

Temporal changes in native and exotic vegetation and soil characteristics following disturbances by feral pigs in a California grassland

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Abstract

Invasive species that increase prevailing disturbance regimes can profoundly alter the composition and structure of ecosystems they invade. Using both comparative and manipulative approaches, we investigated how native and exotic vegetation and soil characteristics at a coastal grassland site in northern California changed through time following disturbances by feral pigs (*Sus scrofa*). We quantified these successional changes by comparing pig disturbances of varying ages (2, 14, 26+, and 60+ months) during the spring and early summer of 2001. Our results indicate that species richness of native plants increased slowly but steadily through time following disturbances, whereas richness of exotic species rebounded much more rapidly. Percent cover of native perennial grasses also increased steadily through time after pig disturbance, whereas the cover of exotic perennial grasses, annual grasses and forbs initially increased rapidly after disturbance and then remained the same or subsided slightly with time. The cover of native forbs and bulbs either increased weakly through time following disturbance or did not change substantially. Pools of ammonium and nitrate in the soil did not change greatly through time following pig disturbance. Net mineralization rates for ammonium and nitrate also varied little with age since disturbance, although we did find that nitrate mineralization was greater at intermediate ages in one study. Neither organic matter content or particle size varied significantly with disturbance age. In summary, we have shown that native and exotic plants from different functional groups vary greatly in how they recovered from pig disturbances. Exotic taxa were generally able to rapidly colonize and persist in pig disturbances, whereas native taxa usually exhibited a slow but steady rebounding following pig disturbance. Given our results, and those of others from nearby sites, we suggest that the health of coastal grasslands may be enhanced substantially by eliminating or greatly reducing the size of feral pig populations.

Introduction

Disturbance is widely recognized as a key factor influencing the structure of ecological systems (Sousa 1984; Pickett and White 1985; Pickett et al. 1989). In terrestrial plant communities, disturbance generally increases spatial and temporal

heterogeneity of vegetation (Collins and Barber 1985) and is considered integral to the maintenance of species diversity (Grime 1973; Connell 1978; Huston 1979). However, natural and human-caused disturbances may also threaten native communities because they can promote the spread of invasive, exotic plant species (Mooney

and Drake 1986; Drake et al. 1989; Rejmánek 1989; Hobbs and Huenneke 1992; D'Antonio et al. 1999; Sakai et al. 2001; Cushman et al. 2004). This dual role of disturbance poses significant challenges for applied ecologists and resource managers, who attempt to maintain native species while simultaneously controlling the spread of exotic taxa.

Biotic disturbance agents are a common feature in many terrestrial landscapes and can alter soil characteristics, the structure of plant communities, and the dominance of invasive species (Hobbs and Huenneke 1992; Mack and D'Antonio 1998; Cushman et al. 2004). Disturbances by native mammals – such as pocket gophers, prairie dogs, badgers, bear and bison – create small-scale soil disturbances through burrowing, excavations and wallowing that affect landscapes in diverse and often variable ways (Platt 1975; Huntly and Inouye 1988; Whicker and Detling 1988; Hobbs et al. 1988; Martinsen et al. 1990; Tardiff and Stanford 1998). Biotic disturbances have often been shown to facilitate invasion by exotic plant taxa, which are able to rapidly colonize and become established in these openings (Rice 1987; Hobbs et al. 1988; Peart 1989a; Hobbs and Mooney 1991; D'Antonio 1993; McIntyre and Lavorel 1994; Cushman et al. 2004).

Domesticated mammals have been introduced in many parts of the world and frequently establish feral populations that substantially modify natural disturbance regimes (Cox 1999; D'Antonio et al. 1999). For example, feral goats and sheep on temperate and tropical islands (Coblentz 1978; van Vuren and Coblentz 1987), as well as feral horses and burros in arid habitats of the western U.S. (Cox 1999; Beever and Brussard 2000; Beever et al. 2003), can have large impacts on the ecosystems they invade. Feral pigs (*Sus scrofa*) are an exotic disturbance agent that has also invaded many regions and habitat types of the world and are now found on all continents except Antarctica, as well as many oceanic islands. While foraging for below-ground plant parts and macro-invertebrates, pigs overturn extensive areas of vegetation and associated soil, and create a complex mosaic of disturbance intensities and ages (Barrett 1993; Kotanen 1995; Cushman et al. 2004). A number of studies in a diverse array of habitats and geographical regions have investigated the effects of pig disturbances on the distribution and abundance of

native and exotic plant species (Spatz and Mueller-Dombois 1975; Jacobi 1981; Stone 1985; Aplet et al. 1991; Kotanen 1995; Cushman et al. 2004). In general, these studies have found that pig disturbances are often associated with or actually promote the invasion of exotic plant species, although Cushman et al. (2004) reported that different plant functional groups and grassland patch types varied greatly in their responses to disturbance. Fewer studies have explored the influence of pig disturbances on soil characteristics, and results have been quite variable. For example, Singer (1984) found that pig disturbances in montane forests of the southeastern U.S. were associated with elevated nitrate levels, whereas Moody and Jones (2000) and Cushman et al. (2004) found no such effects in grasslands and oak woodlands in California.

Determining how native and exotic components of a plant community respond to soil disturbances *through time* will be critical for understanding the ecological consequences of these perturbations and the rate and prognosis for recovery. The conventional wisdom is that exotic plants will be able to rapidly colonize and become established in disturbed patches, whereas most native taxa will be slower to respond (see Hobbs and Huenneke 1992; D'Antonio et al. 1999). However, these generalities need to be tested further, and particular attention must focus on the degree to which plant taxa from different functional groups (*sensu* Lavorel et al. 1997) or life forms vary in their responses to disturbance through time. Such an emphasis on successional trajectories will be especially important for resolving key management challenges. For example, will continued soil disturbance maintain plant communities in a highly invaded state that does not allow natives to recolonize? And, when dealing with exotic disturbance agents, would their removal or reduced abundance be a viable restoration technique that fosters the recovery of native components of the community, or would a reduction in soil disturbance simply further the dominance of exotic plants? Understanding these kinds of temporal dynamics in plant communities will be essential for making sound decisions about the management of ecological systems that regularly experience disturbance.

In this paper, we report on results from comparative and exclosure studies that evaluate the

influence of disturbances by feral pigs on a coastal grassland in northern California. Our work addresses three questions: (1) How does grassland vegetation change through time following disturbances by feral pigs, and do native and exotic plants from different functional groups vary in their responses? (2) How does plant-available nitrogen and other soil characteristics (i.e., soil moisture, texture and organic matter) change through time following pig disturbance? and (3) Does the response of vegetation and soil characteristics to pig disturbances through time vary with fine-scale heterogeneity within a grassland ecosystem? Answers to these questions will not only enhance our understanding of the effects of disturbances on vegetation and soil characteristics, but will also assist applied ecologists in predicting the environmental consequences of this exotic disturbance agent.

Study system

Our research was conducted at Salt Point State Park, (38°34'31" N, 123°18'43" W), approximately 120 km north of San Francisco, California in northwest Sonoma County. This coastal grassland has a marine-influenced, Mediterranean-type climate with cool, wet winters and mild summers. Year-round fog and winter rains between October and April account for the average annual precipitation of 920 mm (30 year average; National Weather Service). Soils at the site are derived from the Franciscan rock formation and are classified within the Rohnerville loam series, consisting of loam, silt loam (USGS Soil Survey 1972). The grassland occurs on a coastal terrace at 275 m elevation, is approximately 1.5 ha in size, and is surrounded by a mixed evergreen forest dominated by *Lithocarpus densiflorus* (tanoak), *Arbutus menziesii* (madrone), and *Umbellularia californica* (bay laurel). Vegetation within the grassland is dominated by perennial bunchgrasses, the most common of which are the exotic *Anthoxanthum odoratum* (sweet vernalgrass) and two natives, *Danthonia californica* (California oatgrass), and *Deschampsia cespitosa* (tufted hairgrass) (see Table 1). Interspersed among these bunchgrasses are a mixture of native and exotic herbaceous dicots (forbs), exotic annual

grasses, and native bulbs. Throughout the paper, we use the term exotic (= non-native, non-indigenous, alien) to refer to plant species whose area of origin is Europe and Asian.

Throughout the Salt Point site, there is a striking pattern of small-scale heterogeneity in vegetation (Cushman et al. 2004). Two distinct patch types occur side by side: one is low growing with a mixture of annual and perennial grasses, forbs and bulbs (short patch type), while the other is dominated heavily by bunchgrasses (tall patch type). In these latter patches, both plant cover and aboveground biomass are dominated by *A. odoratum* and *D. cespitosa*. In contrast, short patches do not include *D. cespitosa* and instead are dominated by the native bunchgrass *D. californica* and a species-rich assemblage of exotic annual grasses and forbs. There are no obvious differences in slope, elevation or aspect that might easily explain this distinctive vegetation pattern, which is repeated throughout the grassland. These two patch types vary widely in size, but range from 4 m² to 2500 m² in size, and are most commonly 100 m². Similar small-scale heterogeneity was discussed by Peart (1989a) for a coastal grassland near Sea Ranch, California.

During the wet season each year (November–May), the grassland at Salt Point is heavily disturbed by feral pigs. Most animals are hybrids between two forms: feral domestic pigs (*Sus scrofa domestica*) and introduced Eurasian wild boars (*S. scrofa scrofa*). These disturbance agents are omnivorous and have a diverse and seasonally variable diet that includes invertebrates, fungi, and below-ground bulbs and roots, acorns, as well as aboveground grass and forb foliage (Barrett 1978). Since their introduction into California by Spanish settlers in 1769 (Barrett 1993), populations of feral pigs have increased in size and are responsible for significant disturbances in oak woodlands and grasslands (Kotanen 1995; Waithman et al. 1999). At Salt Point State Park, feral pigs may have been present since the early 1800s, when Russian settlers and fur traders released domestic pigs in the area (Mayer and Brisbin 1991). Although native burrowing animals, such as *Thomomys bottae* (pocket gophers) and *Scapanus latimanus* (moles), are also present in this grassland, pigs are the primary cause of soil disturbances. Typically, they disturb this grassland every

Table 1. Vascular plant species present (✓) and absent (×) from plots used in comparative and exclosure studies to evaluate the responses of plant communities to pig disturbances of differing ages (2-, 14-, 26+ months-old disturbances in the comparative study and 2-, 14-, and 60+ months-old disturbances in the exclosure study).

Plant species	Origin	Functional group	Comparative study			Exclosure study		
			2	14	26+	2	14	60+
APIACEAE								
<i>Eryngium armatum</i>	N	PF	×	✓	✓	✓	✓	✓
ASTERACEAE								
<i>Aster chilensis</i>	N	PF	✓	×	×	✓	✓	✓
<i>Filago gallica</i>	E	AF	×	✓	✓	✓	✓	✓
<i>Hemizonia congesta</i>	N	AF	✓	✓	✓	×	✓	✓
<i>Hypochaeris glabra</i> & <i>Leontodon taraxacoides</i>	E	AF	✓	✓	✓	✓	✓	✓
<i>Psilocarphus tenellus</i>	N	AF	×	✓	✓	×	×	×
BORAGINACEAE								
<i>Plagiobothrys nothofulvus</i>	N	PF	✓	×	×	×	×	×
FABACEAE								
<i>Lotus angustissimus</i>	E	AF	✓	✓	✓	×	×	×
<i>Lotus formosissimus</i>	N	PF	✓	×	✓	✓	×	×
LAMIACEAE								
<i>Prunella vulgaris</i>	N	PF	×	×	×	✓	✓	✓
LINACEAE								
<i>Linum bienne</i>	E	PF	✓	✓	✓	×	×	✓
ONAGRACEAE								
<i>Camissonia ovata</i>	N	PF	×	×	×	✓	×	✓
PLANTAGINACEAE								
<i>Plantago erecta</i>	N	AF	✓	✓	✓	✓	✓	✓
<i>Plantago lanceolata</i>	E	PF	✓	✓	✓	✓	✓	✓
<i>Anagallis arvensis</i>	E	AF	✓	✓	✓	✓	✓	×
RANUNCULACEAE								
<i>Ranunculus californicus</i>	N	PF	✓	✓	✓	✓	×	✓
RUBIACEAE								
<i>Galium parisiense</i>	E	AF	✓	×	✓	×	×	✓
SCROPHULARIACEAE								
<i>Triphysaria eriantha</i>	N	AF	×	×	✓	×	×	×
IRIDACEAE								
<i>Sisyrinchium bellum</i>	N	B	✓	✓	✓	✓	✓	✓
JUNCACEAE								
<i>Juncus bufonius</i>	N	AG	✓	✓	✓	×	×	×
<i>Juncus patens</i>	N	PG	✓	×	✓	×	×	×
<i>Luzula comosa</i>	N	PG	×	×	×	×	✓	✓
LILIACEAE								
<i>Brodiaea terrestris</i>	N	B	✓	×	✓	×	×	✓
<i>Calochortus uniflorus</i>	N	B	✓	✓	✓	✓	×	✓
POACEAE								
<i>Agrostis stolonifera</i>	E	PG	✓	×	✓	×	✓	✓
<i>Aira caryophyllea</i>	E	AG	✓	✓	✓	✓	✓	✓
<i>Aira praecox</i>	E	AG	✓	✓	✓	✓	✓	✓
<i>Anthoxanthum odoratum</i>	E	PG	✓	✓	✓	✓	✓	✓
<i>Briza minor</i>	E	AG	✓	✓	✓	×	×	×
<i>Bromus hordeaceus</i>	E	AG	×	×	×	×	✓	✓
<i>Cynosurus echinatus</i>	E	AG	✓	✓	✓	✓	✓	✓
<i>Danthonia californica</i>	N	PG	✓	✓	✓	✓	✓	✓
<i>Deschampsia cespitosa</i>	N	PG	✓	✓	✓	✓	✓	✓
<i>Holcus lanatus</i>	E	PG	×	✓	✓	✓	✓	×
<i>Vulpia bromoides</i>	E	AG	✓	✓	✓	✓	✓	✓

Plant origin is either native (N) or exotic (E) and functional group includes perennial forbs (PF), annual forbs (AF), bulbs (B), perennial grass/graminoid (PG) and annual grass/graminoid (AG).

year and create a mosaic consisting of different aged disturbances, with the most recent disturbances easily distinguished from older disturbances and the surrounding vegetation (J. H. Cushman, personal observation).

Methods

Study designs

Using both comparative and manipulative approaches, we have evaluated the temporal changes in vegetation and soil properties that occur in response to pig disturbances. We substituted space for time by comparing grassland patches in a single year that had been disturbed by pigs at different times in the past. This kind of cross-sectional or chronosequence comparison is used commonly in ecology to study succession (Pickett 1989; Chapin et al. 1994) and ecosystem dynamics (Vitousek 2002). The objective of this approach is to control for as many environmental variables as possible (e.g. climate, slope, aspect, soil type, vegetation) except time since last disturbance. The strength of this space-for-time approach is that it allows an investigator to address longer-term phenomena in a single field season. The weakness is that it is difficult to control for potentially confounding variables. In addition, the approach requires that investigators are able to accurately reconstruct the age of disturbances, which is often difficult to achieve. Despite these potential shortcomings, we feel that space-for-time substitutions are valid in our study system for the following reasons. First, our comparison plots were in close proximity to each other and thus experienced the same climate. Second, we matched comparison plots so that they had similar topography, soil characteristics and vegetation. And third, in our system, we were able to determine accurately the age of pig disturbances (see below).

In a comparative study, we examined the degree to which vegetation and soil properties differed among three disturbance ages and how these patterns varied between short and tall patch types (see *Study system* for details on patch types). Within a 200 × 200 m study area, we established 36 50 × 50-cm plots that were distributed equally between short and tall patch

types (all plots were matched for slope, aspect and soil type). For each patch type, we located plots within areas of three known disturbance ages: those that had been completely disturbed by pigs in mid March of 2001 (but not since), those disturbed completely in mid March of 2000 (but not since), and those not disturbed since at least mid March of 1999. With sampling of the vegetation and soil in these plots occurring in mid May of 2001, our disturbances were approximately 2-, 14-, and 26+ months-old. In summary, our design consisted of two patch types, three disturbance ages, and six replicates per disturbance age per patch type, for a total of 36 plots.

We established a second study in short vegetation patches at the Salt Point grassland to add a manipulative component to our research and to assess the responses of vegetation and soil to pig disturbances over a longer time sequence than we were able to determine in the comparative study. Having such a longer time sequence is critical for assessing whether the removal of pigs is a viable technique for promoting the recovery of native components of the plant community. Located in an adjacent 100 × 100 m area, this study capitalized on portions of a pig-exclosure experiment that began in 1996 (Cushman et al. 2004). We used eight 2 × 2-m exclosures from this study, each of which had 2 m t-posts at the corners, 1 m woven-wire fencing on all sides, and a strand of barbed wire at ground level along the plot perimeter to prevent pigs from prying up the fencing. We established 24 50 × 50-cm plots in the short patch type distributed equally among three disturbance ages. Eight of the 24 plots were fenced and free from pig disturbances for at least 5 years. In this same area, we also selected eight unfenced plots that were disturbed completely by pigs in mid March of 2001 (but not since) and eight plots that were disturbed completely by pigs in mid March of 2000 (but not since). With field sampling of these plots occurring in mid May of 2001, our disturbances were approximately 2-, 14-, or 60+ months-old. As before, all plots were matched for slope, aspect, soil type and general vegetation characteristics.

Disturbance age and plant community composition

In both the comparative and exclosure studies, we estimated plant species richness and plant cover on

May 17 and 18 of 2001 using point-intercept sampling methods (Bonham 1989). Leaving a 10 cm border inside the 50 × 50-cm sampling frame, we established four parallel transects, each 30 cm long and spaced 5 cm apart. At 5 cm intervals along each transect, we recorded all plant species that hit a sampling rod lowered at a total of 28 points per plot. Following Cushman et al. (2004), we grouped plant species according to their geographic origin (i.e., native or exotic) and then placed them into functional groups based on life history characteristics (see Lavorel et al. 1997). With this scheme, we identified six plant categories: native perennial grasses (which also included two uncommon graminoid species from the Juncaceae: *Juncus patens* and *Luzula comosa*), exotic perennial grasses, exotic annual grasses, native bulbs, native forbs and exotic forbs. Native annual graminoids were represented by only one species (*Juncus bufonius*), which did not occur in sufficient numbers of plots to permit analysis. Exotic bulbs as a group were completely missing from our plots.

Disturbance age and soil properties

We sampled all plots in the comparative and enclosure studies to evaluate the degree to which soil properties varied among pig disturbances of different ages. For soil nitrogen and moisture, we collected samples on March 23 and April 26 of 2001. To extract soils, we used a standard 2-cm diameter soil corer inserted to a depth of 15 cm. For each plot, the top 10 cm of two soil cores were combined into one sample. This corresponded to the range of soil depths that we commonly observed pig disturbances to occur at our study site (J. H. Cushman, personal observation). Samples were returned to the lab and separated into four sub-samples. One 10-g sample was analyzed for ammonium (NH_4^+) and nitrate (NO_3^-) content within 24 h of collection using a 2 M KCl solution (see Binkley and Vitousek 1989), while another sample was placed in a breathable bag and allowed to incubate in the lab at room temperature for 30 days. The resulting extracts were frozen and later analyzed for ammonium (NH_4^+) and nitrate (NO_3^-) content at the University of California DANR Analytical Laboratory (Davis, CA). The difference in nitrogen

between initial samples and those incubated for a month represented an estimate of net mineralization rates. Unextracted soil fractions were dried in a convection oven at 65 °C for 24 h and reweighed to determine soil moisture content. Nutrient values were adjusted to control for differences in soil moisture content. Soil samples collected on March 23, 2001 were air-dried and sent to DANR analytical lab for analysis of particle size and percent organic matter.

Statistical analyses

We analyzed all data using JMP 3.1 statistical software (SAS Institute, Cary, NC). For the comparative study, we evaluated vegetation data using two-way multivariate analyses of variance (MANOVAs), with disturbance age (2, 14, or 26+ months) and patch type (short and tall) as the grouping factors. Plant species richness of native and exotic taxa were the two response variables for the first MANOVA, whereas percent cover of six vegetational groupings were the response variables for the second MANOVA (native and exotic perennial grasses, exotic annual grasses, native bulbs, and native and exotic forbs). In the enclosure study, we assessed vegetation data using a one-way MANOVA, with disturbance age as the sole grouping factor and the response variables identical to those used for the comparative study (only the short patch type was used in the enclosure study). For all MANOVAs with significant disturbance age or disturbance age × patch interaction terms, we proceeded with 'protected' ANOVAs (sensu Scheiner 2001) on individual response variables. As discussed at length by Scheiner (2001), this approach is an effective method for dealing with potential correlations among multiple dependent variables (see Alvarez and Cushman 2002 and Cushman et al. 2004). For all significant ANOVAs, we tested for differences among disturbance ages using post hoc Student–Newman–Keuls' (SNK) multiple range tests (Underwood 1997; Zar 1999). Prior to analyses, we arcsine-transformed all percent cover values in order to meet the homogeneity of variance assumption for ANOVA (as assessed by Cochran's test (Underwood 1997)). For species richness data, heteroscedasticity was met without transformations.

Comparative data on soil properties were evaluated with two separate three-way MANOVAs, with disturbance age, patch type, and sample date (March and April 2001) as the grouping factors (repeated-measure analyses were not used because we sampled soil from different patches of all plots in March and April). Response variables for the first MANOVA were percent soil moisture, ammonium (NH_4^+) and nitrate (NO_3^-) pools, net NH_4^+ and net NO_3^- mineralization rates, whereas the second used percent organic matter, percent sand, percent silt, and percent clay. In the enclosure study, we assessed soil data using two one-way MANOVAs, with disturbance age as the grouping factor. Response variables for the two MANOVAs were identical to those used for the comparative study. As before, 'protected' ANOVAs were performed if there were significant main effects or interaction terms. Prior to the statistical analyses, all percent data were arcsine-transformed and, when appropriate, nitrogen soil data were log-transformed for use in parametric analyses.

Results

Disturbance age and plant community composition

Comparative study

Results from a two-way MANOVA revealed that species richness of native and exotic plant taxa

varied significantly with age of feral pig disturbances ($F_{4,60} = 2.63$, $P = 0.0431$), and there was a trend for this relationship to vary with patch type (disturbance age \times patch type interaction: $F_{4,60} = 2.18$, $P = 0.082$; Figure 1). A subsequent protected ANOVA showed that native plant species richness varied significantly among disturbances of different age ($F_{2,30} = 3.54$, $P = 0.0418$). Results from SNK tests indicated that 2-months-old disturbances had significantly fewer native species than both 14 and 26+ months-old disturbances, which in turn were not different from each other (Figure 1a). A second ANOVA showed that there were insignificant trends for exotic species richness to increase with disturbance age ($F_{2,30} = 2.50$, $P = 0.099$) and for the pattern to be most evident in short patches (disturbance age \times patch type interaction: $F_{2,30} = 2.98$, $P = 0.0662$; Figure 1b). Exotic richness was also significantly greater in short patches ($F_{1,30} = 6.19$, $P = 0.0186$).

In a second MANOVA, the percent cover of all plant functional groups (native and exotic perennial grasses, exotic annual grasses, native bulbs and native and exotic forbs) varied significantly with disturbance age ($F_{12,52} = 8.18$, $P < 0.001$; Figure 2). Results from a protected ANOVA revealed that the cover of native perennial grasses varied significantly with disturbance age ($F_{2,30} = 34.64$, $P < 0.0001$), with this pattern being consistent between short and tall patch types (disturbance age \times patch type interaction: $F_{2,30} = 0.11$, $P = 0.898$). In addition, multiple

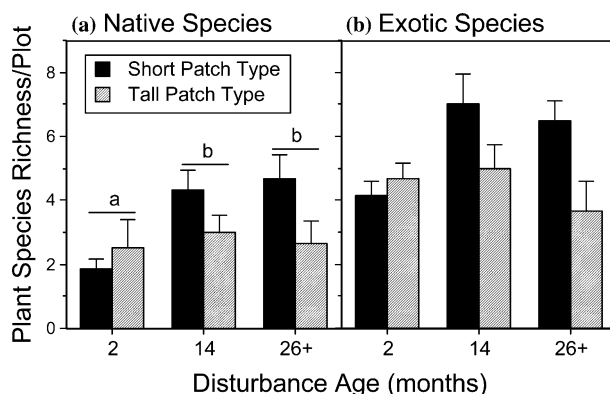


Figure 1. Native and exotic plant species richness per plot (means +1 SE) in feral pig (*Sus scrofa*) disturbances of three different ages (2-, 14-, and 26+ months-old) and two distinctive patch types (short and tall) that occur frequently throughout a grassland study area. Letter above bars correspond to the results from multiple comparison tests.

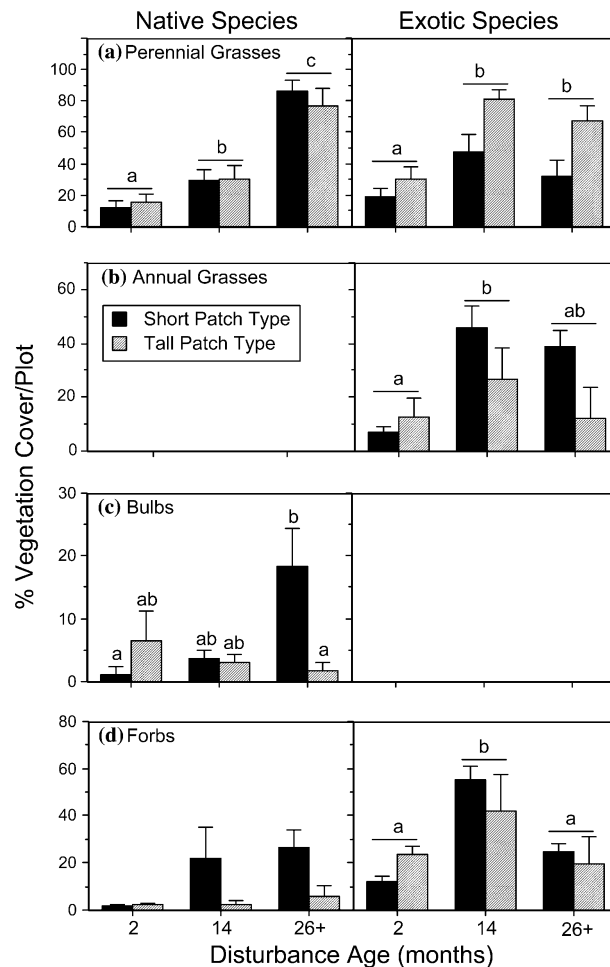


Figure 2. Percent cover (means +1 SE) of native and exotic perennial grasses (a), annual grasses (b), bulbs (c), and forbs (d) per plot in feral pig (*Sus scrofa*) disturbances of three different ages (2-, 14-, and 26+ months-old) and two distinctive patch types (short and tall) that occur frequently throughout a grassland study area. Letter above bars correspond to the results from multiple comparison tests.

comparison tests showed that the three disturbance ages were significantly different from each other, giving rise to a pattern of increasing cover with age (Figure 2a). The cover of exotic perennial grasses also varied significantly across disturbance ages ($F_{2,30} = 8.27$, $P = 0.0014$), with significantly less cover occurring in 2-months-old relative to 14 and 26+ months-old disturbances. Unlike the results for native perennial grasses, we found that the cover of exotic perennial grasses increased rapidly after disturbance, such that SNK tests failed to detect differences in cover values between 14 and 26+ months-old disturbances (Figure 2a). Tall patch types had significantly

greater cover of exotic perennial grasses than short ($F_{1,30} = 12.71$, $P = 0.0012$), but we did not detect an interaction between disturbance age and patch type ($F_{2,30} = 1.20$, $P = 0.316$).

The response of exotic annual grasses and forbs to disturbance age was similar to that for exotic perennial grasses (Figure 2b, d). Percent cover for both groups varied significantly with disturbance age (exotic annuals: $F_{2,30} = 4.58$, $P = 0.0184$; exotic forbs: $F_{2,30} = 6.19$, $P = 0.0056$), with multiple comparison tests indicating that cover initially increasing rapidly after disturbance and then subsiding with time. For exotic annual grasses, cover values were greater in short patches than tall

($F_{1,30} = 6.40$, $P = 0.0169$), and there was a trend for the effects of disturbance age to be greater in short patches than tall (disturbance age \times patch type interaction: $F_{2,30} = 3.03$, $P = 0.063$; Figure 2b). In contrast, we did not detect significant patch effects for exotic forb cover ($F_{1,30} = 0.17$, $P = 0.681$), nor did the effect of disturbance age vary with patch type ($F_{2,30} = 1.17$, $P = 0.324$; Figure 2d).

The temporal responses of native bulbs and forbs to pig disturbance were more complex than we detected for the other plant groups. Although the cover of bulbs varied only weakly with disturbance age ($F_{2,30} = 1.96$, $P = 0.158$), the effect of disturbance age varied significantly with patch type (disturbance age \times patch type interaction: $F_{2,30} = 4.54$, $P = 0.019$). Specifically, the cover of bulbs increased rapidly with disturbance age in short patches (similar to how native perennial grasses responded), but then exhibited a less dramatic pattern in the opposite direction in tall patches (Figure 2c). Cover of native forbs was greater in short patches than tall ($F_{1,30} = 8.44$, $P = 0.0068$), and there were trends for cover to vary with disturbance age ($F_{2,30} = 2.58$, $P = 0.0928$) and for the effects of disturbance age to be greater in short patches than tall ($F_{2,30} = 2.75$, $P = 0.0797$; Figure 2d). In short patches, there was a rapid initial increase in cover from 2 to 14-months-old disturbances, but then cover peaked and increased no further with increasing age. In contrast, tall patches had less cover of native forbs compared to

short patches and did not show changes in cover with disturbance age.

Exclosure study

Results from a one-way MANOVA revealed that the richness of native and exotic species together did not vary significantly with disturbance age ($F_{4,42} = 1.56$, $P = 0.202$). However, as shown in Figure 3, this result was due largely to exotic richness being unaffected by disturbance age. In contrast, as found in the comparative study, there was a trend for native richness to increase with disturbance age.

Unlike our results for species richness, a one-way MANOVA showed that disturbance age had a significant influence on the percent cover of six plant groupings considered collectively – native and exotic perennial grasses, exotic annual grasses, native bulbs and native and exotic forbs ($F_{12,34} = 4.70$, $P < 0.001$; Figure 4). Results from subsequent protected ANOVAs indicated that cover values for both native and exotic perennial grasses were significantly influenced by disturbance age ($F_{2,21} = 6.95$, $P = 0.005$ and $F_{2,21} = 4.0$, $P = 0.034$, respectively). Multiple comparison tests revealed that the cover of native perennial grasses remained low 14 months after disturbance but then increased significantly in 60+ months-old disturbances (Figure 4a). In contrast, the cover of exotic perennial grasses increased significantly 14 months after pig disturbance and remained at these levels in 60+ months-

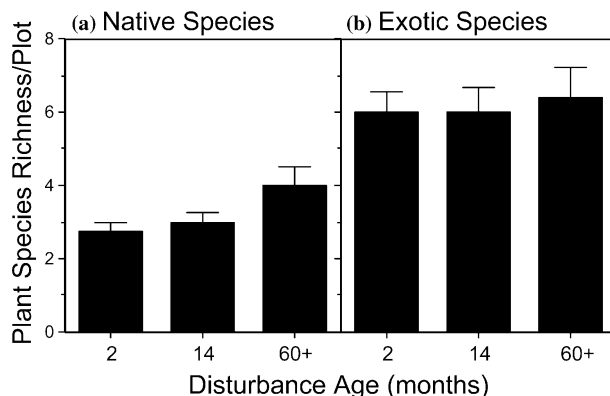


Figure 3. Native and exotic plant species richness per plot (means + 1 SE) as a function of feral pig (*Sus scrofa*) disturbances of three different ages (2-, 14-, and 60+ months-old). Fencing was used to prevent pigs from disturbing the 60+ months-old plots. Letter above bars correspond to the results from multiple comparison tests.

old disturbances (Figure 4a). Exotic forbs were also significantly influenced by disturbance age ($F_{2,21} = 5.57$, $P = 0.011$) and exhibited a response similar to that of exotic perennial grasses, with cover rapidly increasing in 14-months-old disturbances and then remaining the same in 60+ months-old ones (Figure 4d). We detected similar trends of rapidly increasing but saturating cover in response to disturbance age for both exotic annual grasses (Figure 4b; $F_{2,21} = 3.20$, $P = 0.086$). However, the cover of native bulbs and forbs were not significantly affected by the age of pig disturbance

(Figure 4c, d; $F_{2,21} = 1.51$, $P = 0.244$ and $F_{2,21} = 0.37$, $P = 0.697$, respectively).

Disturbance age and soil properties

Comparative study

In contrast to the results for vegetation, the comparative study provided no evidence that soil properties varied significantly with age of pig disturbance. A three-way MANOVA showed that ammonium and nitrate nitrogen pools and net mineralization rates did not vary significantly

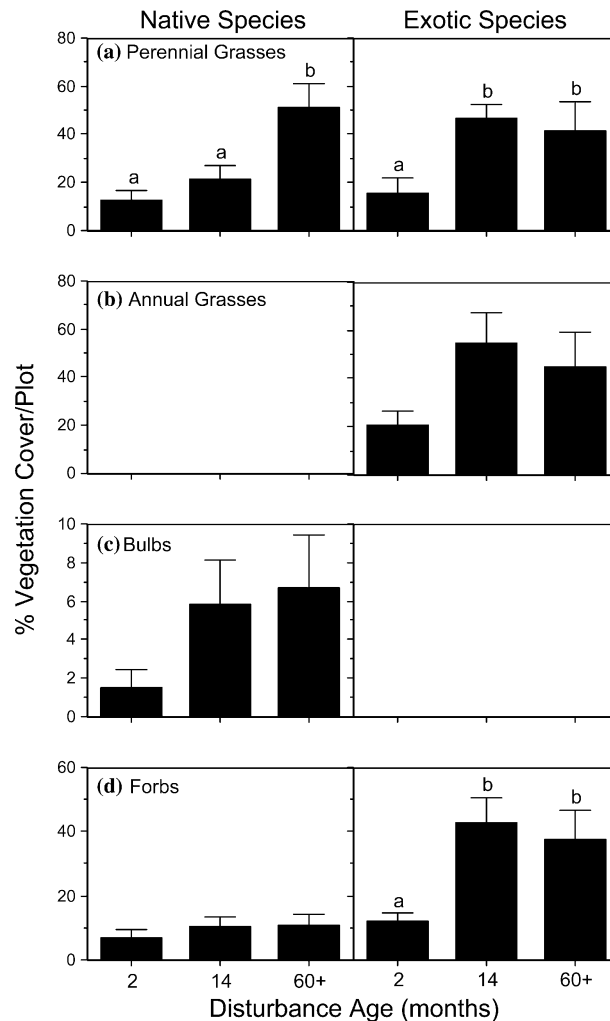


Figure 4. Percent cover (means +1 SE) of native and exotic perennial grasses (a), annual grasses (b), bulbs (c), and forbs (d) per plot as a function of feral pig (*Sus scrofa*) disturbances of three different ages (2-, 14-, and 60+ months- old). Fencing was used to prevent pigs from disturbing the 60+ months-old plots. Letter above bars correspond to the results from multiple comparison tests.

with disturbance age ($F_{10,102} = 1.29$, $P = 0.244$), nor were any of the interaction terms involving disturbance age significant. However, we detected pronounced differences in mineralization rates between patch types ($F_{5,50} = 6.24$, $P < 0.0001$), with rates for ammonium being greater in short patches and those for nitrate being greater in tall patches (Figure 5). An additional MANOVA revealed that soil organic matter and texture (percent sand, silt and clay) did not vary significantly with disturbance age ($F_{8,56} = 1.10$, $P = 0.378$; Table 2a).

Exclosure study

Unlike our results for the comparative study, a two-way MANOVA detected a significant effect of pig disturbance age on soil ammonium and nitrate nitrogen pools and net mineralization rates ($F_{10,68} = 2.15$, $P = 0.032$; Figure 6). Subsequent protected ANOVAs revealed that this was due primarily to the significant effect of disturbance

age on net nitrate mineralization rates ($F_{2,37} = 3.58$, $P = 0.038$), where levels were greater in 14-months-old disturbances and equally low in 2 and 60+ months-old disturbances (Figure 6b). ANOVAs indicated that there was no effect of disturbance age on ammonium and nitrate pools ($F_{2,37} = 2.29$, $P = 0.115$ and $F_{2,37} = 1.86$, $P = 0.171$, respectively) or net ammonium mineralization rates ($F_{2,37} = 0.17$, $P = 0.841$). The MANOVA for soil organic matter and particle size failed to detect a significant effect of disturbance age ($F_{8,38} = 0.29$, $P = 0.963$; Table 2b).

Discussion

Feral pigs are an exotic disturbance agent that now occurs in a diversity of habitat types on all but one continent and many oceanic islands. Our comparative and exclosure studies demonstrated that this invasive mammal is having large

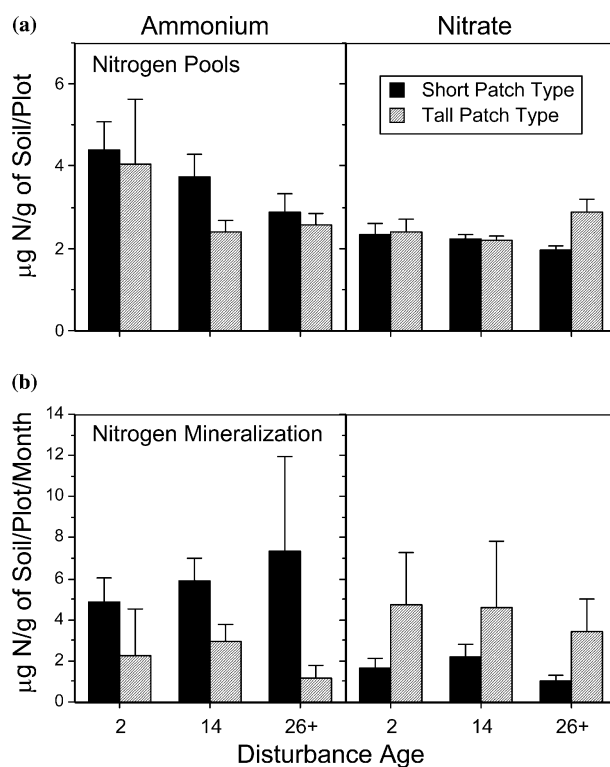


Figure 5. Mean (+1 SE) ammonium and nitrate pools (a) and net mineralization rates (b) in feral pig (*Sus scrofa*) disturbances of three different ages (2-, 14-, and 26+ months-old) and two distinctive patch types (short and tall) that occur frequently throughout a grassland study area.

Table 2. Comparison of mean soil texture (± 1 SE; % sand, silt and clay) in a coastal California grassland for pig disturbances of different ages. These ages were 2, 14 and 26+ months for a comparative study and 2, 14, and 60+ months for an enclosure study.

Soil fraction	Mean percent (± 1 SE)		
	2 months	14 months	26+ months
(a) Comparative study			
Organic matter	3.1 \pm 0.1	3.1 \pm 0.1	3.4 \pm 0.1
Sand	47.4 \pm 1.3	47.5 \pm 1.2	47.3 \pm 0.8
Silt	40.1 \pm 1.3	40.1 \pm 1.1	40.3 \pm 0.7
Clay	12.5 \pm 0.3	12.4 \pm 0.4	12.3 \pm 0.5
Soil moisture	23.1 \pm 0.8	23.2 \pm 1.1	24.9 \pm 0.9
(b) Exclosure study			
Soil fraction	2 months	14 months	60+ months
Organic matter	2.8 \pm 0.1	2.9 \pm 0.1	2.9 \pm 0.1
Sand	49.9 \pm 1.7	50.4 \pm 1.3	50.9 \pm 1.2
Silt	37.2 \pm 1.4	37.2 \pm 0.7	36.9 \pm 0.9
Clay	12.9 \pm 0.6	12.4 \pm 0.7	12.2 \pm 0.6
Soil moisture	21.9 \pm 1.1	21.8 \pm 0.8	21.8 \pm 0.9

impacts on a coastal grassland in northern California, and that native and exotic plant taxa often vary in their responses to disturbances of differing ages. We have found that the richness

of native plant species was reduced immediately following pig disturbance and then increased slowly through time (Figures 1a and 3a). In contrast, species richness of exotic plants was either

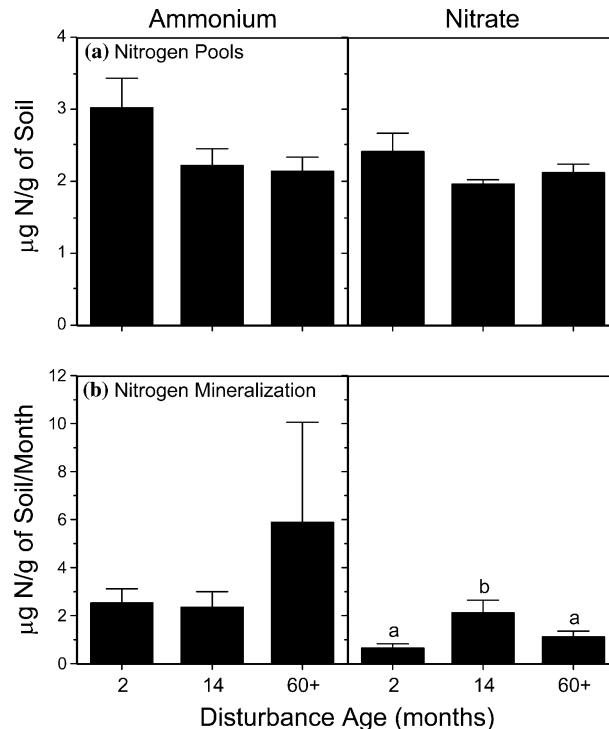


Figure 6. Mean (± 1 SE) ammonium and nitrate pools (a) and net mineralization rates (b) for March and April 2001 as a function of feral pig (*Sus scrofa*) disturbances of three different ages (2-, 14-, and 60+ months-old). Fencing was used to prevent pigs from disturbing the 60+ months-old plots. Letter above bars correspond to the results from multiple comparison tests.

similar across different disturbance ages, as found in the exclosure study (Figure 3b), or showed only a weak and saturating trend of increasing richness with disturbance age, as found in the comparative study (Figure 1b). Such findings are in line with a number of other studies from diverse geographical regions and habitat types, which have documented that small-scale soil disturbances by mammals can facilitate invasion by exotic plant species (Rice 1987; Hobbs et al. 1988; Peart 1989a; Hobbs and Mooney 1991; D'Antonio 1993; McIntyre and Lavorel 1994; Cushman et al. 2004). In general, invasive taxa more commonly possess life history characteristics that enable them to colonize rapidly and become established in disturbances: they often produce abundant amounts of seed that either persist in the soil of disturbed areas or disperse in from surrounding patches (Peart 1989b; Kotanen 1996, 1997a, b). However, not all studies have found that native and exotic plant taxa respond differently to biotic soil disturbances. For example, in a nearby coastal grassland (~130 km north of our site), Kotanen (1995) reported that native and exotic richness responded similarly to pig disturbance: the richness of both groups initially decreased during the first year following disturbance and then rebounded to levels similar to or sometimes greater than those in undisturbed plots after two years.

Although members of the same functional group, native and exotic perennial grasses recovered from pig disturbance in markedly different ways. During the five years of our chronosequence analysis, percent cover of native perennial grasses recovered at a consistently slower rate than exotic members of this functional group. Other studies of coastal grasslands in northern California have also found that native bunchgrasses were slow to colonize pocket gopher mounds (Peart 1989a) and experimental soil disturbances (Kotanen 1997a). Differences in life history characteristics may partially explain this result. In general, perennial bunchgrasses tend to be longer lived and take several years to reach reproductive maturity (Jackson 1985; Briske and Derner 1998). In fact, one of two native perennial bunchgrasses in this system, *Deschampsia cespitosa*, can live up to 60 years and commonly takes up to five years to flower (Gatsuk et al.

1980). Also, bunchgrasses allocate more resources to root and vegetative biomass during the growing season and less to reproduction (Jackson and Roy 1986). As a result, their seeds are relatively rare in the seed rain and natural recruitment is low (Peart 1989b; Dyer et al. 1996; Hamilton et al. 1999; Seabloom et al. 2003). The comparatively poor colonizing ability of native perennial grasses – including *Deschampsia*, which dominates our site (Peart 1989a, b) – has been documented by other studies of grasslands in California (Bartolome and Gemmill 1981; Jackson and Roy 1986; Stromberg and Griffin 1996; Hamilton et al. 1999). Indeed, colonizing ability has been identified as an important factor leading to the large-scale conversion of native perennial grasslands to exotic annual grasslands (Jackson 1985).

The slower recovery of native perennial grasses to pig disturbance may also result from competition with exotic grasses and forbs. Numerous studies have shown that exotic annual grasses in California are more effective at acquiring light and water than *Nassella pulchra*, and reduce the growth and seed production of this common native perennial grass (Bartolome and Gemmill 1981; Dyer et al. 1996; Holmes and Rice 1996; Dyer and Rice 1997, 1999; Hamilton et al. 1999). Exotic annual forbs have also been shown to out compete native bunchgrasses for inorganic nitrogen and reduce their biomass (Hooper and Vitousek 1997; Scott et al. 2001). Little is known about the competitive effects of *Anthoxanthum odoratum* – the dominant exotic perennial grass in our system – on native perennial grasses. However, we suspect that this invader competes intensively with native bunchgrasses, given that both taxa are long-lived, invest heavily in below-ground biomass, and appear to overlap greatly in their zones of resource use in the soil throughout the year (see Cushman et al. 2004).

Despite the slow rate at which native bunchgrasses recover from pig disturbance, their cover increased steadily with time since disturbance for both the comparative and exclosure studies. 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. Although clonal growth is often critical for colonization of small

soil disturbances in grasslands (e.g. Goldberg and Gross 1988), our field observations suggest that these increases in native bunchgrasses were due primarily to recruitment from seed and not clonal expansion (see also Kotanen 1996). Other studies in nearby coastal grasslands corroborate our findings on the temporal responses of native bunchgrasses to disturbance. For example, Kotanen (2004) found that native perennial graminoids exhibited a slow but steady increase in abundance over a 10-year-period following experimental soil disturbances. In addition, Corbin and D'Antonio (2004) documented that native perennial bunchgrasses became competitively dominant to exotic annual grasses over a four-year period. Collectively, these studies and our results suggest that, if given sufficient time in the absence of further soil disturbances, native bunchgrasses can rebound and come to dominate coastal grasslands, even in the face of considerable abundance of exotic vegetation.

In marked contrast to native perennial grasses, we found that all three exotic plant groups – forbs and both annual and perennial grasses – increased greatly in cover after just one year following pig disturbance and remained at these elevated levels or decreased slightly in subsequent years. We hypothesize that such rapid but saturating increases are best explained by life history characteristics. As has been discussed frequently, exotic grasses and forbs commonly possess traits – such as high germination rates, short life cycles, fast growth rates, well-developed dispersal abilities, and intensive resource allocation to reproduction – that allow their populations to undergo rapid growth following disturbances (Baker 1965; Bazaz 1986; Rejmánek and Richardson 1996). In other coastal systems, two researchers have reported somewhat different results from ours for exotic annual grasses. Peart (1989a) found that *Vulpia myuros*, an exotic annual grass, was better than four native bunchgrass species at colonizing gopher mounds during the first year following disturbance, but was replaced by these bunchgrasses the second year. Kotanen (2004) also found that exotic annual grasses increased in abundance during the first three years following experimental disturbances in coastal grasslands, but had decreased to low levels after

10 years. At this point, we are unclear whether such variation among these three neighboring sites in northern California was due to differences in plant species composition, the type or intensity of soil disturbance, or prevailing precipitation and temperatures regimes during the study periods.

For both the comparative and exclosure studies, pig disturbances of differing ages did not vary significantly in their soil characteristics. There were no differences among disturbance ages for ammonium and nitrate pools and net ammonium mineralization rates, and we also failed to detect differences for soil texture, moisture or organic matter. The only significant effect was detected in the exclosure study, where soils in 14-months-old disturbances had higher net nitrate mineralization rates than 2- and 60+ months-old disturbances. This difference was not found in the comparative study, and the mineralization effect from the exclosure study cannot be explained by vegetation differences, as intermediate aged disturbances never had vegetation that differed significantly from new and old disturbances. Although not evaluating the effects of disturbance age, a few studies have considered the influence of pig disturbance or experimental disturbances on soil characteristics. In a four-year experiment, Cushman et al. (2004) found no evidence for an effect of pig disturbances on ammonium and nitrate pools and mineralization rates at our Salt Point study site. Similarly, Moody and Jones (2000) found no correlation between pig disturbances and changes in soil pH, moisture, nitrogen pools and total carbon for oak savannas on Santa Cruz Island, off the coast of southern California. In contrast, Kotanen (1997a) found that simulated disturbances in a coastal grassland in northern California had greater ammonium levels than undisturbed areas, although there was no effect for nitrate. In addition, Singer et al. (1984) found that pig-disturbed soils had elevated nitrate levels relative to adjacent undisturbed areas in deciduous forests of the southeastern U.S. One potential explanation for the absence of effects in our system may be that the Salt Point grassland has been disturbed intensively by pigs each year for an extended period (e.g. 20+ years), which in turn has caused significant changes in soil characteristics prior to

the establishment of our comparative and exclosure studies. If this were the case, further disturbance to the soil by pigs might not have effects on soil characteristics. Another possibility is that pig disturbance levels, although substantial (see Cushman et al. 2004), were not sufficient to alter soil characteristics at this site, which is relatively level and may not have experienced increased leaching or erosion following disturbance. However, regardless of the explanation, variation in soil characteristics does not seem sufficient to explain the vegetation changes that we have detected. Instead, other factors – such as space clearing by pigs which provides greater opportunities for colonization and reduced intensity of competition – are probably responsible for the vegetation changes discussed below.

The view that disturbance facilitates the colonization and establishment of exotic species has become widely held in invasion biology (D'Antonio et al. 1999). Less clear is what happens to native and exotic taxa through time following a disturbance event. The conventional wisdom is that exotic plants colonize disturbances rapidly, become established and even abundant in their novel environment, and subsequently prevent native taxa from reestablishing (Hobbs and Huenneke 1992). A successional analysis by Rejmánek (1989) supports part of this generalization, as he found that exotic plant species from an assortment of habitats in North America and Europe came to dominate communities during early successional stages. However, Rejmánek's data also revealed that this dominance by exotics decreased steadily over a 50 to 60-year-period. Thus, while it is clear that exotic plant species thrive in recently disturbed habitats, these invaders may not be able to persist and remain dominant through time. Our work also provides partial support for the conventional wisdom on biological invasions, as we found that exotic plants recolonized vigorously over time following pig disturbance. However, we did not detect a decrease in the dominance of exotics over time, as found by Rejmánek, but such patterns may take longer than the duration of our study to appear. Most surprising to us – and indeed encouraging – was that native taxa recovered slowly but steadily from pig disturbance, even though exotic plant groups remained dominant. Studies by Peart (1989a, b), Corbin and D'Antonio (2004),

Kotanen (2004) and others have detected similar resiliency of native plant taxa in coastal grasslands. Collectively, such findings suggest that removing or reducing the size of feral pig populations should be an effective technique for restoring native perennial grasses in coastal systems. Unfortunately, we suspect that this resiliency may be specific to coastal grasslands, where the long summer drought of these Mediterranean-type climates is tempered by maritime influences. The temporal responses to pig disturbances in more interior grasslands and savannas may be substantially different, with native plant groups being less able to recover from disturbances under the more arid conditions that prevail in these regions.

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