

Assessing the residual effects of *Carpobrotus edulis* invasion, implications for restoration

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Received: 12 October 2007 / Accepted: 28 February 2008 / Published online: 8 April 2008
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Abstract We examined whether the residual effects on soil caused by the invasion of *Carpobrotus edulis*, common iceplant, would inhibit the reestablishment of a native plant species. *Carpobrotus edulis* interacts both directly by suppressing the growth and establishment of other plants and indirectly by altering soil chemistry. We tested whether the residual effects of *C. edulis* resulted in lowered germination, survival, growth, and reproduction of *Gilia millefoliata*, a rare dune annual. We compared *G. millefoliata* planted in plots previously occupied by *C. edulis* to *G. millefoliata* planted in plots that previously had native vegetation. Each plot received three treatments: seed, transplant, and unplanted, and were censused every three weeks until senescence. *Carpobrotus edulis* had strong negative effects on the germination, survival, growth, and reproduction of *G. millefoliata*. *C. edulis* lowers soil pH and increases organic content due to the recalcitrance of tissue to decomposition, which may have evolved as a mechanism to facilitate recolonization and invasion.

Keywords *Carpobrotus edulis* · Demography · Ecosystem engineers · Ecosystem-level effects · *Gilia millefoliata* · Habitat restoration · Invasive species · Residual effects

Introduction

One of the biggest threats to biodiversity in California is the invasion and establishment of introduced species. The result of a successful invasion is the progressive and often irreversible homogenization of plant communities often characterized by a single species exerting control over the processes of the entire ecosystem (D'Antonio and Vitousek 1992; Wisser et al. 1998). Long-term effects of biological invasions are not only loss of biodiversity but permanent changes to ecosystem processes by altering system-level rates of resource supply, the trophic structure of the invaded area and disturbance regimes (D'Antonio and Vitousek 1992). Biological invasions are a significant threat to native ecosystems because, in addition to out competing native species, invasions alter environmental conditions and resource availability (D'Antonio and Vitousek 1992), which produces potentially long-term residual effects.

The ecological impacts of invasive exotic plant species on native plant communities can result from pathways of direct or indirect effects from the invader. Direct effects of the invader include allelopathy,

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direct competition with native species for resources or space, and rapid preemption of resources following disturbance (D'Antonio and Haubensak 1998). Indirect effects include habitat modification; i.e., alteration of natural disturbance regimes, alteration of substrate stability and geomorphology, alteration and simplification of food webs, and alteration of soil chemistry and chemical processes (D'Antonio and Haubensak 1998). Multiple pathways may be involved in an invasion, which can make diagnosing the impact on ecosystem level processes very complicated and prescribing appropriate habitat restoration problematic.

Understanding the ecological impacts of an invasion is an essential first step in determining a strategy for restoration of an invaded habitat. If the ecological impacts of an invasive species are caused by directly competing with native plants for resources or physical space, then removal of the invader may be sufficient to initiate successful reestablishment of native species to the community. However, if the ecological impacts are due to indirect species interactions then merely removing the invasive species may be insufficient to initiate successful restoration. It is necessary to diagnose the indirect interactions that facilitated the invasion process and determine if these interactions have produced residual effects that impact the invaded ecosystem after the invader has been removed. Residual effects may result from the physical modification of the environment by the invader and may persist for some period of time after removal of the invader. Once the residual effects of an invader on a native plant community have been characterized, the problem can be studied and recommendations can be made about how to reverse the effects and restore the native plant community.

Methods

We tested the hypothesis that the residual effects on soil from the invasion of *Carpobrotus edulis* would inhibit reestablishment of a native plant species after *C. edulis* has been removed. Changing soil chemistry and nutrient availability may not only hasten the invasion process but could physically modify the soil environment over time, resulting in residual impacts to the soil. We conducted experiments to determine if residual effects impact a population of *Gilia*

millefoliata, a rare dune annual, after *C. edulis* has been removed. We investigated whether the residual effects of *C. edulis* result in lowered germination, survival, growth and reproduction of *G. millefoliata*. We compared the demographic attributes of cohorts of *G. millefoliata* planted in native vegetation to cohorts of *G. millefoliata* planted in areas where *C. edulis* had been removed. Cohorts planted in plots where iceplant had been removed (simulating a restoration area) were compared to cohorts planted in plots where iceplant had not invaded but where the native vegetation had been removed (control). If there are residual effects from the *C. edulis* invasion then we would have expected lowered germination, survival, growth, and reproduction in the cohort planted in plots previously occupied by *C. edulis*.

Study species

Common iceplant, *Carpobrotus edulis* (Aizoaceae), is a South African species that invades coastal plant communities from the North Coast of California to Mexico (Hickman 1993). *Carpobrotus edulis* was originally introduced to California to stabilize soil along railroad tracks in the early 20th century and was later planted along highways and used to stabilize coastal sand dunes (Albert 1995). *Carpobrotus edulis* has escaped cultivation and successfully invaded native coastal plant communities in California (D'Antonio 1993; D'Antonio et al. 1993; Albert 1995).

Carpobrotus edulis is a prostrate, succulent perennial forming large clonal swarms up to 20 m in diameter (D'Antonio 1990, 1993). *Carpobrotus edulis* grows from multiple axes rooting where nodes contact the soil, and spreads radially at rates as high as 1 meter per year (D'Antonio 1990; Albert 1995). Branches often grow over one another, resulting in a thick mat of live and dead plant material up to 40 cm in depth (D'Antonio 1990). *Carpobrotus edulis* produces fleshy indehiscent fruits and also reproduces vegetatively.

Gilia millefoliata (Polemoniaceae) is an annual plant native to the northern coastal region of California (Hickman 1993), and is listed by the California Native Plant Society as a 1B rare species. *Gilia millefoliata* is a small herbaceous annual, 8–30 cm in height, and reproduces primarily via seed production (Hickman 1993). We chose to study *G. millefoliata* because of its annual life style, its occurrence in habitats commonly

invaded by *C. edulis*, and because natural populations of *G. millefoliata* have declined as a result of habitat loss by *C. edulis* invasion.

Study site

We conducted the experiment at the U.C. Davis Bodega Marine Reserve (BMR) in Bodega Bay, California (33.32°N & 123.04°W). The climate of the reserve is Mediterranean, characterized by cool, wet winters and foggy summers with an average annual temperature of 15.8°C. Annual rainfall averages 79 cm and occurs mostly between November and early April.

The study was conducted on Mussel Point at 40 m above sea level, an area of the reserve characterized by yellow bush lupine series vegetation dominated by yellow bush lupine (*Lupinus arboreus*) and coyote brush (*Baccharis pilularis*) and introduced annual grassland series vegetation (Sawyer and Keeler-Wolf 1995). *Carpobrotus edulis* and exotic annual grasses have extensively invaded both habitats. The spread of *C. edulis* on Mussel Point has been well documented by aerial photographs taken annually since 1955. The reserve managers began actively controlling the spread of *C. edulis* on Mussel Point in 1997, mainly by use of the herbicide Roundup®.

Experimental design

We collected preliminary data in May 2000 for six life history characters on individuals of *G. millefoliata* from a single population located on the Old South Dune at the U.C. Davis Bodega Marine Reserve. Number of fruits was the life-history characteristic that had the highest coefficient of variation, so we used it in a power analysis for a paired, one-tailed *t*-test to determine the appropriate sample size. We estimated effect size by multiplying the mean number of fruits by Cohen's value of a medium effect magnitude (0.35) (Cohen 1977). The results of the power analysis indicated that a sample size of 40 was necessary to achieve 80% power.

Experimental subjects consisted of a treatment patch of *C. edulis* and an adjacent control patch of native vegetation. We chose 40 patches of *C. edulis* on Mussel Point and cleared all above ground biomass and litter from a 0.5 m × 1.5 m plot in the

center of each *Carpobrotus edulis* patch. In the native vegetation adjacent to the *C. edulis* patch we removed all above ground biomass and litter from a 0.5 m × 1.5 m area. Treatment and control plots within each subject were placed at the same aspect, parallel to each other on the slope, to minimize any microclimate variation within each subject. Each 0.5 m × 1.5 m plot was caged to prevent herbivory by deer or jackrabbits, but allow access to the plants by pollinators. Cages were constructed using a PVC frame covered with 2.54 cm diameter poultry netting.

Field implementation

Three 0.5 m² randomly assigned sub-plots were placed within each 0.5 m × 1.5 m plot and received the following treatments: (1) sown with *G. millefoliata* seed, (2) transplanted with *G. millefoliata* seedlings and (3) unplanted. In each seed cohort plot, twenty *G. millefoliata* seeds were divided into four groups of five seeds each. Seeds were sown at the end of the dry season, before the onset of the winter rains in late October 2000. To prevent the seeds from blowing away, a translucent plastic tree protector tube was placed around each seed grouping. Protector tubes were removed after seeds germinated. For the transplant cohort, seedlings were propagated at the San Francisco State University greenhouse and installed in the field plots in January 2001 (at the time when *G. millefoliata* seedlings began to emerge). Each transplant plot was planted with twelve seedlings, in four groups of three seedlings each. Each unplanted plot was left unplanted to serve as a control. Unplanted plots were regularly monitored to check for the emergence of *G. millefoliata* from the seed bank.

We measured life history characters for each cohort of seeds or transplants planted in field plots (e.g., seed germination, survival, number of stems, and mean leaf length, number of leaves, basal rosette diameter, plant height, number of flowers, and number of fruits). We counted and measured *G. millefoliata* transplants approximately every three weeks from December 26, 2000 to May 10, 2001. At the time of each census we counted all the surviving individuals from both seed and transplant cohorts and measured all the life history characters present on the plants at the time of the census. On May 28, at the end of the census period, we collected all of the plants for processing in

the lab. *G. millefoliata* planted from seed began emerging by the middle of December 2000.

Soil analysis

To quantify soil characteristics in treatment and control plots within each subject, we collected soil samples just prior to transplanting seedlings. Each sample was analyzed for soil moisture content (gravimetrically), organic content (by combustion), and pH (using a hydrated sample and pH probe). We compared differences in these soil characteristics within subjects (between native vegetation plots and plots where *C. edulis* had been removed).

Data analysis

To test whether there was a significant difference in germination, survival, growth, and reproduction of *G. millefoliata* between native vegetation plots and plots where *C. edulis* had been removed, we used a two-factor (treatment & date) repeated-measures experimental design. Within each subject, control plots (defined as plots placed in native vegetation) were compared to treatment plot (plots within *C. edulis* patches, where *C. edulis* had been removed). We report *F*-tests adjusted for non-sphericity of the variance-covariance matrices using the Greenhouse-Geisser epsilon; hence some degrees of freedom are non-integer (Muller and Barton 1989).

Results

Germination and survival

Seed germination began in late December 2000 and three times more *G. millefoliata* seeds germinated in native vegetation than in *C. edulis* patches (Fig. 1a). Cumulative seed germination was low at the end of the study; 17% of the *G. millefoliata* germinated in native vegetation soils and only 6% of the seeds in *C. edulis* soils germinated.

Gilia millefoliata planted or sown in native vegetation soils had higher survival rates than when planted or sown in *C. edulis* soils (Table 1 and Fig. 1b and c). A higher percentage of transplants survived long enough to produce seed compared to plants grown from seeds sown in the field.

Growth

Among the surviving plants, there were no differences in growth in the seed cohort between native vegetation and *C. edulis* soils (Table 1 and Fig. 2). However, there were significant differences in roughly all of the growth measures for the transplant cohort (Table 1 and Fig. 3). Plants transplanted into native vegetation soils produced 3–4 times more leaves, were four times taller, and had fully developed basal rosettes that were four times larger in diameter compared to those in *C. edulis* soils (Fig. 3).

Reproduction

Gilia millefoliata began flowering in early-April, approximately 4 months after germination, and flowering lasted until mid-May. Overall, both *G. millefoliata* cohorts produced very few flowers. Rates of flowering and fruiting did not differ among treatments for the few plants surviving from the seed cohort (Table 1 and Fig. 4). However, transplants in native vegetation soils had significantly more flowers than those in *C. edulis* plots (Fig. 4c). At the peak of flowering, transplants grown in native vegetation soils produced an average of 3–4 flowers, while transplants in *C. edulis* soils produced only one flower per plant. Plants began developing fruits and went to seed in mid-April. Plants in the native vegetation plots produced more fruits than the *C. edulis* plots, but not significantly so (Fig. 4b and d).

Soil characteristics

We found no significant differences in soil moisture content between native vegetation soils and *C. edulis* soils. Soil organic content was higher in *C. edulis* soils (mean = 3.29% ± 0.604), compared to native vegetation soils (mean = 2.45% ± 0.157). The average pH in control plots that had never been invaded by *C. edulis* was significantly higher than in *C. edulis* soils (paired *t* = 6.3, *df* = 33, *P* = 3.99 × 10⁻⁷, mean pH in native vegetation soils = 6.07 ± 0.100, mean pH in *C. edulis* soils = 5.51 ± 0.100).

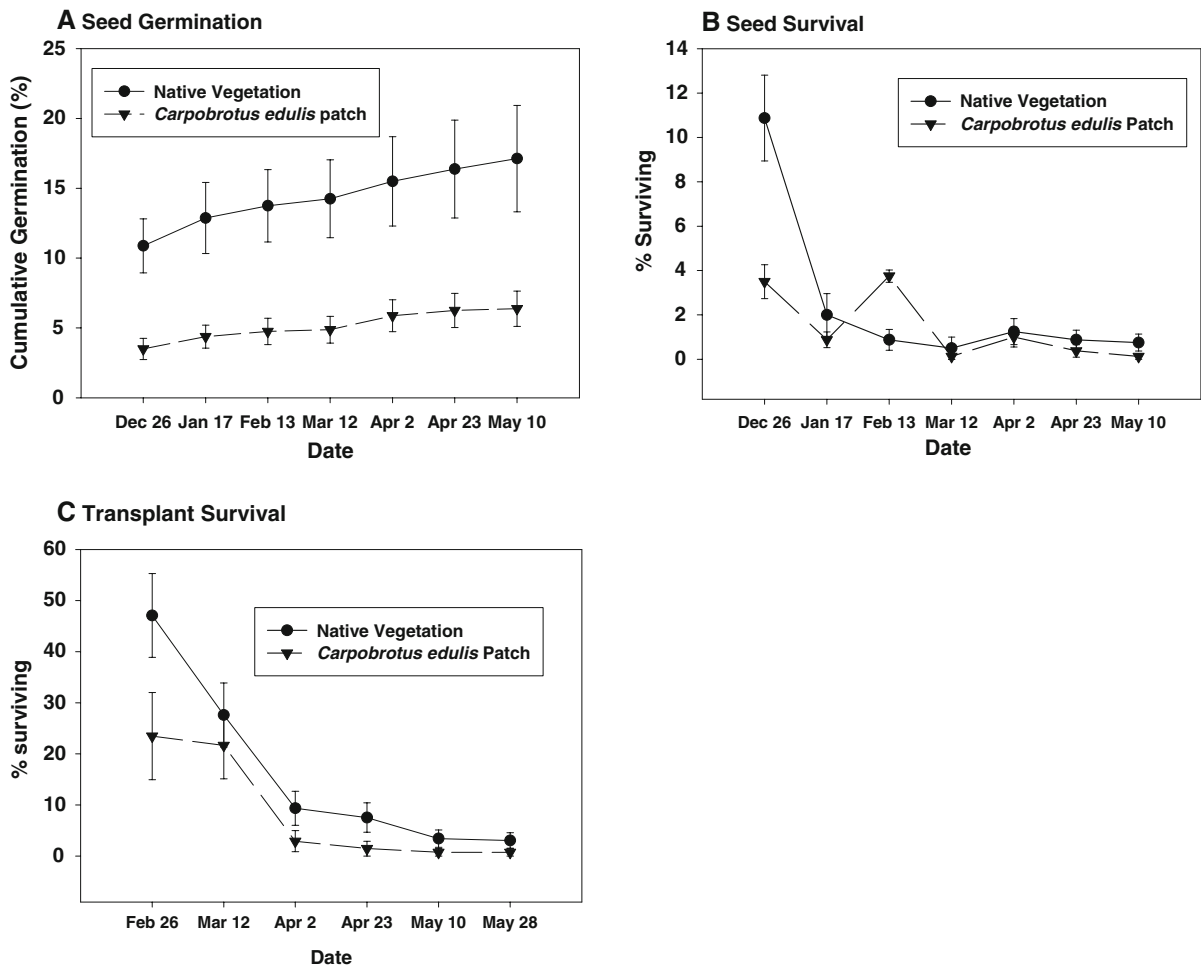


Fig. 1 Seed and transplant survival and seed germination of *G. millefoliata* in soil previously occupied by native vegetation and in soil previously occupied by *C. edulis*

Discussion

Effects on *Gilia millefoliata*

Carpobrotus edulis had strong negative effects on the germination, survival, growth, and reproduction of *G. millefoliata*. In addition, there were clear differences in soil characteristics between native vegetation and *C. edulis* invaded habitats. *Carpobrotus edulis* apparently modifies habitats as a mechanism of invasion, which consequently serves as an obstacle to habitat restoration. When *C. edulis* invades native California coastal habitats it “surrounds and grows over” the living vegetation and creates a monospecific stand within a few years (D’Antonio and

Mahall 1991). Over time *C. edulis* builds up a deep duff layer where chemicals from the dried succulent leaves combined with potential exudates from the live plant material may slowly leach into the soil, reducing soil pH which may affect germination, survival, growth, and reproduction of plants growing in that soil (C.M. D’Antonio and B.E. Mahall, unpublished).

When planted in soils previously occupied by *C. edulis*, *G. millefoliata* had large reductions in growth and reproduction, as well as more rapid mortality. In fact, most plants in *C. edulis* soils suffered mortality within 48 h of planting. For those plants that did survive in *C. edulis* soils, growth and reproductive characteristics were all suppressed relative to plants

Table 1 Repeated measures analysis of variance for vegetative and reproductive traits

Life-history character	Date			Treatment			Date by treatment		
	df	F	P	df	F	P	df	F	P
Seed cohort									
Germination rate	1.3, 49.6	9.17	0.000	1, 39	14.23	0.010	1.2, 47.9	1.43	0.244
Survival	1.8, 71.7	24.55	0.000	1, 39	10.00	0.030	1.8, 73.4	12.18	0.000
Number of leaves	1.2, 3.6	1.27	0.344	1, 3	0.49	0.533	1.2, 3.5	1.92	0.550
Leaf length	1.4, 4.3	1.23	0.354	1, 3	0.77	0.444	1.3, 3.9	2.37	0.206
Basal rosette	1, 4	0.31	0.607	1, 4	2.02	0.228	1, 4	0.11	0.757
Number of stems ^a				7	0.75	0.476			
Number of flowers	1, 4	2.43	0.194	1, 4	0.95	0.385	1, 4	2.43	0.194
Number of fruits	1, 7	0.06	0.811	1, 7	0.40	0.547	1, 7	0.74	0.426
Transplant cohort									
Survival	1, 22	20.91	0.000	2, 44.8	12.90	0.000	2.1, 45.7	5.22	0.000
Number of leaves	1.9, 55.6	6.39	0.001	1, 30	9.00	0.070	2.4, 70.9	1.70	0.184
Leaf length	3, 92.4	7.54	0.000	1, 30	26.62	0.007	3, 91.4	2.00	0.119
Basal rosette	1.1, 5.7	2.70	0.155	1, 5	8.41	0.034	1.1, 5.3	0.66	0.461
Number of stems	1.3, 6.6	6.56	0.034	1, 5	4.81	0.080	1.2, 5.8	1.70	0.248
Plant height	1, 5	12.23	0.017	1, 5	8.77	0.031	1, 5	0.02	0.896
Number of flowers	1.2, 4.7	4.18	0.098	1, 4	19.16	0.012	1.2, 4.6	1.90	0.236
Number of fruits	1, 5	0.06	0.811	1, 5	0.40	0.547	1, 5	0.80	0.412

^a Number of stems was a paired *t*-test in seed cohort

grown in areas never invaded by *C. edulis*, ultimately resulting in decreased seed production. Such suppressed growth and reproductive success will make it difficult to establish populations of *G. millefoliata* in restoration projects involving the removal of *C. edulis*. In addition, transplants were larger and produced more fruit than plants grown from seed; therefore transplanting may be the preferred planting strategy to insure higher reproductive success in the first year following restoration. Another strategy might be to compensate by over-seeding to overcome low fecundity or wait to plant *G. millefoliata* until the residual effects of *C. edulis* are diagnosed and the soil is ameliorated. Furthermore, the residual effects from *C. edulis* invasion may affect other species of native plants inhibiting successful restoration of previously invaded sites.

Mechanisms of invasion of *C. edulis*

Carpobrotus edulis interacts both directly and indirectly while invading and dominating native plant communities. During the invasion process, *C. edulis* directly competes with native plants for space,

suppressing the growth of mature native shrubs and the establishment of native seedlings (Albert 1995). Additionally, *C. edulis* directly competes with native plant species for water, reducing their growth, survival, and reproduction (D'Antonio and Haubensak 1998). *C. edulis* also appears to interact indirectly with native plants by altering soil chemistry (C.M. D'Antonio and B.E. Mahall unpublished), which may aid its invasion of native plant communities and hinder the reestablishment of native plants after its removal.

We found significantly lower pH and higher organic content in soils previously invaded by *C. edulis* in comparison to soils with native vegetation as did C.M. D'Antonio and B.E. Mahall (unpublished). The acidification of soils by *C. edulis* affects soil fertility which can inhibit nitrification and both decrease the availability and increase leaching of calcium and magnesium (D'Antonio and Haubensak 1998; C.M. D'Antonio and B.E. Mahall, unpublished). Although soil acidification occurs naturally over time with succession, it occurs on a shorter time scale with *C. edulis* invasion (C.M. D'Antonio and B.E. Mahall, unpublished). The residual effects of *C. edulis*

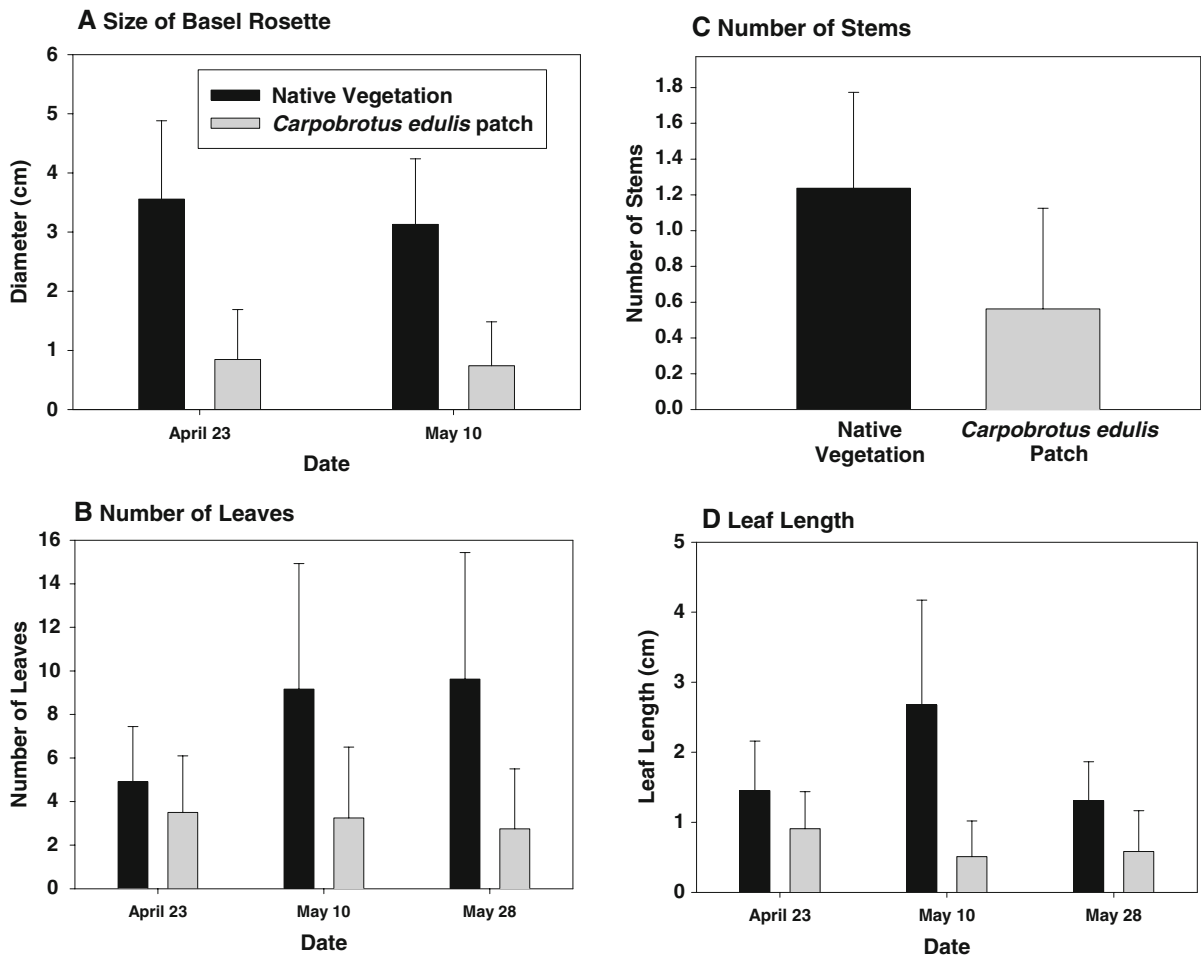


Fig. 2 Vegetative traits of *G. millefoliata* from seed cohort in soil previously occupied by native vegetation and in soil previously occupied by *C. edulis*. Bars and points depict

treatment means, and error bars represent ± 1 standard error. Legend in part A refers to all four subplots

originate at least in part from the dense mat of slowly decomposing roots, leaves, and stems of *C. edulis* that slowly leach into the soil, depleting nitrogen and lowering soil pH and Ca. C.M. D'Antonio and B.E. Mahall (unpublished) added *C. edulis* litter to sites that had not previously been invaded by *C. edulis* and achieved a significant reduction in soil pH and Ca, but not as great as that observed under mats of live *C. edulis*. Hence, the changes in soil chemistry we observed are likely to be caused at least in part by leaching from *C. edulis* litter. The recalcitrance of *C. edulis* tissue to decomposition could have evolved as a mechanism to facilitate recolonization when clones die back. C.M. D'Antonio and B.E. Mahall (unpublished) found the reduction of soil pH persisted for several years after removal of *C. edulis* suggesting

that, depending on the soil type, soil conditions would need to be ameliorated before restoration.

Besides its effects on soil pH and nitrogen availability, *C. edulis* may disrupt osmotic levels in the soil similar to *Mesembryanthemum crystallinum*, another member of the Aizoaceae family (Vivrette 1973; Vivrette and Muller 1977). *Mesembryanthemum crystallinum* retains salt in its leaf tissue and trichomes and releases the salt into the soil after leaf senescence. The leaching of salt into the soil beneath *M. crystallinum* changes soil osmotic levels and creates an osmotic gradient that draws water out of neighboring plants, resulting in desiccation and death. Since *C. edulis* invades habitats similar to *M. crystallinum*, it is possible that *C. edulis* indirectly competes with native plants by changing soil osmotic

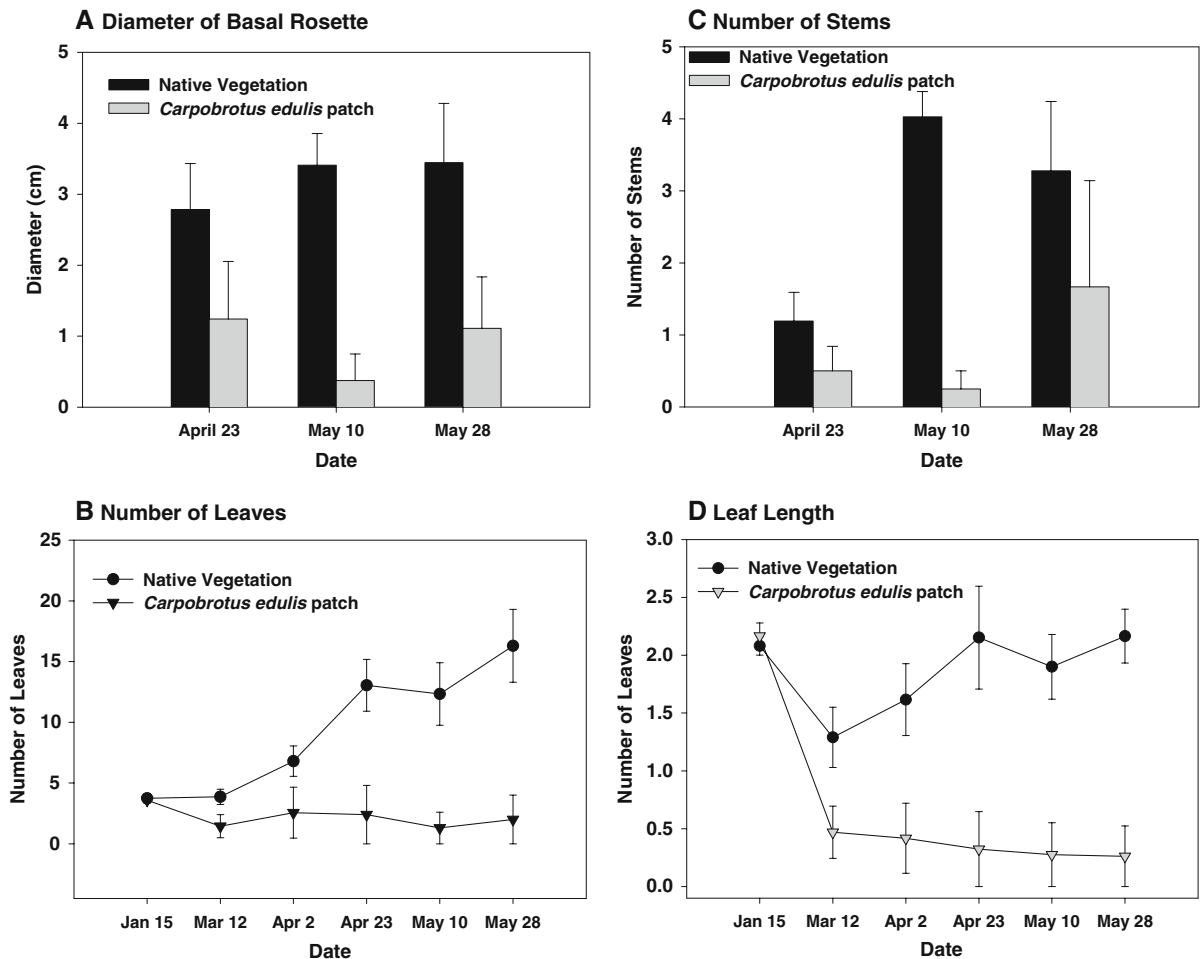


Fig. 3 Vegetative traits of *G. millefoliata* from transplant cohort in soil previously occupied by native vegetation and in soil previously occupied by *C. edulis*. Bars and points depict treatment means, and error bars represent ± 1 standard error

levels. C.M. D'Antonio and B.E. Mahall (unpublished) also found increased sodium levels and decreased nitrate levels in soils invaded by *C. edulis*. The decrease in nitrate affects the activity of nitrifying bacteria (Haynes and Goh 1978). Decreases in calcium from *C. edulis* invasion affect plant growth and cell function (C.M. D'Antonio and B.E. Mahall, unpublished).

Invasive species as ecosystem engineers

Other studies have shown that invasive species greatly influence vegetation composition and change soil chemistry. Mack and D'Antonio (2003) found that changes in vegetation composition, resulting from an exotic grass invasion, altered soil nitrogen

availability in a Hawaiian woodland. Brooks (2003) found that changes in soil nitrogen increased the dominance of an invasive annual in the Mojave Desert. Mitchell et al. (1999) found that areas invaded by *Betula* sp. showed changes in soil chemistry that made heathland restoration problematic. In addition to soil chemistry, invasive plants have been found to alter the soil biota (Reinhart et al. 2003; Reinhart and Callaway 2004) although this phenomenon is not yet well documented.

It is becoming more accepted that some invasive species, such as *C. edulis*, may actually change ecosystem function, acting as "ecosystem engineers" (Alvarez 1999; Alvarez and Cushman 2002; Hobbs and Humphries 1995; Mack and D'Antonio 2003; Vitousek and Walker 1989; Walker and Vitousek 1991).

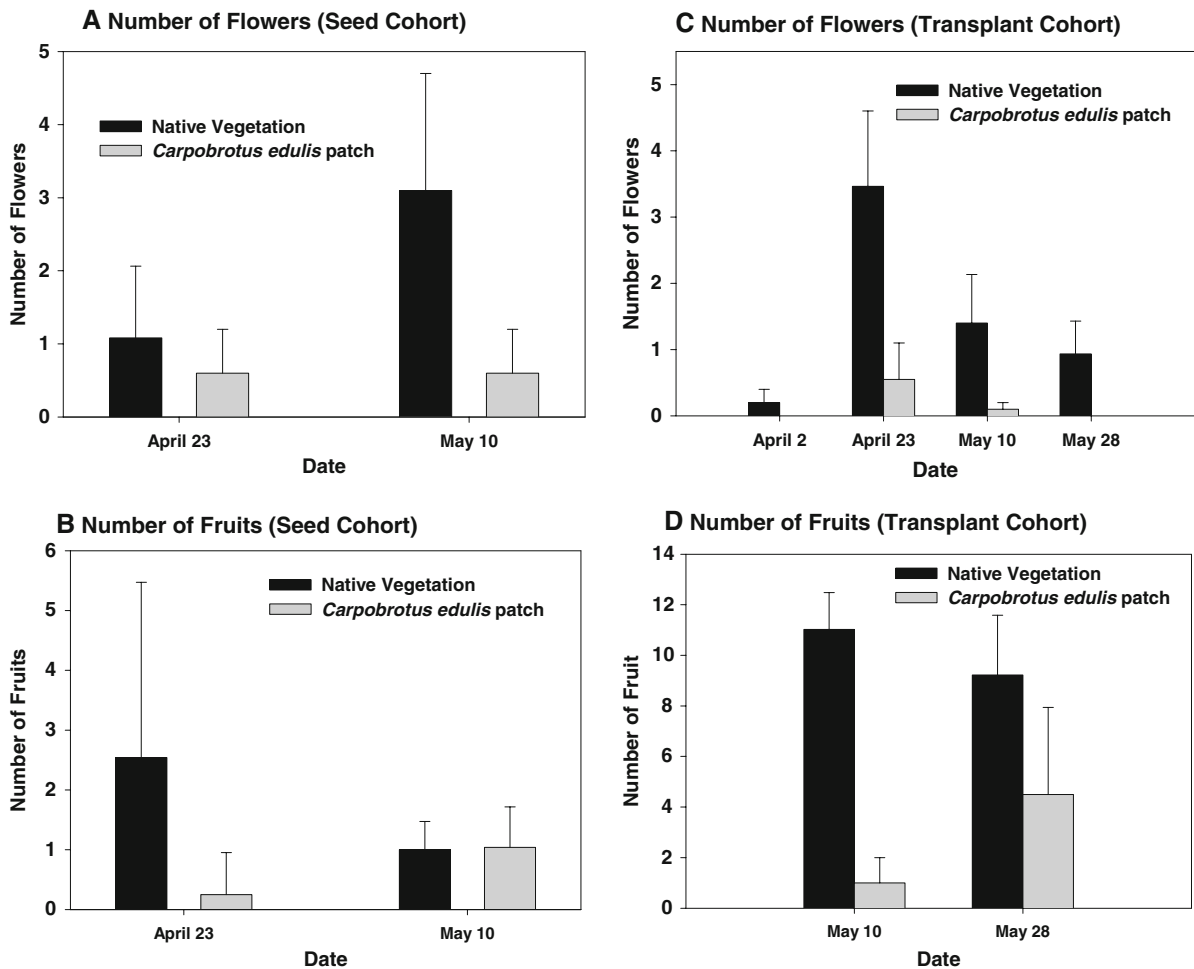


Fig. 4 Reproductive traits of *G. millefoliata* from seed and transplant cohort in soil previously occupied by native vegetation and in soil previously occupied by *C. edulis*. Bars and points depict treatment means, and error bars represent ± 1 standard error

Ecosystem engineers exert control over ecosystem processes and create conditions that favor their own survival, in this case, to the detriment of the native plant community. As we have seen with *C. edulis*, this can occur via multiple potential mechanisms. While this is an interesting ecological phenomenon, diagnosing the effects of ecosystem engineers can prove problematic when multiple mechanisms are working simultaneously. Restoration ecologists are recognizing the importance of addressing the soil environment in planning restoration projects (T. Griggs, personal communication). On sites that have a history of invasion by an ecosystem engineer it will be important to either diagnose and ameliorate residual effects in the soil prior to a successful restoration (Mack et al. 2001) or compensate for the additional mortality in the

planting design. These solutions may be hard to apply without detailed knowledge of the ecosystem changes wrought by the engineer and the biology of the native species of concern.

Future directions

It is important to isolate the mechanism or mechanisms by which *C. edulis* exerts control over soil pH and chemistry. It is also important to examine possible undocumented effects on soil microbial and invertebrate communities, as well as to mycorrhizae since *C. edulis* is not mycorrhizal. Furthermore, it would be useful to determine if the residuals effects of *C. edulis* are widespread among other species in coastal plant communities, and if

such residual effects are common among invasive plants in other ecosystems.

Acknowledgements We thank G. LeBuhn, V.T. Parker, M. Albert, K. Strathmann, and T. Griggs for their guidance; B. Manning and M. LaForce for help with soil analysis; P. Connors and R. Tinsman for access to the UC Bodega Reserve; Carla D'Antonio for providing unpublished data, and M. Andres, L. Berlin, S. Bernstein, B. Breckenridge, J. Caldwell, B. Clark, M. Hammer, C. Hartsough, L. Kough, J. Levy, C. Low, S. O'Neil, B. Porter, J. Rickman, and K. Upson for help with the fieldwork.

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