COMMUNITY LEVEL CONSEQUENCES OF A BIOLOGICAL INVASION: 
EFFECTS OF A NON-NATIVE VINE ON THREE PLANT COMMUNITIES

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ABSTRACT

Biological invasions by non-native species are a global phenomenon that have the capacity to dramatically alter native communities and ecosystems. Despite the alarming rate and scale of these invasions, surprisingly few studies have explored the effects of exotic plant species on the communities they invade. This shortage is particularly troubling because land managers require such information to prioritize control activities and address future challenges. In this study, I investigated the influence of cape-ivy (Delairea odorata; Asteraceae), a non-native vine from South Africa, on the species richness, diversity and composition of three coastal plant communities in northern California. Using both experimental and non-experimental methods, this research demonstrated that plots invaded by cape-ivy contained significantly fewer plant species and exhibited lower species diversity than plots lacking cape-ivy. These effects were consistent across three different habitat types – coastal scrub, willow riparian and alder riparian. Invasion by cape-ivy also significantly reduced the abundance and richness of seedlings in all three habitat types. These results indicate that cape-ivy has had significant negative impacts on three divergent plant communities, and that control of this invasive plant should be a major priority for land managers.

Chair,

signature

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INTRODUCTION

Biological invasions by non-native species are a worldwide phenomenon that threaten to dramatically change communities and ecosystems (Elton 1958; Smith et al. 1985; Groves and Burdon 1986; Mooney and Drake 1986; Drake et al. 1989; Cowling 1992; Vitousek et al. 1992, 1996; Vitousek 1994; Cronk et al. 1995; Williamson 1996; Luken et al. 1997; Gordon 1998). Invasions in terrestrial systems have received most of the attention (see references above), but there is now mounting evidence that marine and freshwater environments are also subject to a tremendous influx of non-native taxa (Carlton and Geller 1993; Carlton 1996; Ruiz et al. 1997; Lee et al. 1999; Ruiz et al. 1999). Given the current rate and spatial scale of biological invasions, the costs of control, and the unfortunate reality that eradication is rarely achieved, detailed information on the consequences of these human-caused additions is urgently needed so that resource managers can prioritize control activities and more effectively allocate limited funds to the protection and restoration of biological diversity.

The majority of studies addressing plant invasions have focused on the characteristics of invasive species (Noble 1989; Huenneke and Vitousek 1990; Binggeli 1996; Reichard 1997), the process of invasion (Vivrette and Muller 1977; Huenneke 1990; D’Antonio 1993; Rejmanek 1996; Auge et al. 1997), effects of disturbance on invasion success (Hobbs and Huenneke 1992; D’Antonio and Dudley 1995), and the attributes of invaded systems (Gerrish et al. 1980; Orians 1986; Versfeld and van Wilgen 1986; Crawley 1987; Harrington 1991; Rejmanek 1996; Hulst 1997; Wiser et al. 1998). Far less attention has focused on the impacts of invasive plants species on the communities and ecosystems they invade. A number of studies have shown that non-native plant species can alter ecosystem-level characteristics of the areas they invade (see reviews by Vitousek 1986, 1990; Mack and D’Antonio 1998). They can modify water availability (Mueller-Dombois 1973; Vitousek 1986), soil fertility (Vitousek et al. 1987, 1989 and 1991; Musil 1993; Stock et al. 1995; Christian and Wilson 1999), fire frequency and magnitude...
(Whisenant 1990; Hughes et al. 1991; D'Antonio and Vitousek 1992), and geomorphic characteristics (Cooper 1967; Craig et al. 1978; Reckendorf et al. 1978).

Despite the global magnitude of the invasive plant problem and increasing efforts to restore invaded landscapes, surprisingly few studies have documented the community level effects of invasive plants on the regions they invade (McCarthy 1997; Woods 1997). Exotic plants are often assumed to alter plant species composition, richness, and/or diversity, but after extensive literature search, I have found only nine studies worldwide that evaluate such effects. Four of these studies assessed community effects using field experiments (Luken 1990; Musil 1993; Holmes et al. 1997; McCarthy 1997), whereas the other five were non-experimental (Kelly 1981; Cross 1982; Richardson et al. 1989; Maekawa 1991; De Winton 1996). Although specific results varied among studies, the general pattern was for invaded communities to exhibit reduced plant species richness compared to their uninvaded counterparts. It is tempting to conclude from these results that individual non-native plant species have consistent effects on the communities they invade. However, based on this limited and geographically restricted set of studies, I believe that such a conclusion is premature and warrants further investigation.

A key trait that characterizes most successful plant invaders is that they have broad physiological tolerances and colonize diverse habitat types (Baker 1974; Noble 1989; Rejmanek 1996; Auge et al. 1997). These habitats often vary markedly in biotic and abiotic conditions, and such differences should influence the abundance and subsequent impact of exotic plant species on resident assemblages. However, I know of only one study that has quantified the effects of the same non-native plant species on multiple habitat types (Maekawa 1991). Since activities to control the abundance and spread of invasive plants are often justified by the assumption that exotic taxa reduce the richness, diversity and composition of indigenous plant species in the regions they invade (Randall 1996), studies on the habitat-specific effects of invaders are critical so that land managers can determine which of the many non-native species are the most disruptive to biological diversity.
Here, I summarize research that addresses the effects of cape-ivy (*Delairea odorata*) on three coastal plant communities in northern California. Although this South African species has become dominant in a wide variety of habitat types in the region, there are no studies that evaluate the impacts of this extremely invasive plant. I conducted both experimental and non-experimental research to address the following questions: 1) Does cape-ivy influence species richness, diversity and composition of the plant communities it invades? 2) Does invasion by cape-ivy alter seedling recruitment? and 3) Are the effects of cape-ivy on plant communities consistent across three different habitat types? Answers to these questions will contribute to our understanding of the effects of individual species on plant communities, and will also provide land managers with urgently needed information on the effects of a highly invasive species.

**STUDY ORGANISMS AND SITES**

Cape-ivy (*Delairea odorata*; formerly *Senecio mikanioides*) is a perennial evergreen vine native to the Cape Province of South Africa, where it occurs naturally in extremely low abundance in fog forests at elevations above 2000 m (J. Balciunas, personal communication). The leaves and stems of this herbaceous plant are hairless and possess a thick waxy cuticle. In California, cape-ivy flowers in December and January but does not appear to produce viable seed (C. Bossard, personal observation). Viable seed is produced in Australia and Hawaii, but most California infestations are self incompatible (M. Robison, personal communication). Individual plants grow year-round, expand vegetatively through prolific stolon production, and regularly form large patches several hectares in size. In spring of 1995, I documented growth rates of 0.3 m per stolon per month, with each stem node capable of rooting on contact with the soil surface. Cape-ivy also breaks apart easily, allowing transported fragments to form new patches. Over time, cape-ivy forms a dense blanket of vegetation due to the layering of new growth over older
stolons, giving rise to a thick fibrous root mass composed of stolons and adventitious roots up to 10 cm thick at soil level.

Although its exact introduction date into North America is not known, cape-ivy was a popular houseplant in the late 1800s (McDonald 1975). In California, it escaped cultivation in Berkeley as early as 1899 (M. Robison, personal communication), and in Marin County as early as the 1940s (Howell 1949). In Hawaii, cape-ivy apparently became established in the wild as early as 1910 (Cuddihy et al. 1990). Over the past two decades, the range of cape-ivy has expanded exponentially throughout many coastal regions of California and Oregon, as well as northern Spain and Australia (M. Robison, personal communication) and the islands of Hawaii and Maui.

The three regions used in this study were located in Golden Gate National Recreation Area (GGNRA) within San Francisco and Marin Counties in northern California. All study regions were located within 15 km of each other and range in elevation from 4-95 m (see Figure 1 and Table 1). These regions are characterized by Mediterranean-type climate, with 90% of the annual precipitation occurring between the months of October and April. Annual precipitation for the region averages 50 cm per year, and mean monthly temperatures range from 9-17°C. Prior to the creation of the GGNRA in 1972, the sites experienced varying degrees of human disturbance including agriculture, grazing and military occupation. Grazing occurred only in the Tennessee Valley study region and ceased in 1985.

The first study region (referred to as coastal scrub) was located on coastal bluffs of the Presidio at the southwestern end of the Golden Gate Bridge. Vegetation at this location is characterized by coastal scrub and dominated by California blackberry (Rubus ursinus), coyote brush (Baccharis pilularis), poison oak (Toxicodendron diversilobum), California lilac (Ceanothus thrysiflorus), herbs and grasses. The second study region (referred to as willow riparian) was located in the Marin Headlands in Tennessee Valley. Dominant vegetation consist of arroyo willow (Salix lasiolepis), blue gum (Eucalyptus globulus) with
an herbaceous understory or rushes (*Juncus effusus* and *J. phaeocephalus*), California blackberry (*Rubus ursinus*) and herbs. The third study region (referred to as alder riparian) was located among riparian vegetation along Redwood Creek, south of Muir Woods National Monument. Overstory vegetation is comprised of red alder (*Alnus rubra*), willow (*Salix* sp.), and California Bay (*Umbellularia californica*). The understory consists of herbs and sparse native shrubs or small trees. There were a total of 87 plant species found within these three locations; 13 species of shrubs and trees, 54 herbaceous species, and 20 terrestrial and wetland grass species (Table 2). Fifty-seven percent of the plant species were native and forty-three percent were non-native. Although each habitat type was characterized by a dominant woody species, only fifteen percent of the total species were trees and shrubs, while eighty-five percent consisted of herbs and grasses. Eighty percent of the tree species, eighty-eight percent of all shrubs and all non-vascular species detected were native. Of the sixty-eight herbaeous species, thirty-three species were native and thirty-five were non-native (Table 2).

**METHODS**

*Non-Experimental Study*

In 1996, I conducted a non-experimental study to evaluate the association between cape-ivy invasion and plant species richness, diversity and composition. I established five blocks within each of three habitat types (coastal scrub, willow riparian or alder riparian), with 20 plots distributed equally among the five blocks. Each block was comprised of two zones of equal size: one invaded by cape-ivy and an adjacent zone of comparable substrate and habitat characteristics that lacked cape-ivy. Within a block, two 1.5 x 1.5 m plots were randomly placed in each of the two zones. Invaded zones had been occupied by cape-ivy for 5-10 years (Table 1) and cape-ivy cover averaged 88%. All five blocks for a given habitat type were located within 1 km of each other and all blocks averaged 15 x 30 m in size.
Using three different methods, I sampled the vegetation in each of three study habitat types (60 plots) during the early spring (February 27 – April 15) and summer (May 1 – July 1) of 1996. To estimate species-specific percent cover, I used point-intercept sampling methods and established four equally spaced, parallel transects 0.38 m apart, within each of the 1.5 x 1.5 m plots. I lowered a thin sampling rod vertical to the transect line and recorded all plant species that touched the rod at 25-cm intervals along each transect (for a total of 20 points per plot). Because multiple hits at a sampling point were common, total vegetation cover often exceeded 100%. To determine plant species richness in each plot, I searched the entire area of each plot and noted all plant species rooted within the plot. To quantify seedling abundance, I placed a 0.5 x 0.5 m sampling quadrat in the center of each plot and recorded the identity and abundance of all seedlings. Cape-ivy was included in all species richness counts. All values were calculated separately for each sampling season.

**Experimental Study**

In 1996, I initiated a two-year cape-ivy reduction experiment to more directly evaluate the influence of cape-ivy on plant assemblages. Within each of the three habitat types, I established 30 plots distributed equally among five blocks that were invaded extensively by cape-ivy (these were the same invaded areas as used for the non-experimental study; see above). There were six 1.5 x 1.5 m plots in each of 15 blocks, which I randomly assigned to one of three treatment levels; ivy reduction, soil and vegetation disturbance, and no manipulation or control (two replicates per level). The disturbance plots served as a control for soil and vegetation disturbance that was caused by removing cape-ivy in the reduction plots. I disturbed and removed cape-ivy in manipulation plots three times during this two-year experiment: April-May 1996, May -July 1996, and June-July 1997. I removed cape-ivy from the reduction plots by carefully weeding them by hand to minimize plot disturbance. Plots were disturbed by inserting a garden fork 8-10 times into the soil to a depth of 5 cm.
Using the same methods as described for the non-experimental study, I sampled the vegetation within all 90 experimental plots three times during the early spring (February - April) and summer (May - July) of 1996 and summer of 1998 (June-July).

**Statistical Analyses**

I analyzed most experimental and non-experimental data using three-way ANOVAs in the JMP 3.1 statistical program (SAS Institute). For the non-experimental ANOVAs, invasion status (cape-ivy present, absent), region (coastal scrub, willow riparian, alder riparian), and season (spring, summer) were the grouping factors, and block (1-5) was nested within habitat types. Non-experimental response variables for these analyses were total plant species richness and diversity (H'). Experimental ANOVAs were similar except that cape-ivy manipulation (reduction, disturbance and control) replaced invasion status as the single grouping factor in the model. Prior to all analyses, data were log transformed to equalize variances. For both experimental and non-experimental studies, log transformations did not equalize variance for data on seedling abundance and bare ground. Thus, I analyzed them using Kruskal-Wallis tests, with invasion status, region and season as grouping factors for the non-experimental study, with blocks nested within region. For the experimental study, cape-ivy manipulation and region were the grouping factors, with blocks again nested within region.

**RESULTS**

**Non-Experimental Study**

As shown in Figure 2a, plots invaded by cape-ivy contained 34% fewer plant species on average than plots lacking cape-ivy (see the invasion status main effect in Table 3a). Although plant species richness varied significantly among the three habitat types, the insignificant status x region interaction term indicates that the negative association between invasion and richness was consistent across these different habitat types (Table 3a). I also detected significant seasonal variation in plant species richness associated with the presence
or absence of cape-ivy, as indicated by the significant status x season interaction term (Table 3a). Although cape-ivy invaded plots had lower richness in both seasons, the reduction was significantly larger in the spring than in the early summer.

Overall, cape-ivy invasion was correlated with substantial changes in the species composition for all three habitat types. Plots invaded by cape-ivy contained 31% fewer native species than uninvaded plots (Table 4). Patterns for non-native plants were similar, there were 32% fewer plant species detected in plots containing cape-ivy (Table 4). Plots invaded by cape-ivy also exhibited reduced grass and forb richness, but there was no significant change in shrub richness compared to uninvaded plots (Table 4). Invaded plots contained 78% fewer annual species and 10% fewer perennial species compared to uninvaded plots; there were significantly more species associated with cape-ivy in the summer than the spring (Table 4).

On average, plant species diversity ($H'$) was 27% lower in plots invaded by cape-ivy compared to those free of this invasive species (Figure 2b, Table 3b). There was an insignificant trend for the effect of cape-ivy to vary among habitat types, due to the lack of influence of cape-ivy on diversity in willow riparian habitats. As was true for species richness, diversity was significantly lower in plots containing cape-ivy during the spring versus the summer (see the status x season interaction term, Table 3b).

Data from this study also demonstrate that invasion by cape-ivy is strongly correlated with seedling recruitment (Figure 3a). There were 88% fewer seedlings present in plots invaded by cape-ivy compared to non-invaded plots. Significant changes in seedling composition were also associated with cape-ivy invasion in all three habitat types. Overall, invaded plots contained 77% fewer seedling plant species on average than plots lacking cape-ivy, with equally significant reductions in both the spring and summer seasons (Table 4). Invaded plots contained 65% fewer species of native plant seedlings, 81% fewer species of non-native plant seedlings, and 77% fewer forb species seedlings than those lacking cape-ivy (Table 4).
There was a significant reduction (56%) in the average amount of bare ground in cape-ivy invaded plots in all three habitat types (Figure 3b). I measured an average of 6% bare ground in uninvaded plots and only 2.5% in invaded plots and there was significantly more bare ground in the spring than summer season among the three habitat types (see status x season interaction terms, Table 3d).

**Experimental Study**

As shown in Figure 4a, repeated attempts over a two year period to remove cape-ivy were successful in significantly reducing its cover (Table 5a). These reductions had a significant effect on plant species richness, with removal plots containing 32% more species on average than control plots (Figure 4b). The effect of reduction on richness varied significantly among blocks and habitat types, as indicated by the significant status x region and status x block interaction terms (Table 5a). Cape-ivy reduction had the greatest effect on species richness in the coastal scrub habitat (48% increase), compared to riparian willow and alder habitats (both increased 24%). Most of the change in species richness was due to an increase in seedling recruitment, particularly that of grasses and forbs. After two years, the cape-ivy reduction plots had 400% more seedlings than control plots and 571% more than the ivy disturbance plots (Figure 4b; Table 6).

**DISCUSSION**

In this study, I have provided results from two concurrent studies which each demonstrate that the non-native perennial vine, cape-ivy (*Delairea odorata*), has had significant negative effects on plant communities in northern California. In a non-experimental study, plots invaded by cape-ivy exhibited significantly reduced species richness and diversity ($H'$) compared to uninvaded plots. Cape-ivy invasion was also associated with significant changes in community composition, reducing the richness of most plant life forms – native and non-native taxa as well as annual and perennial herbs and grasses. In addition, the abundance and species richness of seedlings was significantly
lower in plots invaded by cape-ivy. Results from a field experiment strongly support these findings and demonstrate that they are due to the negative effects of cape-ivy, rather than differences between invaded and uninvaded areas. Results from both experimental and non-experimental studies clearly indicate that the negative effects of cape-ivy were consistent across three markedly different plant communities — coastal scrub, riparian willow and alder riparian.

One of the most striking features of this study concerns how closely the experimental and non-experimental results parallel each other. In the non-experimental study, plant species richness was 34% lower in invaded plots compared to uninvaded ones. At the same time, richness was reduced by virtually the same amount (32%) when cover of cape-ivy was experimentally reduced in plots for two years. Both studies also demonstrated that seedling recruitment was drastically reduced in the presence of cape-ivy, and that annuals and small-statured perennials were the most affected life forms. Such close agreement is impressive and gives added weight to my non-experimental results. In addition, the strong similarity may shed light on the speed with which cape-ivy alters the communities it invades, since the reduction experiment demonstrated that the invaded plant communities responded to the removal of cape-ivy relatively quickly — i.e., within two years.

Cape-ivy possesses two life history characteristics that are associated with highly invasive species: tremendous growth capacity and an ability to tolerate widely varying environmental conditions (Baker 1974; Noble 1989; Rejmanek 1996; Auge et al. 1997). In the GGNRA, cape-ivy growth rates range from an average of 0.35 m per month in a *Eucalyptus* forest to 1.35 m per month in an alder riparian habitat (M. E. Alvarez, personal observation). In just 10 years, cape-ivy expanded 700% within coastal scrub and alder riparian habitats (G. Hoban and M. Vaghti, unpublished data). This species has also become established in 15 different plant community types, ranging from coastal bluff scrub to upland California Bay forests (M. E. Alvarez, personal observation). Not only does this
vine grow rapidly, but it can also rebound quickly and completely from prolonged periods of freezing winter weather (R. Peterson, personal communication). Cape-ivy also has a thick waxy cuticle that enables it to survive summer drought conditions.

One possible explanation for the dramatic effects of cape-ivy may involve the degree to which non-native species match the life forms present in the communities they invade. Invaders with novel life forms may have broad effects on different life forms, leading to the alteration of community structure and decreased diversity (Vitousek 1986). Examples of invasive plants that are considered to be novel growth forms for a particular habitat include Tamarisk sp. in the southwestern U.S., water fern (Salvinia molesta) in African lakes, and the trees Schinus and Melaleuca in the Florida Everglades (Vitousek 1986). Cape-ivy is one of only two stoloniferous, evergreen, perennial vines found in the three habitat types in my study region. The only other species with a similar growth form is Rubus ursinus, but it is not an effective climber because of its woodiness. Cape-ivy's vigorous vining growth form allows it to "forage" for resources by growing up shrubs and trees (up to 15 m in height) and intercepting more light, while its stolons travel along the soil surface, forming a dense groundcover. As resources are located, these same stolons then serve as an asexual reproductive system, enabling cape-ivy to produce adventitious roots and expand even farther into the landscape. Not only must plants compete with the prolific aboveground vining stems of cape-ivy, but these same stems sprout roots on contact with soil, providing cape-ivy with a mobile and opportunistic root system, ideal for colonizing bare soil beneath shrubs and between herbs, as well as covering them with a new season of growth. In addition to its novel growth form, the phenology of cape-ivy growth further compounds its negative effects on plant communities. The most rapid cape-ivy growth occurs during the spring, precisely when plants species in this Mediterranean-type climate undergo maximal growth.

According to Woods (1997), invasive plant species are likely to alter plant communities via two contrasting pathways, depending on the characteristics of the
invader. First, invaders may eliminate species with similar life histories, as in the spread of Monterey pine into *Eucalyptus* forests in Australia (Burdon and Chilvers 1983) or into fynbos in South Africa (Armstrong and van Hensbergen 1996). Alternatively, invaders may reduce the richness of species with dissimilar life histories, such as the invasion of *Rhododendron ponticum* into the British Isles (Cross 1982). Results from my research suggest that the second scenario, rather than the first, is the case for cape-ivy. The first scenario does not apply because a) there are very few plant species in my system that resemble cape-ivy and b) those taxa that share some life history characteristics with cape-ivy (i.e., perennial species with a vining habit or robust rhizomatous growth, such as *Rubus, Vicia, Stachys, Scrophularia*, *Urtica*, and *Marah*) were the least affected by invasion. The second scenario was supported because, like *Rhododendron*, cape-ivy had consistently negative effects on all understory species with dissimilar life history characteristics. In riparian habitats, cape-ivy invasion transforms the understory community from a mixture of both annual and perennial herbs, shrubs and bare ground to a community blanketed with 78% cape-ivy cover. In the scrub habitat, cape-ivy cover averaged 90% and smothered almost all of the short-statured herbs.

Although I did not directly investigate the mechanisms by which cape-ivy alters plant species richness, I hypothesize that the impressive growth capacity of this vine allows it to become a dominant competitor. Competitive advantage is the most commonly cited explanation for why invaders thrive (Vitousek 1986; Blossey and Notzold 1995; Woods 1997). Other investigators have shown that some invasive plant species exhibit superior growth rates or resource allocation compared to natives in the same environment. For example, Japanese honeysuckle (*Lonicera japonica*) outcompeted a native congener (*Lonicera sempervirens*) in the southeastern U.S. (Schierenbeck et al. 1994). On the Pacific coast, European dune grass (*Ammophilla arenaria*), has superior resource allocation capabilities compared to those of American dune grass, *Leymus mollis* (Pavlik 1983). Cape-ivy also fits another generalization which states that most successful invaders of
natural systems are perennials characterized either by prolonged periods of juvenile growth or aggressive clonal growth (Silvertown 1982). Interestingly, both the aforementioned *Lonicera* and *Ammophilla* are also characterized by aggressive clonal growth.

Cape-ivy may alter environmental conditions in areas it invades by reducing light levels and monopolizing below-ground space for roots. Cover values for plant communities invaded by cape-ivy were higher than those for uninvaded habitat, providing evidence that cape-ivy intercepts light that would otherwise reach shorter plants or the soil surface. If light levels are significantly reduced, then it is reasonable to assume that only plants capable of germinating and growing under low light levels would coexist with cape-ivy, such as the non-native annual herb *Gallium aparine*, which I observed in 20% of my study plots among all three habitat types. This reasoning is also consistent with Huenneke's (1995) findings that the non-native herb *Dipsacus sylvestris* significantly reduced light levels and subsequently reduced habitat quality for a native biennial thistle. A reduction in light may explain why the plant growth forms most reduced by cape-ivy's presence were either annuals, seedlings or non-rhizomatous short-statured perennials. In contrast, the richness of rhizomatous and mature woody perennial species were least affected, decreasing by only 4% in the three habitat types.

In addition to competition for light, cape-ivy may also compete for other resources such as water or nutrients. Invaded plots contain a layer (up to 10 cm deep) of dense adventitious cape-ivy roots, which overlap with those of herbs and grasses in the upper soil horizon. Numerous studies have demonstrated that certain non-native plants – such as pines (Swank and Douglass 1974; Dye 1996), *Tamarix* sp. (Busch et al. 1995; Owens 1996), *Carpobrotus edulis* (D'Antonio and Mahall 1991) and exotic grasses (Danielson and Halvorsen 1991; Gordon and Rice 1993) – outcompete natives for water. Non-native plants may also successfully outcompete natives for soil nutrients, as in the case of phosphorus competition between *Agropyron spicatum* and *Agropyron desertorum* (Caldwell et al. 1985). Studies have also shown how competition can adversely affect
native species. For example, the root structure of a native shrub was altered by its association with *Carpobrotus* (D'Antonio and Mahall 1991). Eissenstat et al. (1988) has also shown that superior water extraction by a non-native grass, *Agropyron desertorum*, led to reduced survival, growth, reproduction and late-season water potential of the native shrub, *Artemesia tridentata*.

In addition to competition, cape-ivy may alter growth or germination conditions for plants in a number of ways, including the alteration of soil temperatures, humidity, or the composition of microbes or invertebrates. Reduced seedling abundance in areas invaded by cape-ivy may suggest that the seedbank is depleted. Although I did not investigate it, the reproductive success of parent plants may also be altered due to direct competitive interactions or environmental modifications caused by cape-ivy, thereby further contributing to seed bank decline. It is also possible that the seed bank has not changed significantly since time of invasion, but that conditions for germination in the presence of cape-ivy are just not being met. Data from my study support this explanation, since there was a large experimental response in seedling recruitment due to cape-ivy removal. There was also a significant seedling germination response in the disturbance plots. It would be interesting to monitor seedling recruitment over time to observe the seedbank response after cape-ivy is permanently eliminated. Regardless of cause and effect, seed banks could become depleted as invasion time increases, reducing not only community diversity, but the ability of the entire plant community to respond to future environmental change.

The research presented in this paper provides one of the most comprehensive studies to date documenting the effects of non-native plant species on the communities they invade. Using both experimental and non-experimental studies, I have shown that cape-ivy has had significant negative effects on species richness, species diversity, seedling abundance and the understory composition in three different habitat types. Both studies clearly show that cape-ivy had consistently negative effects across three markedly different habitat types in northern California – coastal scrub, riparian willow and alder riparian.
Demonstrating whether cape-ivy had consistent or inconsistent effects is important because non-native species often invade more than one kind of habitat, and their effects on native plant community composition can exhibit tremendous spatial variation. If a central objective of land managers is to maintain biodiversity, then one of the first management activities should be to identify those invasive species that are having the greatest negative effects on plant communities. Without detailed ecological studies examining the effects of invaders, it is difficult for land managers to determine which invaders have large effects and which are minimal ones. Such studies are crucial because they support science-based management decisions regarding the use of limited funds for the protection and restoration of biological diversity. While state, national and international efforts to control exotic plant taxa are increasing, management programs have not even taken this first step. Although California has an abundance of invaders (Mooney 1986), the research presented here constitutes one of the first studies to document their effects on plant communities. My hope is that this study will provide land managers with a sound basis for prioritizing efforts to control cape-ivy throughout northern California.
Figure 1. Location of the three cape-ivy study sites in the San Francisco Bay Area, California.
Figure 2. Plant species richness (a) and total plant diversity (b) per plot within three habitat types as a function of the presence or absence of cape-ivy (*Delairea odorata*). Vertical lines correspond to one standard error.
Figure 3. Seedling abundance (a) and percent bare cover (b) per plot within three habitat types as a function of the absence or presence of cape-ivy (*Delairea odorata*). Vertical lines correspond to one standard error.
Figure 4. Cape-ivy (Dezairea odorata) cover (a), plant species richness (b) and seedling abundance (c) per plot within three habitat types as a function of three treatment levels: control, vegetation disturbance and cape-ivy reduction. Vertical lines correspond to one standard error.
Table 1. Characteristics of the three sites used for cape-ivy experimental and non-experimental studies.

<table>
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<tr>
<th>Habitat Type</th>
<th>Coastal Scrub</th>
<th>Willow Riparian</th>
<th>Alder Riparian</th>
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<td>San Francisco</td>
<td>Marin</td>
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<td>S, SE</td>
<td>E, SE</td>
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<td>clay loam, alluvial</td>
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Table 2. Plant species found within cape-ivy study plots in three regions of northern California (coastal scrub, riparian willow and riparian alder habitat).

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Table 3. Results from three-way ANOVAs for a non-experimental field study evaluating the difference between total species richness, diversity, seedling abundance and bare ground in the presence or absence of cape-ivy (*Delairea odorata*) among plant communities in northern California. Status refers to the presence or absence of cape-ivy. Region refers to the three different habitat types; scrub, willow riparian and alder riparian. Species richness (a) and seedling abundance (c) were log transformed (common) for statistical analysis.

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### d. Bare Ground - % Cover

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Table 4. Mean species richness and seedling abundance (± 1 standard error) in the presence or absence of cape-ivy (*Delairea odorata*) among three different habitat types; scrub, willow riparian and alder riparian in northern California.

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<tr>
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<td>2.9 ± 0.41</td>
<td>4.7 ± 0.77</td>
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<td>2.3 ± 0.59</td>
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<tr>
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<td>3.2 ± 0.44</td>
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<td>alder</td>
<td>1.3 ± 0.13</td>
<td>2.1 ± 0.31</td>
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<td>0.9 ± 0.61</td>
</tr>
<tr>
<td>willow</td>
<td>0.1 ± 0.35</td>
<td>0.2 ± 0.09</td>
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<tr>
<td>alder</td>
<td>0.7 ± 0.13</td>
<td>1.0 ± 0.17</td>
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Table 5. Results demonstrating a) percent cover of cape-ivy (*Delairea odorata*), and evaluating the influence of cape-ivy on b) total plant richness and c) abundance of seedlings in experimental plots among three plant communities in northern California. Three-way ANOVAs were used to analyze cape-ivy cover and species richness while a Kruskal-Wallis ANOVA for nonparametric data was used on seedling abundance. Treatment refers to one of three different levels; control, vegetation disturbance and cape-ivy reduction. Region refers to three different habitat types; scrub, willow riparian and alder riparian. Species richness (a) and seedling abundance (b) were log transformed (common) for statistical analysis.

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Table 6. Total abundance of seedlings within plots in which cape-ivy was either present (controls) experimentally reduced in cover (ivy reduction) or disturbed (ivy disturbance) n=12. Data are presented for three habitat types (coastal scrub, alder riparian and willow riparian) and two time periods: two months after cape ivy reduction and disturbance treatments (1996) and two years later (1998).

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