Invasive Pine Tree Effects on Northern Coastal Scrub Structure and Composition

Robert J. Steers, Susan L. Fritzke, Jen J. Rogers, James Cartan, and Kaitlyn Hacker*

Vegetation that becomes overtopped usually experiences a decrease in abundance or species richness. When an overtopping plant alters the physiognomy of the existing vegetation (e.g., trees invading a shrubland), ecosystem processes can also be dramatically altered. Worldwide, Monterey pine (*Pinus radiata*) cultivars have been planted in Mediterranean-like climates and are known to invade surrounding natural communities. Ecological impacts resulting from these invasions have been widely investigated; however, the effects from solitary pine trees on the vegetation they overtop are lacking. Furthermore, studies on the impact of *P. radiata* cultivars from the California floristic province, where *P. radiata* is native, do not exist. In coastal California, north of the present-day range of native *P. radiata* stands, cultivars of this species have invaded northern coastal scrub vegetation. To determine the impact of pine invasion on species richness and structure in this habitat, floristic surveys were conducted in 20 blocks that consisted of invaded and uninvaded plots. An invaded plot contained two subplots located under the canopy of an isolated pine tree, whereas a paired, uninvaded plot contained two subplots located in coastal scrub adjacent to each pine. Pine trees selected ranged in size from 2.8 to 119 cm (1.1 to 46.9 in) basal diameter. Our results demonstrate that understory native cover and species richness are negatively correlated with tree size. Understory exotic plant cover and richness of species other than *P. radiata* did not show any correlation with tree size, mainly because exotic plants had a very low abundance overall.

Nomenclature: Monterey pine, *Pinus radiata* D. Don.

Key words: Assisted migration, neonative, pine cultivar, *Pinus radiata*, species richness, succession.

Competition for resources is a primary driver of plant composition and structure (Aerts 1999; Grace and Tilman 1990; Grime 1979; Grubb 1977). When a species overtops another, such as with competition for light, the effect is often one of decreased performance by the understory species (Howard and Newton 1984; Schwinning and Weiner 1998; Weiner 1990). Likewise, when a species overtops an assemblage of plants, the outcome often alters the structure of the vegetation and can decrease species richness in the community below. These effects can be documented whether or not the overtopping species is native or exotic (Alvarez and Cushman 2002; Briggs et al. 2005; Gutierrez et al. 1993; Hobbs and Mooney 1986; Jackson et al. 1990; Lopez-Pintor et al. 2006; Miller et al. 2000; Reinhart et al. 2005; Rejmánek and Rosén 1992; Shmida and Whitaker et al. 1981).

Mechanisms that explain why overtopped vegetation becomes altered are numerous. Pugnaire et al. (1996) postulated several interrelated mechanisms that could cause species richness to decrease under an overtopping plant: The area under the overtopping plant canopy (1) lacks heterogeneity, (2) contains deleterious amounts of litter, (3) has low light availability, and (4) includes increased competition. Lopez-Pintor et al. (2006) attributed lower species richness under overtopping species to canopy effects (light and temperature amelioration) and edaphic effects (nutrient enrichment). Lastly, decreased light, allelopathy, altered biogeochemical cycles, and root interference have all been attributed to differences in herbaceous plant structure or composition between open grassland vs. adjacent oak (*Quercus* spp.) tree understories in Californian woodlands and savannas (Callaway et al. 1991; Jackson et al. 1990; Marañón and Bartolome 1993; Parker and Muller 1982).

In contrast, the effect of an overtopping species can sometimes be facilitative, especially in stressful environments (Pugnaire et al. 2004). In a study examining the

Management Implications

It is not surprising that large, invading trees would affect or alter the vegetation of treeless communities. Understanding what types of changes are taking place is critical for determining how and when invasive tree removal or other types of management practices should be implemented. Based on our results, to minimize the negative effects of invading trees on native plant cover and species richness in coastal scrub habitat, invasive trees should be removed as early in their stage of growth as possible. Furthermore, removing invasive trees before they become reproductively mature can also help control their spread, although this was not a focus of our study. In our study, we demonstrate how the effect of an invasive tree species can be understood from just one point in time by sampling the understory of several different-sized trees. *Pinus radiata* is one of the most widely planted trees in the world, so these findings and methods may be helpful to a broad audience and applicable to other invaded habitat types, although the ecological impacts of this species could be different in other parts of the world. These methods may also be useful for studying the effects of invasive tree species in general. In our study area, one of the management objectives is to preserve the mosaic of coastal scrub and grasslands that are habitat for numerous special-status species. Therefore, understanding how the primary vegetation type (coastal scrub) is altered by an exotic tree can provide justification for spending resources on control methods. Although there is compelling evidence that the invasive pines in our study area are derived from cultivars bred for commercial purposes, additional genetic work from the study area should be done to confirm that assessment. We argue that cultivated *P. radiata* with an unknown origin would be ill-suited for in situ conservation of native *P. radiata* or for use as neonate populations. There also could be significant differences in how cultivars vs. native strains of *P. radiata* behave (growth rate, fitness, ability to spread with and without fire cues, among others), which could affect how they are managed.

by exotic pines as time increases (Richardson et al. 1994) and because invasive species control is exponentially less costly and more efficient when performed at an early stage of invasion (Mack et al. 2000; Naylor 2000; Rejmánek and Pitcairn 2002), understanding when effects from invading plants become apparent can help prioritize the timing of removal. Effects to overtopped vegetation by invading trees or shrubs are likely to be significant, even when individual invaders are small, but relatively little information exists on invasive species effects at early stages.

The purpose of this study was to document the effect of solitary *P. radiata* trees on native vegetation and to determine how vegetation structure and species composition under *P. radiata* trees relate to tree size. Because invasive *P. radiata* cultivars can exhibit continuous recruitment (Richardson and Brown 1986), solitary individuals of varying size can be found throughout a landscape undergoing invasion, such as at our study site (Figure 1). Our primary hypothesis was that as solitary trees increase in size they would displace a greater amount of native plant cover and species richness in their understories. In addition, we also hypothesized that litter depth, litter cover, and overstory *P. radiata* cover would increase in sampling plots as tree size increased.

Materials and Methods

Study Organism. *Pinus radiata* is native to the California floristic province, with native populations at just three mainland sites: Punta del Ano Nuevo in San Mateo County, CA; the Monterey Peninsula in Monterey County, CA; and near Cambria in San Luis Obispo County, CA, as well as on two islands off the Pacific coast of Baja California, Mexico (Guadalupe and Cedros Islands). In the past, *P. radiata* occupied a much broader distribution along the California coast; Pliocene (Late Tertiary) remains have been uncovered from Point Reyes, CA, approximately 115 km (71.5 mi) north of its present-day distribution, and Pleistocene remains have been found in Laguna Niguel, CA, approximately 365 km to the southeast (Millar 1999). During the late Tertiary and through the Quaternary, climate fluctuations resulted in expansions, contractions, colonizations, and extirpations of distinct *P. radiata* populations along the California coast. Like the present day configuration of isolated populations, it is believed that past populations of *P. radiata* exhibited a similar metapopulation distribution. Thus, these isolated populations likely experienced genetic bottlenecks as they fluctuated with climatic conditions (Millar 1999). Alternatively, Axelrod (1982) hypothesized that the prehistoric distribution of *P. radiata* was larger and more widespread along the California coast but underwent significant range restrictions associated with warming during the xerothermic period that eventually led to our present-day extant

vegetation under increasingly older shrubs in a semiarid environment, annual species richness increased with shrub age, except at the oldest stage, where richness finally decreased as competitive interference became more important (Pugnaire et al. 1996). Likewise, Tewksbury and Lloyd (2001) found a facilitative effect on understory species richness in xeric portions of a tree species range but an opposite effect in relatively mesic portions of its range. When reviewing the literature on species richness and productivity, Mittelbach et al. (2001) found that a hump-shaped relationship occurred most frequently.

One of the most widely planted tree species in the world is the Monterey pine (*Pinus radiata* D. Don), which is invasive on several continents (Richardson and Rejmánek 2011; Richardson et al. 1994; Simberloff et al. 2010). *Pinus radiata* has been shown to affect the structure and composition of the vegetation it overtops (Brockerhoff et al. 2003; Ogden et al. 1997; Richardson et al. 1989), but no such study, to our knowledge, has specifically evaluated the impacts from solitary *P. radiata* individuals. Because treeless, natural areas can become increasingly colonized

Figure 1. Invasive *Pinus radiata* cultivars of varying age are common among the coastal scrub covered hillsides of southern Marin County, CA.

populations. Currently, *P. radiata* is listed as critically endangered in California by the California Native Plant Society (CNPS 2011) and all extant native populations are protected as Environmentally Sensitive Habitat by the California Coastal Commission, pursuant to Section 30107.5. As a vegetation type, native *P. radiata* forests rank among the highest in global conservation importance (Sawyer et al. 2009). Large-scale coastal development in combination with other threats, like pathogens (e.g., pine pitch canker) and genetic contamination, bring uncertainty to this species long-term persistence (Millar 1999; Rogers 2004).

Pinus radiata trees have been selected for desired silvicultural traits and have been planted throughout the world, becoming invasive species in many locales (Lanner 1999; Richardson et al. 1994). Some of the same traits that make this species commercially successful (e.g., rapid growth rate) are also associated with its invasiveness. For example, *P. radiata* exhibits a short juvenile period, large seed mass, and a short time between large seed crops, which allows it to be successful in novel environments (Rejmánek and Richardson 1996; Richardson et al. 1994). In California, naturalized *P. radiata* trees found growing beyond the present-day distribution of native populations are referred to as invasive *Pinus radiata* cultivars (PRCs) if their presence is due to human influence (Cal-IPC 2011). It is believed that most of the invading *P. radiata* trees found outside of their native range are derived from commercial cultivars developed in New Zealand (Rogers 2004), including those growing in Golden Gate National Recreation Area (Edberg et al. 1994), where this study took place. Thus, we consider all *P. radiata* trees in our study area to be invasive PRCs. From a biological perspective, *P. radiata* are also considered invasive species because they are nonnative here and cause environmental harm (this study).

Study Area. The study area was located in southern Marin County, CA, within the Marin Headlands portion of Golden Gate National Recreation Area. Before inclusion in the National Park Service in 1972, the Marin Headlands were occupied by the United States Army, who planted PRCs around human habitations, which appear to be the primary source of the PRCs in the study area based on historical, aerial photographs (unpublished data). Invasive PRCs are widely scattered throughout southern Marin County recruiting in coastal scrub and grassland vegetation. Recruitment appears continuous because pine trees of various sizes can be found in any locale (e.g., Figure 1). In some areas, recruitment has been dense and small stands of PRCs exist, forming forested vegetation; however, over much of the landscape, isolated trees or small patches of trees with a few to several individuals are more common. Our study site was limited to the southernmost east–west-trending ridge of hills in Marin County. Soils along this ridge are well-drained, shallow, and gravelly loams (NRCS 2010). Elevation ranges from about 80 to 280 m (263 to 919 ft), and the climate is Mediterranean, with almost all measured precipitation occurring from October through May, although input from fog during the summer months is unquantified but potentially significant (Corbin et al. 2005). Mean annual precipitation is assumed to be about 50 cm yr^{-1} (20 in yr^{-1}), based on a weather station 5.4 km to the south at a similar elevation and distance from the coast (WRCC 2011). Sampling of vegetation was limited to coastal scrub. Therefore, the results of this study are inapplicable to grasslands or other vegetation types. The coastal scrub of the study area can be classified as northern coastal scrub (Ford and Hayes 2007) with coyotebrush (*Baccharis pilularis* DC.) as the dominant shrub and California sagebrush (*Artemisia californica* Less.), sticky monkeyflower (*Mimulus aurantiacus* Curtis), California coffee berry (*Frangula californica* Eschsch.), and poison-oak [*Toxicodendron diversilobum* (Torr. & A. Gray) Greene] as common to locally abundant shrubs.

Methods. Isolated individuals representing PRCs, which varied in size from saplings to large, mature trees, were selected within the dense coastal scrub vegetation found along the southernmost ridge of hills in Marin County. No PRCs found growing in grasslands or grassland\coastal-scrub ecotones were used. Isolated individuals were those trees not growing among, or adjacent to, other PRCs or to other tree species. Furthermore, selected individuals had to be devoid of shading effects or litter inputs blown in from surrounding trees. Isolated PRCs were searched for and surveyed on all available aspects and slopes that lacked recent human disturbances, like abandoned roads, quarries, military/gunnery installations, among others. In addition, all trees that showed signs of pine pitch canker infection, based on California Department of Forestry guidelines

(CDF 2010), were avoided. Where isolated trees of similar dimension were located in close proximity to each other (e.g., within the same stand of coastal scrub), one was randomly chosen for sampling. Twenty PRCs that varied in size from saplings to large mature individuals were used in this study. For each PRC selected, the canopy width was measured from the uphill to downhill side of each tree, and the basal diameter of each tree was measured as well.

To determine the impact of PRC invasion on species richness and vegetation structure of the northern coastal scrub vegetation of the study area, floristic surveys were conducted in 20 blocks, centered on the 20 isolated PRCs found growing in coastal scrub vegetation. Each block consisted of an invaded and uninvaded plot. An invaded plot contained two subplots located under the canopy of the isolated PRC, whereas a paired, uninvaded plot contained two subplots located in coastal scrub adjacent to the isolated PRC. Vegetation sampled in invaded plots was done using a 1-m by 0.5-m quadrat placed in two locations under the canopy of every PRC, between the dripline and the base of the tree trunk on both the uphill and downhill sides of the trunk. The parameters measured within each quadrat included species richness, percentage of cover (bare ground, litter, understory vegetation, and the PRC canopy), and litter depth (taken at center of quadrat and 25 cm off center to the right and left, facing uphill). Cover was based on visual estimation and was aided by use of a gridded quadrat. Vegetation sampling in the uninvaded plot was done by randomly placing two quadrats of the same dimensions used in understory plots within the surrounding uninvaded matrix coastal scrub, in areas at least 20 m from the tree but no more than 50 m away. These uninvaded sites also had to be void of any pine tree litter and had to be at a similar slope, aspect, and topographic formation as the reference tree. Uninvaded reference sites were always placed in the same coastal scrub stand as their corresponding invaded plots. The same parameters measured in invaded quadrats were also measured in uninvaded quadrats.

Data Analyses. Paired *t* tests were used to compare mean native species richness and mean total native plant cover in uninvaded vs. invaded plots. Linear regressions were used to evaluate how coastal scrub vegetation parameters change with increasing size of the overtopping PRC, using parameters measured in understory quadrats against basal diameter and canopy diameter as dependent variables, separately. To examine how overtopped coastal scrub changes compared with paired uninvaded coastal scrub as tree size increases, nonmetric multidimensional scaling (NMS) was used to ordinate all invaded and uninvaded plots in two ways: (1) based on the percentage of cover of all native plant life forms (shrubs, perennial forbs, perennial grasses, annual forbs, and ferns), and (2) based

on the presence-absence of all species rooted in each quadrat. A random starting configuration with 50 runs of real data was used in the autopilot mode with medium speed for both NMS analyses. Then, a multiresponse permutation procedure was performed using a Euclidean distance measure for the cover data and a Sorenson distance measure for the presence-absence data to determine whether uninvaded and invaded plots formed significantly different groupings at $\alpha = 0.05$ (McCune and Mefford 2006). Lastly, using scores taken from axis 1, from each separate ordination, which explained the most variance both times, the difference between paired invaded and uninvaded plots were calculated and regressed against the corresponding basal diameter of the PRC in the invaded plot to see whether dissimilarity in vegetation, based on (1) cover, and (2) species composition (presence-absence), increases as a function of tree size. For all analyses, parameters measured in the two quadrats per invaded or uninvaded plot were averaged together so that $n = 20$ for all statistical analyses. Statistical analyses were performed using SYSTAT 12 (SYSTAT 2007) and PC-ORD Version 5 (McCune and Mefford 2006).

Results

Differences between Uninvaded and Invaded Vegetation. Other than *P. radiata* cultivars, 94 vascular plant species were documented during the study; 70 of which were native. The most common plant species found in uninvaded reference coastal scrub, were *M. aurantiacus*, *B. pilularis*, *T. diversilobum*, *A. californica*, soap-plant [*Chlorogalum pomeridianum* (DC.) Kunth], and brackenfern [*Pteridium aquilinum* (L.) Kuhn], with a frequency of 75, 68, 68, 50, 48, and 38%, respectively, based on 40 quadrats. Within invaded (under *P. radiata*) coastal scrub, the most common species were *T. diversilobum*, *B. pilularis*, *C. pomeridianum*, *M. aurantiacus*, *F. californica*, Torrey's melicgrass (*Melica torreyana* Scribn.), and *P. aquilinum*, with a frequency of 70, 38, 38, 28, 23, 23, and 23%, respectively. A paired *t* test showed that mean native species richness in invaded plots was lower compared with uninvaded plots ($t = 6.9246$; P < 0.001) by 3.3 species (Figure 2). The most common exotic species in both uninvaded and invaded scrub was the annual forb, common chickweed [*Stellaria media* (L.) Vill.], at 18 and 13% frequency, respectively. Another exotic annual forb, scarlet pimpernel (*Anagallis arvensis* L.), was also as frequent as *S. media* in uninvaded scrub but was present in only one invaded quadrat.

Among uninvaded coastal scrub plots, mean native shrub cover was 65% ± 4.2 SE. Also, average native plant cover of perennial grasses, perennial forbs, annual forbs, and ferns was 8.3 ± 3.1, 9.3 ± 2.4, 2.2 ± 0.7, and 10% ± 2.6 SE, respectively. No native annual grasses were found. In
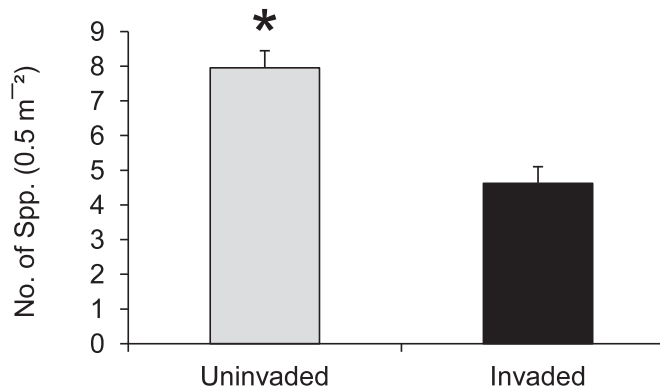

A) Total Native Cover
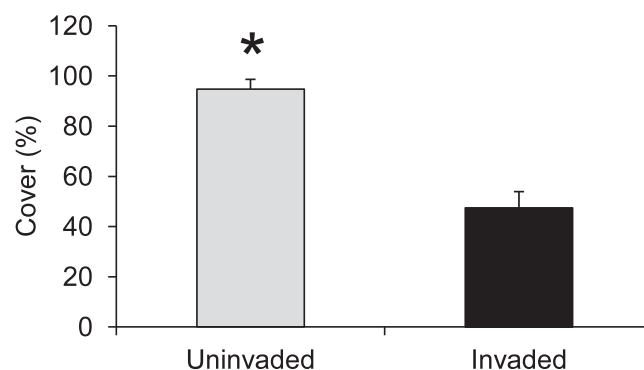
B) Total Native Richness

Figure 2. (A) Mean native cover, and (B) native richness in open, uninvaded coastal scrub vs. sampling plots located in coastal scrub beneath the canopy of an invasive, *Pinus radiata* cultivar. Asterisks indicate significant differences between invaded and uninvaded plots, based on paired *t* tests at $\alpha = 0.05$.

uninvaded coastal scrub, mean exotic plant cover of shrubs, perennial forbs, annual grasses, and annual forbs, was 0.1 ± 0.1, 0.2 ± 0.2, 2.5 ± 1.2, and 1.5% ± 0.5 SE, respectively. No exotic perennial grasses were found in uninvaded coastal scrub, but erect veldtgrass (*Ehrharta erecta* Lam.) was found in one invaded quadrat. Among invaded scrub plots, native shrub cover was 31.9% ± 5.7 SE. Average native plant cover of perennial grasses, perennial forbs, annual forbs, and ferns in uninvaded scrub was 2 ± 1, 8.9 ± 2.7, 1.1 ± 0.3, and 3.6% ± 1.4 SE, respectively. Among invaded plots, all exotic plant life forms exhibited cover values less than 1%. A paired *t* test showed that mean total native cover in invaded plots was 47.3% less than that found in uninvaded plots, which was statistically significant ($t = -2.8384$; P = 0.007) (Figure 2).

Changes in Invaded Vegetation as Tree Size Increases. The PRCs used in this study ranged in size from 2.8 to

Table 1. Results of linear regressions showing the relationship between the size of isolated *Pinus radiata* trees (basal diameter and crown diameter) and the parameters measured under the canopies of those trees.

Undercanopy parameters	Basal diam			Crown diam		
	R^2	Coefficient	P value	R^2	Coefficient	P value
Canopy coverage by *P. radiata*	**0.239**	**0.297**	**0.029**	**0.267**	**0.018**	**0.02**
Bare ground						
Cover	0.002	−0.006	0.862	0	0	0.941
Litter						
Cover of *P. radiata* litter	**0.536**	**0.491**	**0.000**	**0.467**	**0.026**	**0.001**
Cover of other plant litter	**0.266**	**−0.162**	**0.02**	0.14	−0.007	0.104
Litter depth	**0.292**	**0.069**	**0.014**	**0.23**	**0.003**	**0.032**
Exotic plants						
Species richness	0.002	−0.001	0.85	0.011	0	0.662
Absolute total cover	0.038	0.011	0.41	0.167	0.001	0.073
Native plants						
Species richness	**0.23**	**−0.027**	**0.032**	**0.229**	**−0.002**	**0.033**
Shrub richness	**0.284**	**−0.021**	**0.016**	**0.24**	**−0.001**	**0.028**
Perennial grass richness	0.004	−0.001	0.794	0.003	0	0.805
Perennial forb richness	0.016	0.004	0.592	0.01	0	0.676
Annual forb richness	**0.202**	**−0.007**	**0.047**	**0.26**	**0**	**0.021**
Fern richness	0.027	−0.002	0.493	0.024	0	0.515
Absolute total cover	0.176	−0.323	0.066	0.166	−0.018	0.075
Shrub cover	**0.239**	**−0.333**	**0.029**	**0.228**	**−0.018**	**0.033**
Perennial grass cover	0.056	0.028	0.316	0.09	0.002	0.199
Perennial forb cover	0.001	0.011	0.887	0	0	0.94
Annual forb cover	0.134	−0.012	0.112	0.09	−0.001	0.198
Fern cover	0.01	−0.017	0.67	0.003	0	0.83
Relative total cover	0.033	−0.037	0.442	0.143	−0.004	0.1
Relative shrub cover	0.089	−0.249	0.201	0.093	−0.014	0.192

119 cm basal diameter and from 0.66 to 20.90 m crown diameter. Basal and crown diameter were positively correlated (R^2 = 0.876, P < 0.001). Trees selected occurred on north-, east-, south-, and west-facing aspects but only on slopes that averaged 24 ± 0.9° SE. In invaded plots, cover of the *P. radiata* canopy above quadrats ranged from 17.5 to 100% with a mean of 73.9% ± 5.09 SE, litter depth ranged from 2.3 to 21.4 cm with a mean of 8.9 cm ± 1.1 SE, cover by *P. radiata* litter ranged from 1.5 to 80% with a mean of 39.7% ± 5.6 SE, and the cover of plant litter from species other than *P. radiata* ranged from 0 to 35.5% with a mean of 12.4% ± 2.6 SE.

When examining the correlation of tree size with abiotic and biotic parameters measured beneath tree canopies, basal diameter typically had stronger correlations with the measured parameters than canopy diameter (Table 1). Mean cover of bare ground, which was low across all invaded (3.2% ± 1.3 SE) and uninvaded plots (4.6% ± 1.1 SE), did not change with tree size. Cover by *P. radiata* litter and litter depth were both positively

correlated with tree size, whereas litter from all other plant species, which was mostly from native shrubs (data not shown), was negatively correlated with tree size (Table 1). Several biotic parameters also showed significant correlations with increasing tree size (Table 1); total species richness of native plants, native shrub species richness, and native annual forb species richness were all negatively correlated with increasing tree size. Also, native shrub cover was negatively correlated with increasing tree size (Table 1).

When comparing native cover of shrubs, perennial grasses, perennial herbs, annuals, and ferns between uninvaded and invaded scrub, the NMS analysis did not result in a solution, although the separation of uninvaded and invaded plots was visually distinct along axis 1 (Figure 3). The proportion of variance represented by each axis, based on the r^2 between distance in the ordination space and distance in the original space was 45.1, 4.7, and 35.7% for axis 1, 2, and 3, respectively. In addition, axis 1 had a very low proportion (7.84%) of randomized runs
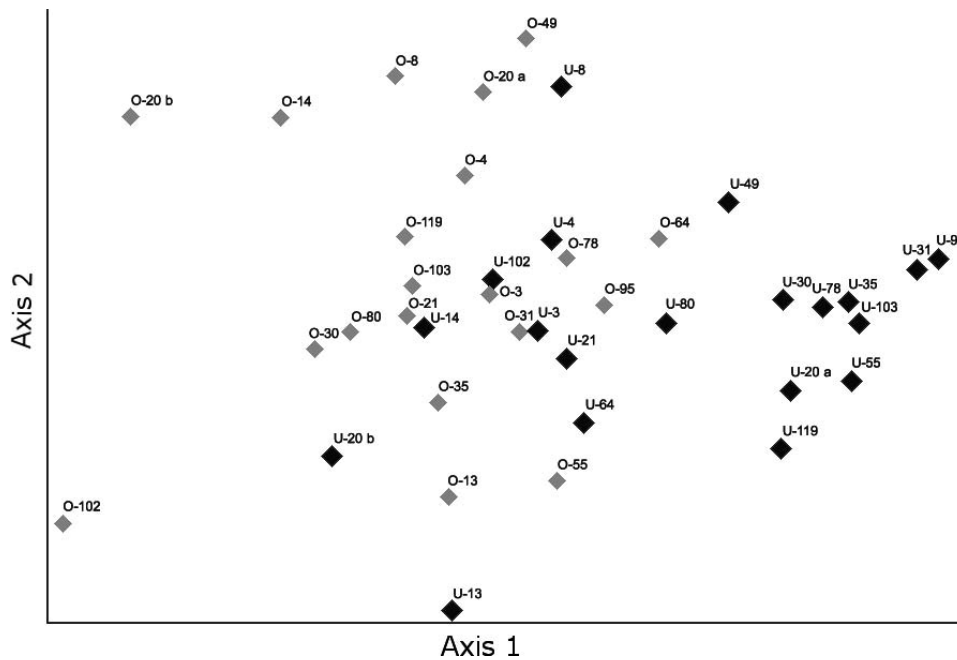
Figure 3. A nonmetric multidimensional scaling ordination using the native cover of shrubs, perennial grasses, perennial herbs, annuals, and ferns from uninvaded and paired, invaded coastal scrub plots. Invaded plots are black and marked with a "U," for understory, with their corresponding basal diameter (cm) listed. Uninvaded plots are grey and marked with an "O," for in the open, and the basal diameter of the tree under which their paired, invaded plots were located are displayed after the dash.

with stress at or less than observed stress, as opposed to the other axes, which had much higher proportions (54.9 and 96.08% for axes 2 and 3, respectively). Thus, axis 1 was more meaningful than the other axes in the ordination. Although the NMS did not result in a solution, the multiresponse permutation procedure did reveal a significant difference between uninvaded and invaded plots ($A = 0.131$; $P < 0.0001$). Finally, when the difference in axis 1 scores between paired uninvaded and invaded plots were regressed against the corresponding basal diameter of the paired invaded plot, linear regression revealed a significant positive correlation ($R^2 = 0.337$, $P = 0.007$) (Figure 5).

When comparing species composition with the presence-absence data between uninvaded and invaded scrub, the NMS analysis resulted in a three-dimensional solution with a final stress of 21.509 and instability of 0.006 after 200 iterations. Mean stress in 50 runs with real data for axes 1, 2, and 3 were 48.818, 26.401, and 21.572, respectively. Thus, the addition of axis 3 did not substantially reduce the stress of the ordination, so only the results from axes 1 and 2 are shown (Figure 4). The multiresponse permutation procedure also revealed a significant difference between uninvaded and invaded plots ($A = 0.016$; $P = 0.009$). Finally, when the difference in axis 1 scores between paired uninvaded and invaded plots were regressed against the corresponding basal diameter of the paired invaded plot, linear regression revealed a significant positive correlation ($R^2 = 0.285$, $P = 0.015$) (Figure 5).

Discussion

Effects on Structure and Species Composition. Although vegetation sampling was performed under trees of different sizes, invaded plots were collectively different than uninvaded plots in structural and compositional parameters. Paired t tests revealed significant differences in total mean native cover and total mean native species richness. Then, when comparing uninvaded plots with invaded plots based on the multiresponse permutation procedure, a significant difference between uninvaded and invaded plots was again detected both for cover and species composition (presence-absence).

Several understory or undercanopy parameters measured in invaded plots showed significant correlations with increasing tree size. Notably, native shrub cover and species richness parameters were negatively correlated with tree size, whereas the cover and depth of *P. radiata* litter was positively correlated. Thus, as invading pine trees increase in size, the cover and species richness of native plants decrease, whereas the canopy cover of *P. radiata* increases and a thick layer of *P. radiata* litter accumulates. Invasive PRCs in Australia have also been shown to produce relatively large amounts of litter directly below tree canopies, which may influence understory species and fuel properties (Williams and Wardle 2007). In addition, it was revealed that as trees increase in size, dissimilarity in native vegetation increases between uninvaded and invaded plots based on cover and species composition using axis 1 scores
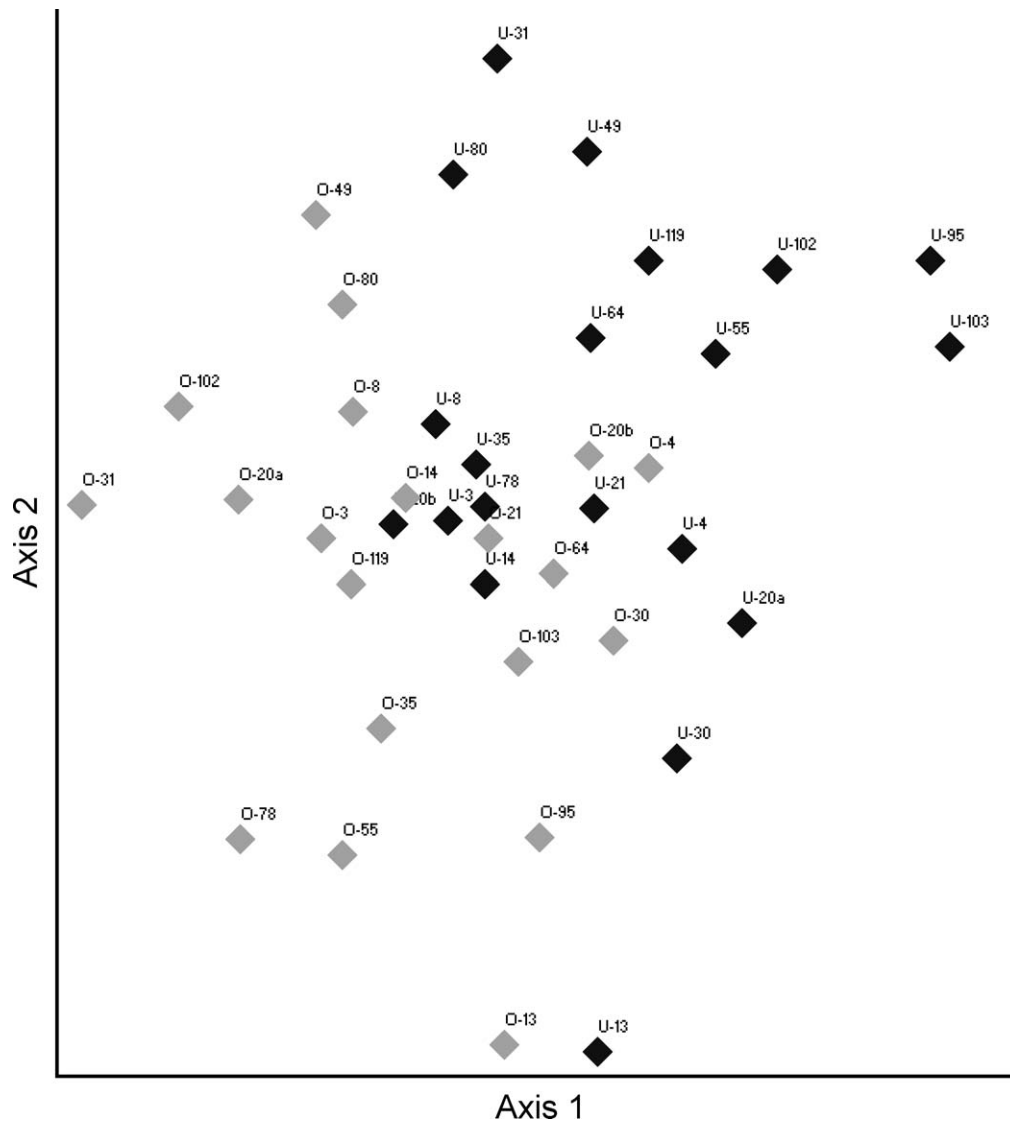
Figure 4. A nonmetric multidimensional scaling ordination using presence-absence data from uninvaded and paired, invaded coastal scrub plots. Invaded plots are black and marked with a "U," for understory, with their corresponding basal diameter (cm) listed. Uninvaded plots are grey and marked with an "O," for in the open, and the basal diameter of the tree under which their paired, invaded plots were located are displayed after the dash.

from two separate NMS ordinations. Thus, it is clear that isolated *P. radiata* trees exert a strong negative influence on the northern coastal scrub vegetation they overtop. To minimize this negative influence, PRCs should be removed at the earliest stage of growth as possible.

We limited our sampling to coastal scrub vegetation even though *P. radiata* trees were also observed recruiting in open grasslands and in the ecotone between grasslands and coastal scrub. If *P. radiata* trees are more successful at establishing in locations with relatively low cover of shrubs, such as canopy gaps in the coastal scrub, then this could have affected our results. Canopy gaps would have different initial conditions (e.g., lower shrub cover but higher species richness) than closed-canopied areas where the uninvaded

plots were placed. However, the smallest PRCs sampled were all found growing out of dense, closed-canopied vegetation (pictures not shown). Shrub cover for the five smallest trees used (ranging from 2.8 to 13.6 cm basal diameter) was $64.5\% \pm 6.2$ SE for uninvaded and $53.4\% \pm 10.3$ SE for invaded plots and was not statistically different between these habitats ($t = -2.3474$; $P = 0.079$). Furthermore, we observed hundreds of seedlings and saplings growing under, and emerging from, dense northern coastal scrub vegetation in our study area. We do not think our results were influenced by inadvertently sampling PRCs that had grown in places that initially contained canopy gaps or areas with relatively low shrub cover, although it is impossible to know with

A) Plant Cover

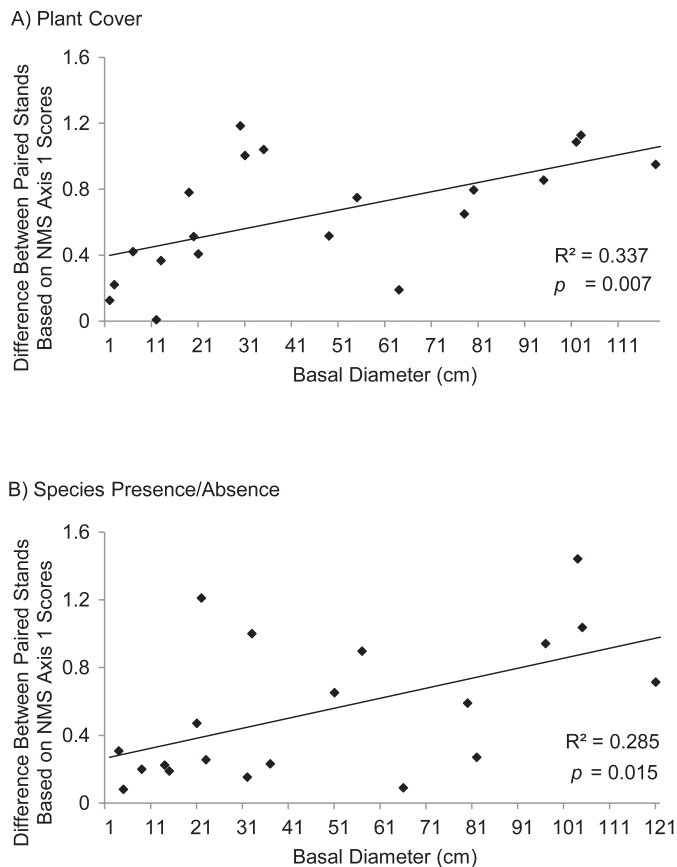## B) Species Presence/Absence

Figure 5. Linear regressions showing the relationship between tree size (basal diameter) and dissimilarity in vegetation, (A) based on plant cover, and (B) species composition (presence or absence). Dependent variables for (A) and (B) were obtained by calculating the difference in axis-1 scores between paired sampling plots from the corresponding nonmetric multidimensional scaling ordinations presented as Figures 3 and 4, respectively.

certainty for every tree (invaded plot) sampled, especially the larger ones. Lastly, paired invaded and uninvaded plots were located in close proximity to one another within the same stand of coastal scrub. Uninvaded plots were on the same slope, aspect, and topographic position as their paired invaded plots were. All coastal scrub stands used appeared to have uniform shrub coverage in the discrete portions of the stands where sampling took place. Thus, any inherent differences in initial coastal scrub vegetation between paired plots were minimized to the fullest extent possible.

Effects on Ecosystem Processes. Invading plant species are known to alter ecosystem processes (Henderson et al. 2006; Levine et al. 2003; Mack et al. 2000), and when they change the physiognomy of the vegetation they colonize, these alterations are often dramatic (Brooks et al. 2004; Le Maitre et al. 1996). There are many examples of invasive

Pinus species transforming grasslands or shrublands into forests (Richardson et al. 1994; Simberloff et al. 2010). Impacts to ecosystem processes resulting from type conversions include negative changes to vegetation structure and species composition, altered wildlife habitat, altered soil nutrients, altered biogeochemical cycling, altered hydrology, altered fuel volume, and altered fire regimes, among others. Although ecosystem processes were not investigated in our study, it is likely that the effects from invading *P. radiata* in northern coastal scrub would be similar to those documented from other Mediterranean-like climates where *P. radiata* has already invaded (Gaertner et al. 2009; Richardson et al. 1994; Simberloff et al. 2010).

Application to Successional Processes. Successional processes in central and northern coastal California can proceed from shrubland to woodland vegetation in the absence of disturbances (Callaway and Davis 1993, 1998; Russell and McBride 2003; Van Dyke and Holl 2001; Zavaleta and Kettley 2006). Where succession is taking place, evergreen broad-leaved tree species, such as coast live oak (*Quercus agrifolia* Née) and bay laurel [*Umbellularia californica* (Hook. & Arn.) Nutt.], or conifers like Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco], are important colonizers of shrubland communities. As succession takes place, the richness and abundance of coastal scrub species are expected to decrease as scrub becomes colonized and overtopped by these native trees. However, other more shade-tolerant vascular plants may eventually take residence in the understories of these trees based on observations from mature woodlands and forests (Sawyer et al. 2009). In our study area, *P. radiata* had colonized coastal scrub vegetation much more rapidly than any native tree species and in more places than the native tree species are likely to occur, such as in very close proximity to the seashore or on exposed, south-facing slopes. Thus, although native trees that colonize coastal scrub may cause similar impacts as *P. radiata*, the rate at which they colonize coastal scrub and their spatial distribution appear much different from that of *P. radiata*, at least in our study area (R. J. Steers, personal observation).

If isolated PRCs coalesce and form stands with continuous canopies in our study area, then native species richness might eventually increase in those stands when species adapted to *P. radiata* forest conditions establish. Over time, those stands might resemble native *P. radiata* stands found further south (Sawyer et al. 2009), which share many native plant species with those in our study area. However, it is also possible that other invasive plants associated with forests and woodlands in our study area, such as *E. erecta*, English ivy (*Hedera helix* L.), French broom [*Genista monspessulana* (L.) L. Johnson], English holly (*Ilex aquifolium* L.), among others, could establish

instead of native species and preclude the formation of stands that resemble native *P. radiata* forests. Because this study focused on isolated trees, many of which were young, we are not able to infer future successional trajectories (although see Lazarotti 2004). Finally, if PRCs act like other serotinous coastal conifers from the central coast, then fire succession of the coastal scrub community could be dramatically altered because fire would be expected to increase the spatial extent of *P. radiata* at the expense of coastal scrub, similar to what happened with bishop pine (*P. muricata* D. Don) following the nearby Point Reyes National Seashore Vision Fire (Forrestel et al. 2011; Harvey et al. 2011).

Conservation. One of the primary management goals for our study area is to protect its special status species and their habitats, principally the mosaic of coastal scrub and grasslands that blanket the Marin Headlands. Because this study demonstrates that invasive PRCs can dramatically alter the structure and species composition of coastal scrub, the most abundant vegetation type in the study area, continued removal of PRCs should be implemented. This study showed that, as tree size increases, negative alterations to coastal scrub also become greater. Thus, removing trees when they are as small as possible will minimize their negative effects. Although not investigated, removal of trees before they reach reproductive maturity would also help control their spread. Furthermore, serious consideration should be made to removing large PRCs surrounding structures, regardless of their cultural significance because those trees are a major source of propagules in the study area. Pine pitch canker (CDF 2010) has killed some PRCs in the study area, but it appears unlikely that it will eliminate all of the PRCs, so active removal efforts are necessary to keep trees in check. Eradication of PRCs from Golden Gate National Recreation Area and surrounding wildlands should also be explored. Rejmánek and Pitcairn (2002) have determined that it is usually possible to eradicate plant infestations ≤ 1,000 ha (2,471 ac). The spatial extent of PRCs in southern Marin County should be quantified, and eradication should be pursued, if possible. In addition, other invasive tree species in the study area, such as black acacia (*Acacia melanoxylon* R. Br. ex Ait. f.), Tasmanian blue gum (*Eucalyptus globulus* Labill.), and Monterey cypress [*Hesperocyparis macrocarpa* (Hartw.) Bartel] may also affect coastal scrub in ways similar to that of the PRCs (e.g., decreased shrub cover and reduced native species richness in the understory). Because treeless vegetation can be highly altered by colonizing trees, other invasive tree species besides PRCs should also be the focus of removal efforts if resources are available.

Part of the mission of the National Park Service is to preserve unimpaired the natural resources of each park for future generations. Global change is making this mission difficult when invasive species, nitrogen deposition, climate change, and other phenomena are acting at scales well beyond the borders of each park. Relating to climate change and the uncertain future of *P. radiata* forests in the three native mainland locations along the California coast, Millar (1998, 1999) and Millar et al. (2007) have proposed that where *P. radiata* exist outside of the current native range, these places should be used to harbor neonative populations to aid in the long-term conservation of this species. Because *P. radiata* formerly occupied portions of coastal Marin County during the Pleistocene, current *P. radiata* populations found here could be kept in place and used as neonative populations.

There are several considerations that land managers should address before allowing current *P. radiata* populations in coastal Marin County to serve as neonative populations. First, pine forests may not be a desirable vegetation type or compatible with existing management objectives (e.g., protection of special status species and viewsheds, among others). Second, if land managers accept PRCs as neonative populations, they must also be willing to accept all of the potential changes to habitats and ecosystem processes that will occur as *P. radiata* trees become dominant, which are reviewed above. Third, if land managers embrace this neonative conservation strategy, it also follows that these recruiting pines should be afforded the same special status and legal protection as native *P. radiata* in natural forests. Fourth, the lack of information on the origin and breeding of the PRCs poses a problem if they are to be used for the long-term conservation of this species.

Most of the silvicultural breeding of *P. radiata* has occurred outside California in New Zealand. Unfortunately, it is believed that many of the invading trees on the central coast of California are derived from these commercial sources (Edberg 1994; Rogers 2002, 2004). Furthermore, it is unknown what differences commercial cultivars exhibit in growth rate, seed production, ability to release seed without fire cues, recruitment rates, and other characteristics, compared with uncultivated plants derived from the native extant forests of California (sensu Whitham et al. 2003, 2006). In addition, it is also unclear which native population of *P. radiata* plants the invading PRCs are derived from, which is important because origin may have a strong influence on behavior (Rogers 2004). It is also unknown whether PRCs are the progeny of more than one of the native extant *P. radiata* populations. Ideally, trees that have been bred for commercial purposes should not be used for the conservation of *P. radiata* forests. Furthermore, because in situ genetic conservation of *P. radiata* is a global priority (Rogers 2002), neonative populations composed of PRCs derived from multiple native forest origins could be counterproductive. Therefore, before accepting PRC populations as neonative populations, further investigations, including genetic work, should be performed to understand tree origin and degree of cultivation.

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