversity (see Connell 1978, Sousa 1984), its influence in human-altered landscapes is complex and presents considerable challenges for resource managers, who attempt to maintain native biodiversity while controlling the spread and impact of exotic species.

The responses of plant communities to disturbance will be determined in part by the life history characteristics of resident species present in the community. Plant taxa from different functional groups (sensu Lavorel et al. 1997) exhibit unique suites of life history characteristics and often vary considerably in their tolerance to disturbance as well as their colonization and competitive abilities (Grime 1979, McIntyre et al. 1995, Lavorel et al. 1999). Native and exotic taxa within the same functional group may also respond differently to disturbance, with the latter being more likely to possess life history traits that allow them to colonize rapidly after disturbance (Hobbs and Huenneke 1992).

Finally, variable outcomes in community responses to disturbance may arise from spatial variation in the dominance of different functional groups and the relative abundance of native and exotic species. Focusing on each of these factors will be critical for developing a predictive framework for understanding community responses to disturbance.

Domesticated mammals have been introduced throughout the world and commonly establish feral populations that can greatly alter natural disturbance regimes (Cox 1999, D'Antonio et al. 1999). For example, feral goats and sheep have been shown to severely increase soil erosion on both temperate and tropical islands by removing plant biomass and trampling vegetation (Mueller-Dombois and Spatz 1975, Coblentz 1978, Scowcroft and Hobdy 1987, Van Vuren and Coblentz 1987). In the western United States, grazing by feral horses was shown to reduce the species richness and abundance of grasses and shrubs as well as the abundance of small-mammal burrow entrances (Beever and Brussard 2000, Beever et al. 2003). In the southwestern United States, grazing and trampling by feral burros reduced plant species richness and cover as well as small-mammal abundance (see Cox 1999). Feral pigs (*Sus scrofa*) are now found in a diverse range of habitats on all continents except Antarctica, as well as many oceanic islands (Mayer and Brisbin 1991). Pigs can greatly increase disturbance levels in areas they invade, by overturning extensive amounts of soil and associated vegetation as they forage for belowground plant tissues (roots, bulbs) and invertebrates (Bratton 1975, Barrett 1978). Studies in New Zealand, Hawaii, and the Great Smoky Mountains in the southeastern United States have suggested that foraging disturbances by pigs are associated with reduced dominance of native plants and increased abundance of exotic taxa (Bratton 1975, Challies 1975, Spatz and Mueller-Dombois 1975, Aplet et al. 1991). At the ecosystem level, studies indicate that pigs may also increase soil mixing and decomposition rates of soil organic matter, increase rates of nutrient mineralization, and decrease rates of nitrogen retention (Singer et al. 1984, Vitousek 1986, Aplet et al. 1991). In contrast to these results, D'Antonio et al. (1999) have suggested that the effects of pig disturbances on grasslands may be less pronounced, and in some cases these ecosystems appear to recover rapidly from pig disturbances (Spatz and Mueller-Dombois 1975, Russell-Smith and Bowman 1992). For example, in a coastal grassland in northern California, Kotanen (1995) found that exotic annual grasses did not dominate native plants as a result of pig disturbance.

Feral pigs are a dominant feature of coastal and inland grasslands in California, and determining their effects on communities is complicated by the unfortunate reality that grasslands in the state are already heavily altered. They have undergone an extraordinary transformation in vegetation: once dominated by native

perennial bunchgrasses, grasslands in California now comprise primarily annual grasses from Eurasia (Heady 1988, Heady et al. 1988, 1992). In addition, grizzly bears (*Ursus arctos horribilis*) were the only native animal that disturbed grassland soils in a fashion similar to pigs (see Tardiff and Stanford 1998), and they have been extirpated from California since the early 1920s (Jameson and Peeters 1988). Thus, because these grasslands are heavily invaded and lack a key disturbance agent, the consequences of adding pigs to the system are unclear. One possibility is that pig disturbances may facilitate the invasion of exotic plant species. Alternatively, pigs may substitute for a lost disturbance agent, clear space in the landscape, interrupt the competitive dominance of exotic species, and thereby create refugia in which native plants can flourish. Only by conducting long-term field experiments can a better understanding of the effects of this exotic disturbance agent be developed.

Here, we summarize the results from research that examines the influences of soil disturbances by invasive feral pigs on a coastal grassland in northern California. Using a four-year exclosure experiment, our research has addressed the following questions: (1) Do pig disturbances alter plant species richness and biomass production of a grassland community, and do native and nonnative plants from different functional groups vary in their responses to disturbances? (2) Does the impact of pig disturbances on plant communities vary with distinctive fine-scale variation in grassland vegetation that occurs at our site? (3) Does the unintentional exclosure of nontarget mammals influence plant community composition or nitrogen mineralization rates in the soil? (4) Can vegetation changes caused by pig disturbances be explained by effects on soil nitrogen mineralization rates? Answers to these questions will expand our understanding of the linkages between biological invasions and disturbance and provide critical insight needed to develop science-based management policies.

Study System

Our research was conducted in a mesic, coastal grassland at Salt Point State Park (38°31′34″ N, 123°43′18″ W), ~120 km north of San Francisco, California in northwest Sonoma County. This coastal system has a mediterranean-type climate with cool, wet winters and warm, dry summers. Rainfall from October through May accounts for the yearly average precipitation of 100 cm. The 5-ha grassland is surrounded by mixed evergreen forest and occurs on a coastal terrace at 275 m elevation. Soils at the site are in the Rohnerville loam series and are described by the USGS as a loam, silt loam.

The plant species at our site fell into one of four functional groups based on life history characteristics and growth forms (see Lavoral et al. 1997). Like many coastal grasslands in California, the site is still domi-

nated by perennial grasses: two native bunchgrasses (*Danthonia californica* and *Deschampsia cespitosa*) and three nonnative species (primarily *Anthoxanthum odoratum*, and to a much lesser extent, *Holcus lanatus* and *Agrostis stolonifera*). Second, although native annual grasses are absent, exotic members of this group are abundant and include *Aira caryophyllea*, *Cynosurus echinatus*, *Vulpia* sp. (probably *myuros*), and *Briza minor*. Third, native nongrass monocots are interspersed throughout the site and include *Sisyrinchium bellum*, *Brodiaea terrestris*, *Calochortus uniflorus*, and *Juncus bufonius* (there are no exotic members in this group). And fourth, herbaceous dicots (forbs) are abundant and include the natives *Plantago erecta* and *Horkelia tenuiloba* as well as the exotics *Linum bellum*, *Leontodon taraxacoides*, *Plantago lanceolata*, and *Hypochaeris radicata*. Woody species were absent from our plots.

The vegetation in this grassland is characterized by striking fine-scale heterogeneity in composition and structure. It consists of a mosaic of two distinctive patch types: a low-growing grassland vegetation (referred to as the short patch type) interspersed among areas of taller vegetation dominated by large bunchgrasses (referred to as the tall patch type). Short patches support a mixture of annual and perennial grasses, forbs, and bulbs, whereas vegetation in tall patches is dominated by *Anthoxanthum* (exotic) and *Deschampsia* (native), both perennial bunchgrasses. The height of vegetation in short patches rarely exceeds 1 m, and is often considerably shorter, whereas vegetation in tall patches commonly exceeds 1 m. These two patch types are variable in size but usually cover an area no larger than 25 m^2 and often as small as 2–4 m^2. The patch types commonly occur side by side in areas that do not differ greatly in slope, aspect, or soil type. Similar small-scale heterogeneity was discussed by Peart (1989) for a nearby coastal grassland in Sonoma County.

Native to Eurasia and North Africa, feral pigs (Suidae) are conspicuous components of coastal grasslands and have occurred in coastal and inland regions of California since at least the 1700s (Barrett 1978, Wood and Barrett 1979, Mayer and Brisbin 1991). In many regions of California, populations are comprised of feral domestic pigs (*Sus scrofa domesticus*), wild boar (*Sus scrofa scrofa*) introduced in the 1900s for hunting, and various hybrid forms. Pigs are omnivorous and have a diverse and seasonally variable diet that includes invertebrates, fungi, and belowground bulbs and roots, acorns, as well as aboveground grass and forb foliage (Barrett 1978). During the wet season each year (October–May), groups of foraging pigs regularly pass through Salt Point State Park and disturb extensive portions of the short and tall patch types at our study site. Although detailed records are not available, pigs have been present in the park for at least the past two decades and probably much longer (R. Pasquinelli, *personal communication*). Pig disturbances are distinctive

and differ greatly from those generated by pocket gophers (*Thomomys bottae*) and moles (*Scapanus latimanus*). Their foraging activity (grubbing) consists of excavating the soil to a depth ranging from 5 to 15 cm. The disturbed vegetation and associated soil may remain in place or pigs may push this material to the side, thereby covering adjacent vegetation.

METHODS

Exclosure experiments

Conducting effective pig-exclosure experiments involves overcoming two challenges. First, one must contend with the reality that pig disturbances are distributed patchily throughout a study site, and there is a high probability that not all unfenced control plots will be disturbed during the course of a study. Simulated pig disturbances might seem to be a solution to this dilemma, but they are open to the criticism that human disturbances do not accurately mimic those of pigs. The second challenge to contend with is that pig fencing may unintentionally exclude other nontarget mammals that themselves may have significant effects on the plant community. If this occurred, it would not be clear whether a significant fencing effect was due solely to pigs, or to the nontarget mammals, or to some combination of the two.

To address these two challenges, in May and June of 1996 we established an exclosure experiment in a grassland at Salt Point State Park. The experiment consisted of 40 2 × 2 m plots distributed throughout our grassland site. Plots were grouped in pairs, with plots within pairs separated by 2–4 m. We matched all pairs with respect to topography, plant species composition, degree of plant cover, and levels of previous pig disturbance. (At this site, we could easily distinguish among pig disturbances that occurred during the past few months vs. those that occurred one or two years previously; J. H. Cushman and T. A. Tierney, *personal observation*.) Twenty-two plots were located in the short patch type, whereas 18 plots were in the tall patch type. (See *Study system* for descriptions of the two patch types.) We randomly assigned plots in each pair to one of two treatment levels: they either received fencing to exclude feral pigs and other medium- to large-sized mammals, or were left unmanipulated and served as controls. All plots had heavyweight t posts at each corner, with the 2-m posts driven 0.75 m into the ground. Exclosure plots received 1 m woven-wire fencing on all sides, with a strand of barbed wire at ground level along the plot perimeter to prevent pigs from prying up the fencing. These fences effectively excluded pigs from all manipulated plots during our four-year study.

During the four years of this experiment, 14 of the 20 unfenced control plots were disturbed by pigs at least once, and along with their fenced counterparts, were used to assess the effects of pigs on vegetation

and soil characteristics. There were 28 plots in all: 16 plots in short patches and 12 in tall patches. The six control plots that were not disturbed by pigs, along with their six fenced pairs, were used to assess the hypothesis that unintentionally excluded herbivores had significant effects on the vegetation in our plots (12 plots in all; 6 plots in each of the short and tall patches). Pigs had disturbed these control plots prior to our study, as there was clear evidence of older pig disturbance in all 40 plots at the outset (J. H. Cushman, *personal observation*). In our system, the nontarget taxa were black-tailed deer (*Odocoileus hemionus columbianus*) and hares (*Lepus californicus*). Smaller herbivores and granivores, such as *Microtus californica* and *Peromyscus maniculatus*, were not excluded by our fencing (J. H. Cushman, *personal observation*).

Disturbance level

In early March for three of the four years of this study (1997, 1998, and 2000), we estimated the amount of areal cover of pig disturbance that occurred in each of the 20 unfenced plots using point-intercept methods (Bonham 1989). We established three parallel and permanent transects within each of the 2×2 m plots, with transects placed randomly after allowing for a 30-cm buffer along the plot perimeter. We then sampled the unfenced plots every 10 cm along each transect for a total of 45 points, and at each point, determined whether the soil and vegetation had been disturbed by pigs during the current rainy season. Our previous work at this site revealed that current-year disturbances were distinguished easily from those occurring in the two previous years (J. H. Cushman and T. A. Tierney, *personal observation*).

Plant community composition

Four years after the exclosure experiment was established, we used standard point-intercept methods (Bonham 1989) to sample the plant community in all 40 plots. To evaluate the effects of our manipulations on plant species richness, we sampled the vegetation along the same three transects used to document disturbance levels. The 30-cm buffer along the plot perimeter was especially important for the vegetation sampling, so as to avoid possible edge effects caused by the fencing. In mid-June of 2000, we sampled all fenced and unfenced plots every 10 cm along each transect for a total of 45 points and recorded the species of each plant hit. (Multiple species were frequently hit per point.) For each plot, we then grouped all plant species by geographic origin (i.e., native or exotic). Sampling in June allowed us to detect the vast majority of plant species in our plots, including spring-flowering species such as bulbs.

At peak biomass in mid-June of 2000, we also quantified aboveground plant biomass in all plots used in the exclosure experiment. We harvested all living aboveground biomass and accumulated dead plant matter (or residual dry matter; RDM) rooted in a sampling ring (0.066 m²) placed in three randomly determined locations within each plot. These samples were pooled and in total represented 5% of the plot area (0.2 m²). In the laboratory, we first separated all material into living and dead biomass and then, following Lavorel et al. (1997), sorted plant biomass into the following functional groups based on life history and growth characteristics: annual and perennial grasses, nongrass monocots, and forbs (herbaceous dicots). We then divided the biomass from each of these four groups into native and exotic categories. We dried all samples at 60°C for 48 hours, and weighed dried biomass immediately after removal from the oven.

Soil nitrogen mineralization rates

In February and March of 2000, during the yearly peak in nitrogen mineralization (J. H. Cushman, *unpublished data*), we sampled the soil in our 40 plots using methods outlined in Binkley and Hart (1989) and Binkley and Vitousek (1989). In four randomly determined locations within each plot, we collected soil using a 2-cm corer inserted to a depth of 15 cm. This corresponded to the range of soil depths at which we commonly observed pig disturbances to occur at our study site (J. H. Cushman, *personal observation*). Soil from each plot was combined, mixed, and then divided into three equal samples. We extracted nitrate (NO_3^-) and ammonium (NH_4^+) ions from a 10-g sample within 24 hours of collection using a 2 mol/L KCl solution, whereas another sample was placed in a breathable bag and allowed to incubate in the laboratory at room temperature for 30 days. The resulting extracts were frozen and later analyzed for NO_3^- and NH_4^+ content at the University of California's DANR Analytical Laboratory (Davis, California, USA). We then calculated net mineralization rates as the difference in ammonium and nitrate content between initial samples and those incubated for a month (micrograms of NO_3^- and NH_4^+ per gram of soil per day). We determined the water content of a third 10-g soil sample so that we could adjust nutrient values for differences in soil moisture at the time of initial collection.

Statistical analyses

We performed all statistical analyses using the JMP 3.2.1 and SAS 8.0 software (both from SAS Institute, Cary, North Carolina, USA). To determine the degree to which pig disturbance levels varied between patch types and among years, we analyzed data on the percentage of disturbance per plot using a repeated-measure ANOVA, with patch type (short or tall) as the grouping factor and year (1997, 1998, and 2000) as the repeated measure. Data on percentage of disturbance were arcsine square-root transformed prior to analysis. To evaluate the influence of pig disturbances on vegetation, we analyzed our data using multifactor MANOVAs, with pig treatment (pigs present or absent),

patch type (short or tall), and pair nested within patch type as the grouping factors in both cases ($n = 28$ plots). Pair was treated as a random factor and Wilks' lambda values were used throughout. Response variables for the first MANOVA were the richness of native and exotic plant species in 2000. Response variables for the second MANOVA were living aboveground dry biomass in 2000 for native and exotic perennial grasses, exotic annual grasses, native nongrass monocots, and native and exotic forbs (biomass data were log transformed prior to analysis to equalize variances). For MANOVAs with significant pig treatment main effects or any significant interaction terms containing pig treatment, we proceeded with "protected" ANOVAs (sensu Scheiner and Gurevitch 2001) on individual response variables. Data on accumulated dead plant material were analyzed with an ANOVA using the same model as employed for the living biomass analyses. Two-way MANOVAs on native and exotic plant species richness and percent cover data collected in June 1996 indicated that fenced and unfenced plots were not significantly different from each other at the start of the experiment (all P values were >0.5).

We also examined the degree to which the amount of pig disturbance influenced native and exotic components of our plant community. To accomplish this, we used linear regression analyses to evaluate the relationship between plant species richness and aboveground biomass and the average area (%) of unfenced control plots disturbed by pigs during three years (1997, 1998, and 2000). We performed separate analyses for native and exotic taxa and log-transformed biomass data to equalize the variance.

Data on soil nitrogen mineralization rates were analyzed using a repeated-measure MANOVA, with pig treatment (pigs present or absent), patch type (short or tall) and pair nested within patch type as the grouping factors, and time (February or March) as the repeated measure. As before, pair was treated as a random factor and Wilks' lambda values were used. Ammonium and nitrate mineralization rates (micrograms of NO_3^- and NH_4^+ per gram of soil per day) were the multiple response variables. Data on soil moisture were analyzed with a repeated-measure ANOVA using the same grouping factors as used in the MANOVA.

To consider the possibility that black-tailed deer and hares were having effects on the plant or soil characteristics in our system, we analyzed data from undisturbed control plots along with their fenced counterparts ($n = 12$ plots). Here, we again used two separate MANOVAs, with herbivore treatment (herbivores present or absent), patch type (short or tall), and pair nested within patch type as the grouping factors in both cases. As before, pair was treated as a random factor, Wilks' lambda values were used, and response variables were the same plant and soil characteristics used previously.
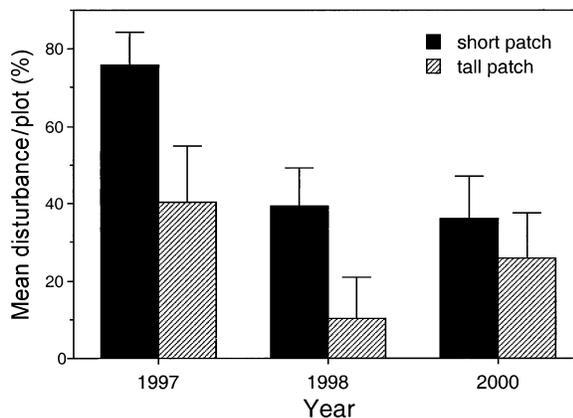

FIG. 1. Percentage area of plots (mean + 1 SE) that were disturbed by feral pigs in each of three years (1997, 1998, and 2000) in short and tall patch types.

RESULTS

Disturbance level

Results from a repeated-measure ANOVA documented that the amount of pig disturbances in our unfenced plots varied significantly among years; disturbance was greatest in 1997 and equally low in 1998 and 2000 (Fig. 1; $F_{2,24} = 12.60$, $P = 0.0002$). This analysis also revealed that there was a trend for short patches to receive more disturbance than tall patches ($F_{1,12} = 3.47$, $P = 0.087$). However, there was no evidence that differences in amounts of disturbance between patch types varied significantly among years ($F_{2,24} = 1.72$, $P = 0.208$).

Plant community composition

Results from a MANOVA indicated that soil disturbances by feral pigs significantly altered the richness of native and exotic species considered collectively (Fig. 2; $F_{2,11} = 30.12$, $P < 0.001$). Subsequent protected ANOVAs showed that this significant MANOVA was due to pig disturbances causing a 24% increase in the number of native plant species (Fig. 2A; $F_{1,12} = 3.58$, $P = 0.083$) and a 29% increase in exotic richness (Fig. 2B; $F_{1,12} = 25.94$, $P = 0.0003$). Although exotic species richness was significantly greater in short patches than tall ($F_{1,12} = 48.09$, $P < 0.0001$), this was not the case for native taxa ($F_{1,12} = 2.70$, $P = 0.126$), and the effect of pig disturbances on species richness did not vary with patch type for either group (treatment × patch type interactions; natives, $F_{1,12} = 0.35$, $P = 0.567$; exotics, $F_{1,12} = 0.29$, $P = 0.598$).

A second MANOVA revealed that soil disturbances generated by pigs had a significant influence on aboveground plant biomass of the different functional groups (Fig. 3; $F_{6,7} = 5.47$, $P = 0.021$), with these effects varying significantly among patch types (treatment × patch type interaction, $F_{6,7} = 5.02$, $P = 0.026$). A subsequent protected ANOVA indicated that pig distur-
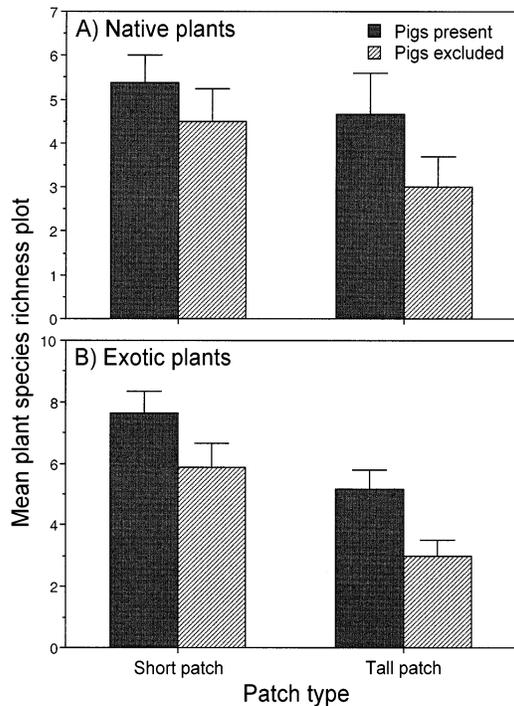
FIG. 2. Plant species richness (mean + 1 SE) of (A) native and (B) exotic taxa as a function of short and tall patch types and whether feral pigs and their soil disturbances were present or excluded.

bances significantly altered the biomass of exotic perennial grasses ($F_{1,12} = 8.16$, $P = 0.015$), with a 52% decrease in tall patches and no effect in short (treatment × patch type interaction, $F_{1,12} = 9.29$, $P = 0.01$; Fig. 3A). In contrast, disturbances had no such effects on native perennial grasses ($F_{1,12} = 0.01$, $P = 0.91$). Exotic annual grasses exhibited a strongly context-dependent response, with pig disturbances causing a 69% biomass decrease in tall patches and a 62% increase in short patches (treatment × patch type interaction, $F_{1,12} = 6.95$, $P = 0.022$; Fig. 3B). The exact opposite response was found for native, nongrass monocots, where pig disturbances decreased biomass in short patches by 56% and increased biomass by 80% in tall patches (treatment × patch type interaction, $F_{1,12} = 6.94$, $P = 0.021$, Fig. 3C). Pig disturbances increased the biomass of exotic forbs ($F_{1,12} = 8.24$, $P = 0.014$), with values increasing by 79% in tall patches and only 15% in short patches (treatment × patch type interaction, $F_{1,12} = 2.5$, $P = 0.139$; Fig. 3C). Similar to the response of native perennial grasses, biomass of native forbs was not adversely affected by pig disturbances ($F_{1,12} = 0.42$, $P = 0.531$). Lastly, we found that pig disturbances reduced the amounts of dead plant material accumulating in plots by 40% ($F_{1,12} = 9.29$, $P = 0.01$; Fig. 4).

As shown in Fig. 5, native and exotic vegetation differed greatly in how they responded to variation in the amount of pig disturbance. Neither richness nor aboveground biomass of native plant species varied significantly with average percent cover of pig disturbance (richness, $y = 4.48 + 0.015x$, $F_{1,12} = 0.53$, $P = 0.481$, $R^2 = 0.042$; Fig. 5A; biomass, $y = 4.60 - 0.018x$, $F_{1,12} = 2.67$, $P = 0.128$, $R^2 = 0.182$; Fig. 5C). In contrast, both exotic richness and aboveground biomass increased with amount of disturbance (richness, $y = 4.74 + 0.046x$, $F_{1,12} = 6.07$, $P = 0.030$, $R^2 = 0.336$, Fig. 5B; biomass, $y = 4.21 + 0.01x$, $F_{1,12} = 9.96$, $P = 0.008$, $R^2 = 0.454$, Fig. 5D).

Results from the herbivore exclosures indicated that, in the absence of pigs, fencing out nontarget mammals (deer and hares) at our site did not have significant effects on the grassland community. A MANOVA revealed that these herbivores did not have a significant influence on the richness of native and exotic plant species in our system ($F_{2,5} = 1.42$, $P = 0.324$). A second MANOVA also indicated that these mammals did not have significant effects on aboveground plant biomass of the different plant functional groups ($F_{6,1} = 0.88$, $P = 0.672$).

Soil nitrogen mineralization rates

Results from a repeated-measure MANOVA indicated that pig disturbances did not have significant effects on ammonium and nitrate mineralization rates (Table 1; $F_{2,35} = 1.50$, $P = 0.237$). Rates did vary significantly between sample dates ($F_{2,35} = 4.56$, $P = 0.017$), with values greater in February for nitrate and greater in March for ammonium. Although soil moisture was significantly greater in February than March ($F_{1,12} = 54.10$, $P < 0.0001$), there was no effect of pig disturbance on soil moisture ($F_{1,12} = 0.80$, $P = 0.389$).

Results from the herbivore exclosures indicated that deer and hares did not influence nitrogen availability at our site. A repeated-measure MANOVA showed that herbivores did not significantly affect ammonium and nitrate mineralization rates ($F_{1,3} = 0.47$, $P = 0.514$). Such findings, along with those for vegetation summarized earlier, strongly suggest that our results from the pig exclusions shown in Figs. 2–5 were due to pig disturbances and not to unintended exclosure of nontarget animals.

DISCUSSION

In this paper, we have summarized results from a four-year exclosure experiment, which documents that the foraging activity of feral pigs had substantial effects on the disturbance regimes (Fig. 1) and vegetation characteristics (Figs. 2–5) of a mesic coastal grassland in northern California. A number of studies have shown that small-scale soil disturbances by mammals can facilitate invasion by plant taxa that possess life history characteristics that enable them to colonize rapidly and become established in these openings (Rice 1987, Hobbs et al. 1988, Peart 1989, Hobbs and Mooney 1991, D'Antonio 1993, McIntyre and Lavorel 1994, Kotanen 1995, 1997a). Our data support this gener-
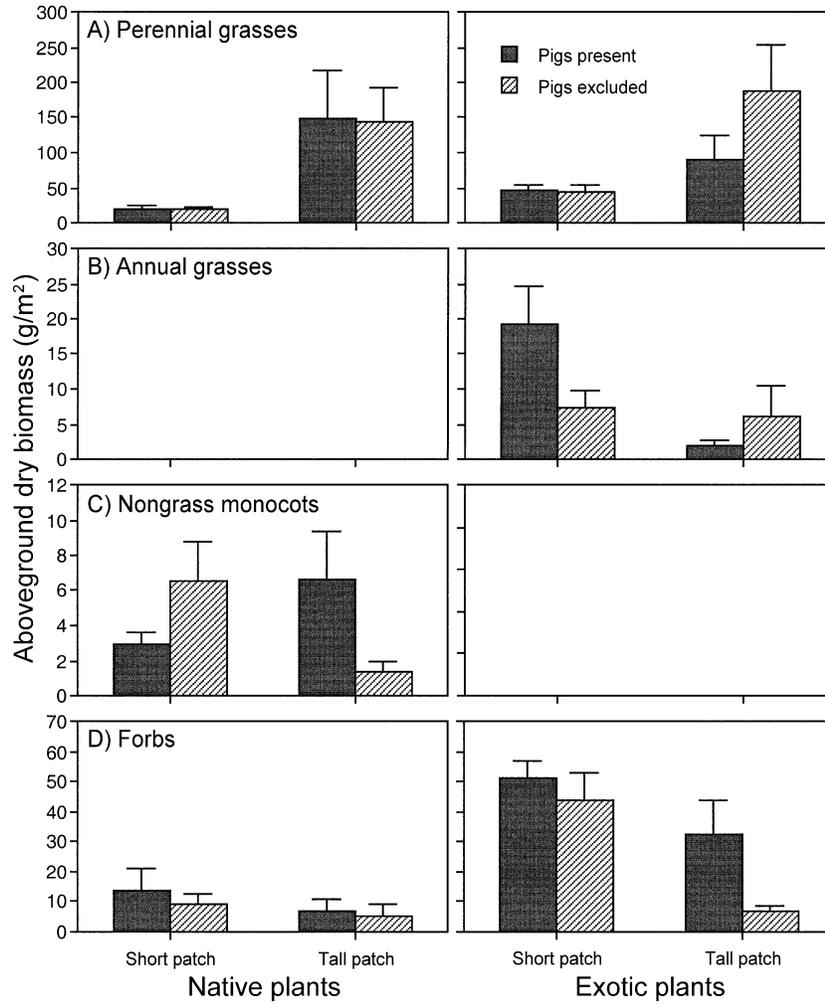
FIG. 3. Aboveground dry biomass (mean + 1 SE) of native and exotic plants as a function of short and tall patch types and whether feral pigs and their soil disturbances were present or excluded. Plants were grouped into functional groups: (A) perennial grasses, (B) annual grasses, (C) nongrass monocots (primarily bulbs), and (D) forbs.
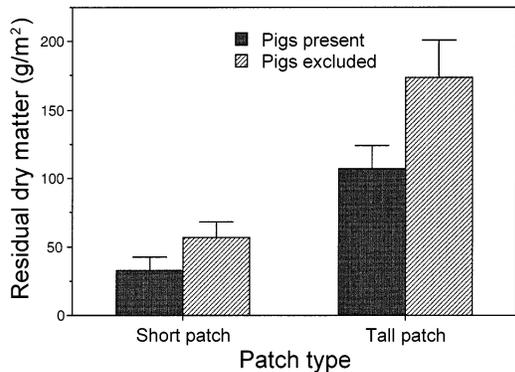

FIG. 4. Residual dry matter (mean + 1 SE) as a function of short and tall patch types and whether feral pigs and their soil disturbances were present or excluded.

alization, as the richness of both native and exotic plant taxa increased in pig-disturbed areas, and exotic richness increased with increasing amounts of disturbance. These plant species are short lived and especially adept at colonizing openings because they produce abundant amounts of seed that persist in the soil of disturbed areas and/or because they disperse into disturbed areas as seed rain from surrounding patches (Peart 1989, Kotanen 1996, 1997a, b). In a nearby coastal grassland (~130 km north of our site), Kotanen (1995) found that pig disturbances initially reduced plant species richness during the first year after disturbance, and then richness rebounded to levels similar to or sometimes greater than those in undisturbed plots. He also found that native and exotic richness responded similarly to pig disturbance. In another study involving responses to simulated pig disturbance, Kotanen (1997a) found that plant species richness either recovered three years following disturbance, or was reduced. Despite the
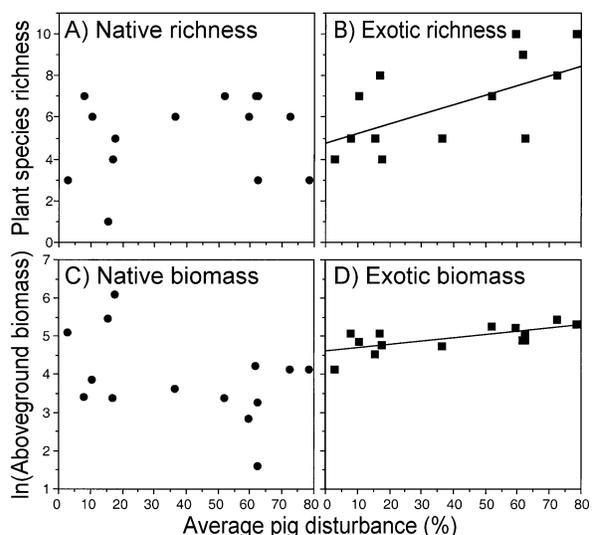
FIG. 5. Relationship between (A, B) plant species richness and (C, D) aboveground dry biomass (g/m²) and percentage pig disturbance averaged over three years (1997, 1998, and 2000) for both native and exotic taxa.

close proximity of study sites, our results differ somewhat from those of Kotanen in that plant species richness was increased by pig disturbances and that exotics exhibited a stronger response than natives. One possible explanation for these differences is that our disturbed control plots consisted of a mosaic of disturbance ages, and individual patches could have been disturbed multiple times during the experiment. In contrast, Kotanen had plots that were disturbed once and then monitored one, two, and in some cases three years after this initial event. (Plots that were disturbed repeatedly were excluded from further study.) Thus, although our experiment did not control for the number of disturbances or disturbance age, it captured the range of disturbance frequencies and ages that characterized this system. A second factor is that Kotanen's study was conducted during 1990–1993 near the end of a six-year drought, whereas ours occurred from 1996 to 2000 when precipitation levels were more substantial. Variability in precipitation is known to have major impacts on grassland systems (Pitt and Heady 1978, Bartolome 1989, Hobbs and Mooney 1991), and the response of our two study sites to pig disturbance may have differed because of these contrasting regimes.

A striking result of our four-year study is that biomass of native perennial grasses was unaffected by pig disturbances. This pattern was robust, as it persisted in the two patch types that were dominated by different native bunchgrass species, *Deschampsia* in tall patches and *Danthonia* in short patches. A possible explanation for our findings is that native bunchgrasses are deep-rooted species and therefore more difficult for pigs to overturn while foraging. Bunchgrasses are well known to allocate extensive resources to belowground tissue

(Jackson and Roy 1986) and can live up to 60 years and grow quite large (Gatsuk et al. 1980). Our observations are consistent with this hypothesis, as pigs rarely overturned established native bunchgrasses and instead rooted around them, or at best disturbed their outer edges. In a nearby coastal grassland, Peart (1989) also found that pocket gophers tended to avoid areas dominated by bunchgrasses, perhaps because these perennials are difficult to disturb. Kotanen (1995) also found that native bunchgrasses (especially *Danthonia*) were not adversely affected by pig disturbances. Another possibility is that some native perennial grasses were very susceptible to pig disturbances and disappeared from the system prior to our study, leaving only species that were more tolerant of frequent soil disturbances. Although we cannot rule out this possibility, it seems unlikely, given that our pig-disturbed grassland did not lack native perennial grass species that were found in adjacent less disturbed grasslands (J. H. Cushman, *personal observation*).

In contrast to the response of native bunchgrasses, we found that pig disturbances dramatically reduced the aboveground biomass of exotic perennial grasses in tall patches at our site. In our plots, 71% of the biomass for exotic perennial grasses was produced by *Anthoxanthum odoratum*, so the reduction of biomass in tall patches may have reflected primarily the response of this species rather than exotic perennial grasses as a group. The next most dominant exotic perennial grass in our system was *Agrostis stolonifera*, which comprised 27% of the biomass for this group. Its response resembled that of *Anthoxanthum* in short patches, where there was no effect of pig disturbance, but there was only a weak trend for *Agrostis* to be less abundant in pig-disturbed plots in tall patches. In any case, the difference in responses of native bunchgrasses and exotic representatives, such as *Anthoxanthum*, may be explained by plant size and the amount and depth of root tissue developed prior to disturbance. Although the total biomass of exotic perennial grasses in our plots was large, individual plants tended to be small, and we hypothesize that these individuals had not produced sufficient amounts of anchoring root tissue to resist disturbance by pigs.

TABLE 1. Mean (±1 SE) ammonium and nitrate mineralization rates (micrograms of NO_3^- and NH_4^+ per gram of soil per day) in soil from plots either disturbed by pigs or protected from such activities.

Patch type	Pig treatment	
	Disturbed	Protected
A) Ammonium (NH_4^+) mineralization		
Short	6.77 (1.08)	7.16 (1.52)
Tall	5.44 (1.16)	5.15 (1.91)
B) Nitrate (NO_3^-) mineralization		
Short	−1.64 (0.31)	−1.42 (0.27)
Tall	−1.66 (0.48)	−0.84 (0.36)

The 52% reduction in biomass of exotic perennial grasses (primarily *Anthoxanthum*) was associated with, and we believe led to, a number of other vegetation changes in tall patches. The reduction created major openings or gaps in the grassland that members of other functional groups were able to exploit. In particular, we hypothesize that the 80% increases in biomass of both exotic forbs and native, nongrass monocots (primarily bulb-producing species) in tall patches was a direct response to the diminished presence of exotic perennial grasses. In both cases, competition with *Anthoxanthum* in tall patches may have prevented these taxa from reaching maximum abundance and therefore biomass. This conclusion seems plausible given that other studies of grasslands and old fields have shown that plants colonizing gaps often experience reduced competition for light and belowground resources (e.g., Goldberg and Gross 1988, Cahill and Casper 2002). However, we were surprised that the biomass of exotic annual grasses did not respond similarly to the reduced prevalence of *Anthoxanthum* in pig-disturbed areas. We suspect that the 69% decrease in biomass of this group in tall patches occurred because of two factors, acting individually or jointly. First, compared to short patches, exotic annual grasses were much less abundant in tall patches, and they may not have been able to capitalize on the gaps because their seeds were less abundant in the soil. Second, the response of exotic annual grasses may have been diminished by intense competition with exotic forbs, which increased dramatically after the decline of *Anthoxanthum*.

The vegetation responses to pig disturbance in short patches were markedly different from those in tall patches. The first difference was that biomass of exotic perennial grasses was not affected significantly by pig disturbances, as it had been in tall patches. The intensity of pig disturbances was greater in short patches than tall, which we suspect kept the biomass of exotic bunchgrasses at low levels and prevented them from rebounding, even after four years of protection from disturbance. The second important difference in short patches was that biomass of exotic annual grasses increased by 62% in response to pig disturbances, whereas it had decreased by 69% in tall patches. The result in short patches was not surprising given that exotic annual grasses are known to respond positively to disturbance (see Hobbs and Huenneke 1992) when adequate seed sources are available. Given their abundance in short patches, exotic annual grasses probably had a well-developed seed bank and extensive seed rain from neighboring undisturbed patches, which enabled them to respond favorably to pig disturbance in short patches. This large increase in annual grasses may also explain the 56% reduction in biomass of native nongrass monocots, with the exotic taxa simply out-competing them for space. An additional or alternative possibility is that these native taxa, which are composed almost entirely of bulb-producing species, were unable to tolerate the high disturbances levels that characterized short patches.

Given the amount of pig disturbance that occurred in our unfenced control plots (Fig. 1), we were surprised to discover that soils from disturbed and protected plots did not differ significantly in net nitrogen mineralization rates (Table 1) or soil moisture levels. Our results were also unexpected given the work of Singer et al. (1984), who found that intensive pig rooting in a southeastern United States deciduous forest was associated with significantly greater nitrate, ammonium, and potassium pools in the soil, even at depths of 100 cm. In addition, working in a mesic forest on the island of Hawaii, Vitousek (1986) found that net nitrogen mineralization was greater in pig-disturbed soils compared to areas protected from disturbance for at least 14 years. In the only other study that has focused on grasslands, Kotanen (1997*a*) assessed the effects of two kinds of simulated pig disturbance on soil nitrogen pools, and found results not substantially different from ours. He found that nitrate pools were not affected by either type of soil disturbance, whereas the results for ammonium were somewhat equivocal. (Levels were higher than controls for one type of simulated disturbance and lower for another.) These results, combined with ours, suggest that soil nutrients in Mediterranean grasslands may not be greatly affected by pig disturbances. Numerous factors could explain the absence of effects in our system. First, the grassland may simply be able to withstand, or recover rapidly from, considerable amounts of soil disturbance without experiencing significant changes in nitrogen availability. This might occur if nutrients did not leach rapidly from the system, but instead collected in the many small depressions that pigs create. Another potential explanation is that our results may have been due to the Salt Point grassland being disturbed intensively by pigs year after year, which in turn caused significant changes in soil characteristics prior to the establishment of our experiment. A third possibility is that pigs did modify soil nitrogen availability, but these effects were masked by our sampling regime. We pooled soil samples from four randomly selected locations within each 2×2 m plot. These areas may have varied in the amount and age of disturbance they received, such that pooled samples merged heavily disturbed soils with lightly disturbed ones and/or recently disturbed soils with those disturbed long ago. Such mixing might have diluted distinct fine-scale patterns that existed within our plots. However, in another study at the Salt Point site, T. A. Tierney and J. H. Cushman (*unpublished data*) also found that the pig disturbances did not substantially alter soil nutrients, texture, or moisture in 2001, even after controlling for the amount and age of pig disturbances. In summary, regardless of which of these factors was operating in our system, variation in soil characteristics does not seem sufficient to explain the many vegetation changes that we have detected. Instead, our

data are more consistent with the notion that changes in the plant community were due to space clearing by pigs that provided greater opportunities for colonization and reduced intensity of competition.

The management implications of this study are complex because we have found that soil disturbances have a mixture of similar and opposing effects on different components of a community. Our results highlight the increasingly common challenges that resource managers must face, regardless of geographic region or habitat type: simultaneously, they must contend with multiple invasive species that interact with each other and native taxa in complex and often unpredictable ways. Our data show that different plant functional groups vary greatly in their responses to disturbance, and that native and exotic members of the same functional group do so as well. Furthermore, our work suggests that annual-dominated and perennial-dominated grasslands will differ markedly in their responses to pig invasion. We suspect that this kind of variability is not unique to feral pigs or the coastal grasslands of California, and suggest that it will be critical for future studies assessing the community-level effects of disturbance to focus explicitly on the responses of taxa from different functional groups and geographical origins, and how they vary with spatial heterogeneity in the landscape. Finally, despite the variability documented in this study, we conclude that the overall effect of feral pigs on grasslands will be to promote further invasion of exotic grasses and forbs. Such homogenization of the community suggests that resource managers should prioritize the protection of coastal grasslands in California that still boast reasonably intact native vegetation, but are declining due to disturbance by feral pigs.

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