RESEARCH REPORT

Vegetation Response after Removal of the Invasive *Carpobrotus* Hybrid Complex in Andalucía, Spain

Jara Andreu, Esperanza Manzano-Piedras, Ignasi Bartomeus, Elías D. Dana and Montserrat Vilà

ABSTRACT

We evaluated the ecological success of the manual removal of *Carpobrotus* species, a putative hybrid complex of a South African perennial mat-forming plant, by comparing treated, noninvaded, and invaded plots across coastal Andalucía in southern Spain. As a measure of the management effectiveness, we quantified the density of *Carpobrotus* seedlings and resprouts in treated plots one year after treatment. Response of the plant community to removal was assessed by comparing native species richness, cover, diversity, and species composition among treatments. Removal greatly reduced to a great extent *Carpobrotus* density. However, successful control will require repeated hand-pulling treatments. Treated plots had a significant increase in species richness, especially annual plants, compared to invaded plots, but both had the same native plant cover and diversity. We found similar species composition between removal and noninvaded plots, indicating that revegetation is not necessary. Long-term monitoring is necessary to determine whether these observed patterns of community response are transient or stable through succession.

Keywords: alien plant, coastal dunes, management, plant diversity, Spain

Given the potential negative impact of non-native plants on native species, ecosystems, and human health and economies (Mack et al. 2000, McKinney and Lockwood 1999, McNeely 2001, Pimentel et al. 2005), control of invasive species has become an important challenge for land managers, as well as a common component of restoration efforts (Zavaleta et al. 2001, Smith et al. 2006). Since removing invasive species requires tremendous time and effort, the potential costs and benefits of managing invaders should be assessed. Such evaluations need to include measures of plant community response, not just such factors as funding and degree of community commitment.

The invasive South African succulent genus *Carpobrotus* (Aizoaceae) is an example of a non-native plant that often dominates plant communities in many Mediterranean regions of the world (D'Antonio and Mahall 1991, D'Antonio 1993, D'Antonio et al. 1993, Vilà et al. 2006). *Carpobrotus* species are crawling, mat-forming, succulent chamephytes (plants with buds near ground level, Raunkier 1977) easily recognized by their succulent, finger-shaped, and triangular-section leaves (D'Antonio 1990, D'Antonio 1993). Introgressive hybridization is very common (Vilà et al. 1998), occurring throughout coastal California between the non-native hottentot fig (*Carpobrotus edulis*) and the putative native sea fig (*C. chilensis*), leading to a high abundance of invasive hybrid morphotypes that compete aggressively with native plant coastal species (D'Antonio 1990, Albert et al. 1997, Vilà and D'Antonio 1998). In Spain, *Carpobrotus* species, known locally as uña de gato, may be hybrids between hottentot fig and Sally-my-handsome (*C. acinaciformis*).

Carpobrotus forms large mats on coastal rocks, cliffs, and sand dunes owing to its profuse clonal growth and long-distance dispersal by vertebrates (D'Antonio 1990, D'Antonio 1993, Traveset et al. 2008). The fleshy fruits bear a large number, often over a thousand, of small seeds (Bartomeus and Vilà 2009) that are eaten and widely dispersed by several mammals such as rabbits (D'Antonio 1990) and rats (Bourgeois et al. 2005). *Carpobrotus* has a long-lived seed bank that can remain viable in the soil for at least two years (D'Antonio 1990). *Carpobrotus* is able to grow from multiple axes, rooting where nodes contact the soil, and spreads radially at rates as high as one meter per year (Wisura and Glen 1993). It competes aggressively with native plant species, achieving high rates of space colonization, which suppresses the growth and establishment of other plants (D'Antonio and Mahall 1991, Albert 1995, Suehs et al. 2004, Vilà et al. 2006). Furthermore, it also interacts indirectly with native

Ecological Restoration Vol. 28, No. 4, 2010
ISSN 1522-4740 E-ISSN 1543-4079

vegetation by altering soil chemistry (Conser and Connor 2009).

It was first introduced as an ornamental plant into Europe around the 17th century at the Leyden Botanical Garden, the Netherlands, and since then it has been cultivated in other European botanical gardens (Fournier 1952). However, the progressive expansion and naturalization in the Mediterranean Basin started in the beginning of the 20th century (Sanz-Elorza et al. 2004). Nowadays, it is considered invasive in Europe (Albania, France, southern UK, Portugal, Italy, Greece, Montenegro, and the Canaries and other Mediterranean islands), northern Africa, southern Australia, New Zealand, and USA (California and Florida) (Sanz-Elorza et al. 2004).

In Spain, it was introduced intentionally for gardening, landscaping, and dune stabilization in the beginning of the 20th century, owing to its fast clonal growth, low water requirements, and showy, large flowers (Sanz-Elorza et al. 2004). Owing to the large extent of invaded areas in coastal communities, it is one of the most costly invasive species in Spain (Andreu et al. 2009). We conducted a regional survey to test the short-term effectiveness of *Carpobrotus* removal and native vegetation response in coastal sand dunes across Andalucía (southern Spain). In particular, we addressed the following two questions: 1) Has *Carpobrotus* been successfully controlled in our study sites one year after treatment? 2) Are native species richness, cover, diversity, and composition after *Carpobrotus* removal similar to reference communities?

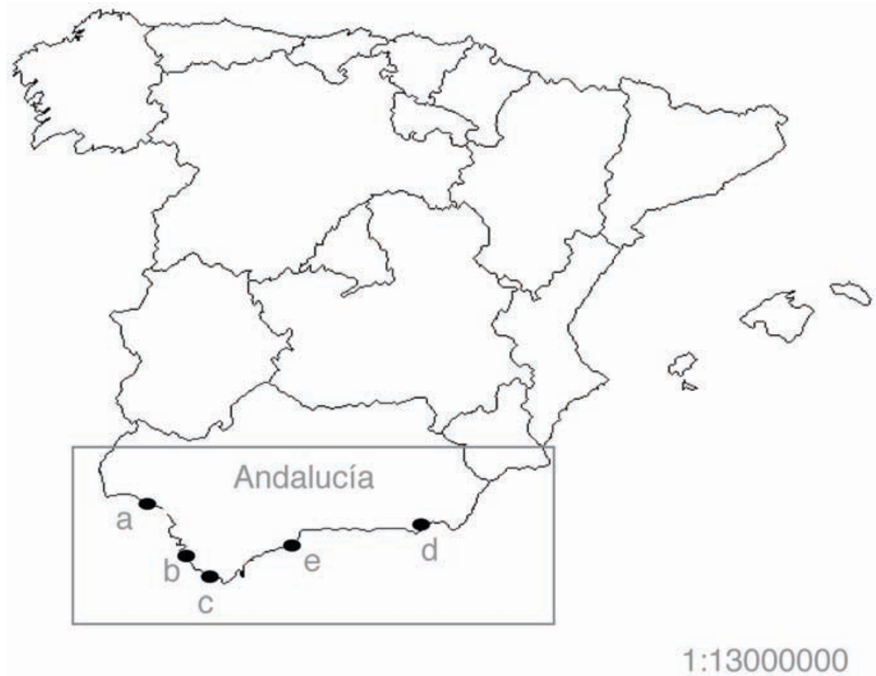

Figure 1. Six experimental sites where *Carpobrotus* was removed and monitored in Andalucía (southern Spain): a) Parador Mazagón (Huelva); b) Punta Camarinal (Cádiz); c) Torrelapeña (Cádiz); d) Artola 1 and 2 (Málaga); and e) Punta Entinas (Almería).

Study Sites & Experimental Design

The study was conducted in six coastal localities in four provinces of Andalucía where *Carpobrotus* had been removed the year before as part of the Andalusian Plan for Control of Invasive Species (Ortega Alegre and Ceballos 2006) (Figure 1). Overall, 300 ha had been treated by hand-pulling *Carpobrotus*. A total of 400 T of plant material was transferred to compost areas. This plant is readily cloned by rooting stem fragments that contain just one node; thus it was crucial to fully remove all individuals and also any buried stems (D'Antonio 1990).

These localities provided a representative sample of the entire Andalusian coast and the typical habitat types where *Carpobrotus* invades worldwide. The vegetation in the study sites is typical Mediterranean coastal shrublands dominated by chamephytes. The main species are European beachgrass (*Ammophila arenaria*, Poaceae), mastic tree (*Pistacia lentiscus*, Anacardiaceae), salvia cistus (*Cistus salviifolius*, Cistaceae), *Silene nicaeensis* (Caryophyllaceae), sweet alyssum (*Lobularia maritima*, Brassicaceae), silver sea stock (*Malcolmia littorea*, Brassicaceae), *Echium gaditanum* (Boraginaceae), and *Anacyclus radiatus* (Asteraceae). The climate is Mediterranean, with warm dry summers and mild, wet winters.

In order to determine effectiveness and vegetation responses to removal treatments, we established the following three treatments: 1) control plots (n = 18) where *Carpobrotus* was not present and there was no history of invasion and vegetation removal management; 2) invaded plots (n = 13) with high *Carpobrotus* cover (circa 70%) and no history of removal; and 3) treated plots (n = 46) where *Carpobrotus* was removed. The distance between plots within a locality ranged from 10 m to 50 m. This approach allowed us to distinguish changes caused by removal, since observing treatment plots over time may not allow differentiation of treatment effects from changes due to natural fluxes (Swab et al. 2008). Table 1 provides details for all six localities about location, habitat, most common plant species, and number and size of plots for each treatment.

The location, number, and size of experimental plots were decided with the aid of land managers one year after *Carpobrotus* removal. Owing to the idiosyncrasies of the removal treatments, caused mainly by differences in the size and spatial position of *Carpobrotus* patches and vegetation

Table 1. Site information for all six localities in an experiment to control *Carpobrotus* in coastal vegetation of Andalucía, Spain. Raunkier life-form of each species is indicated in parenthesis: P = Phanerophyte, T = Therophyte, C = Chamephyte, G = Geophyte, H = Hemicryptophyte.

			Number of Plots (size, in m)		
Locality (Province)	Habitat	Native Species	Invaded	Noninvaded (Control)	Treated
Punta Camarinal (Cádiz)	Rock shores, sea-cliffs, and stable dunes	*Anacyclus clavatus* (T) *Armeria pungens* (H) *Cyperus capitatus* (G) *Euphorbia terracina* (C)	5 (10 × 10)	0	5 (10 × 10)
Torrelapeña (Cádiz)	Shifting and stable dunes	*Ammophila arenaria* (H) *Lotus creticus* (C) *Malcolmia littorea* (C) *Medicago littoralis* (T)	5 (5 × 5)	0	5 (5 × 5)
Artola 1 (Málaga)	Shifting and stable dunes	*Helichrysum stoechas* (C) *Lotus creticus* (C) *Ononis natrix* (C) *Pistacia lentiscus* (P)	0	5 (5 × 5)	5 (5 × 5)
Artola 2 (Málaga)	Shifting dunes	*Cynodon dactylon* (H) *Lotus creticus* (C) *Medicago littoralis* (T) *Pancratium maritimum* (G)	3 (5 × 5)	3 (5 × 5)	3 (5 × 5)
Mazagón (Huelva)	Stable dunes	*Cistus salviifolius* (P) *Medicago littoralis* (T) *Paronychia argentea* (C) *Rumex tingitanus* (C)	0	5 (5 × 5)	10 (2.5 × 2.5)
Punta Entinas (Almería)	Stable dunes	*Cyperus capitatus* (G) *Helichrysum stoechas* (C) *Phagnalon saxatile* (C) *Reichardia tingitana* (T)	0	5 (2 × 10)	5 (2 × 10)

structure, plot sizes were not identical between sites. Plot sizes ranged from 2.5 × 2.5 m (6.25 m^2) to 10 × 10 m (100 m^2).

As a measure of the management effectiveness, density of *Carpobrotus* seedlings or resprouts (hereafter recruits) was determined within each plot as the number of recruits per square meter. *Carpobrotus* recruits were classified depending on their number of leaves in 4 different categories based on increasing branching patterns (<10 leaves, 10–24 leaves, 25–49 leaves, and >50 leaves). Recruits with fewer than 10 leaves were probably seedlings, and those with more than 50 leaves were probably remnants left in place unintentionally when removing the species.

Vegetation response to *Carpobrotus* removal was measured by the point-intercept method. Plant surveys were carried out at 20 cm intervals along the perimeter of the experimental plot by recording all plant species contacting an imaginary vertical line at each interval point. In each plot, we identified all species at 300–1,000 points, depending on the size of the plot. This method provided a record of species composition and abundance in each plot, a measure of plant cover, and, indirectly, an estimation of species richness and diversity.

Most taxa were identified to the species level, with grasses (Poaceae) being pooled, and then labeled as native or non-native and assigned to one of the five Raunkier (1977) plant life-forms. This plant classification system is based on the position of perennating buds in relation to the soil surface: chamephytes, geophytes (survival via underground food-storage organs such as rhizomes, tubers, or bulbs), hemicryptophytes (perennating buds at ground level and aerial shoots die-back), phanerophytes (perennating buds or shoot apices on aerial shoots) and therophytes (survival as seeds—annual or ephemeral plants).

We calculated the relative cover of individual plant species as the proportion of contacts of each species relative to the total number of plant contacts per transect, followed by the relative cover of non-native plants and each Raunkier life-form. Total native vegetation cover was calculated as the total number of contacts of all native species in relation to total number of contacts including bare ground, *Carpobrotus* and other non-native species, if present. We measured the species richness of natives and non-natives. Native diversity was calculated using the Shannon–Wiener diversity index (H), which is sensitive to rare species. All of these response variables were compared between control, invaded, and treated plots.

In order to determine whether, within a site, treated plots exhibited the same species composition as control plots, we calculated the Sorensen Similarity Index (*S*). This index ranges between 1 (same species composition) and 0 (most varied species composition).

Data Analysis

As data did not fit parametric test assumptions, differences in the density of the different leaf categories of *Carpobrotus* recruits were analyzed with Kruskal-Wallis tests. We also performed a multiple comparison test after Kruskal-Wallis to assess differences in leaf categories using the pgirmess package and the Kruskalmc function of R (vers. 2.6.2, R Foundation for Statistical Computing, Vienna, Austria).

Plot sizes differed between sites. Since species richness is dependent on the number of specimens counted and, therefore, on sample size, we transformed observed species numbers to expected values for a given sampling size by rarefaction curves (Sanders 1968, Hurlbert 1971, Gotelli and Colwell 2001) using the rarefy function in the vegan package of R. Rarefaction curves standardized the sampling in each of the plots to the minimum sample size (n = 300), which permits us to use rarefied data to make species richness and diversity comparisons (Gotelli and Colwell 2001). All analyses were with rarefied data.

Some response variables could not be normalized with data transformation. Therefore, differences in native species cover, richness, diversity, and functional group cover between treatments (invaded, control, and treated) were tested with a generalized linear mixed model (GLMM) with a Poisson distribution of errors and a logit link function (Crawley 2002). The logit link function ensures that all the fitted values are positive, while Poisson errors are recommended to deal with integer (count) variables, which are often right-skewed and have variances that are equal to their means (Crawley 2002). Treatment was included as the fixed factor, and site was included as a random factor to account for spatial autocorrelation. Models were run using the glmmPQL function of the MASS package in R. We also calculated the power of our analysis (β) to assess the probabilities of Type II error, given our small sample size. In order to test if *Carpobrotus* removal increased colonization by other non-native species, we compared non-native species cover among treated, control, and invaded plots using the Kruskal-Wallis test. Mean values ± standard errors are given throughout the text.

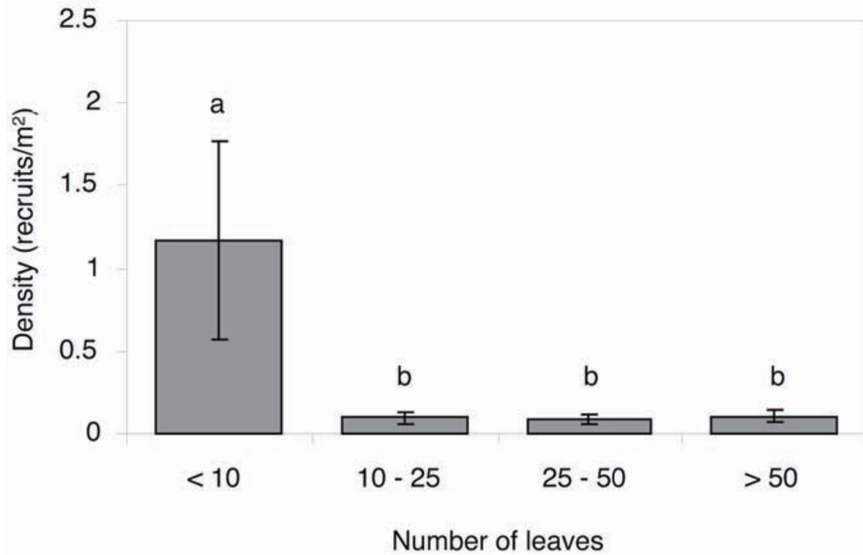

Figure 2. Mean (± SE) *Carpobrotus* recruit density one year after removal from six coastal sites in Andalucía, Spain, grouped by the number of leaves per recruit. Different letters indicate significantly different values (H = 8.74, df = 3, p = 0.032).

Results and Discussion

Effectiveness of Carpobrotus *Removal*

Recruit density in treated plots across sites averaged 0.13 ± 0.09 recruits per square meter. No reestablishment of *Carpobrotus* occurred in 52% of the treated plots. One of the sampled sites (Punta Camarinal) accounted for most of the observed *Carpobrotus* recruits (63%). Recruits with fewer than ten leaves were significantly more abundant than recruits with at least 10 leaves (Figure 2).

Low densities of *Carpobrotus* recruits one year after treatment indicated that short-term management had considerably reduced *Carpobrotus* presence, although it had not eradicated the species. Recruits with fewer than 10 leaves, probably seedlings, were the most abundant, which suggest the importance of the seed bank in the reestablishment capacity of *Carpobrotus*.

Native Plant Species Cover, Richness, and Diversity

The GLMM model revealed significantly higher values of rarefied species richness in treated plots (7.20 ± 0.40) than in invaded plots (6.64 ± 0.29; Figure 3a), indicating that *Carpobrotus* may have an impact on species richness by replacing native species in the communities it invades (Brandon et al. 2004, Hejda and Pyšek 2006, Hulme and Bremner 2006). However, we found no significant differences in total native species cover (Figure 3b) and diversity (Figure 3c). These results are consistent with other case studies (Ogden and Rejmánek 2005, Vidra et al. 2007, Swab et al. 2008, Pavlovic at al. 2009) and probably are due to a low abundance of new recruits and the short-term scale of our study. Neither did we find significant differences between treated and control plots with respect to plant cover, richness, and

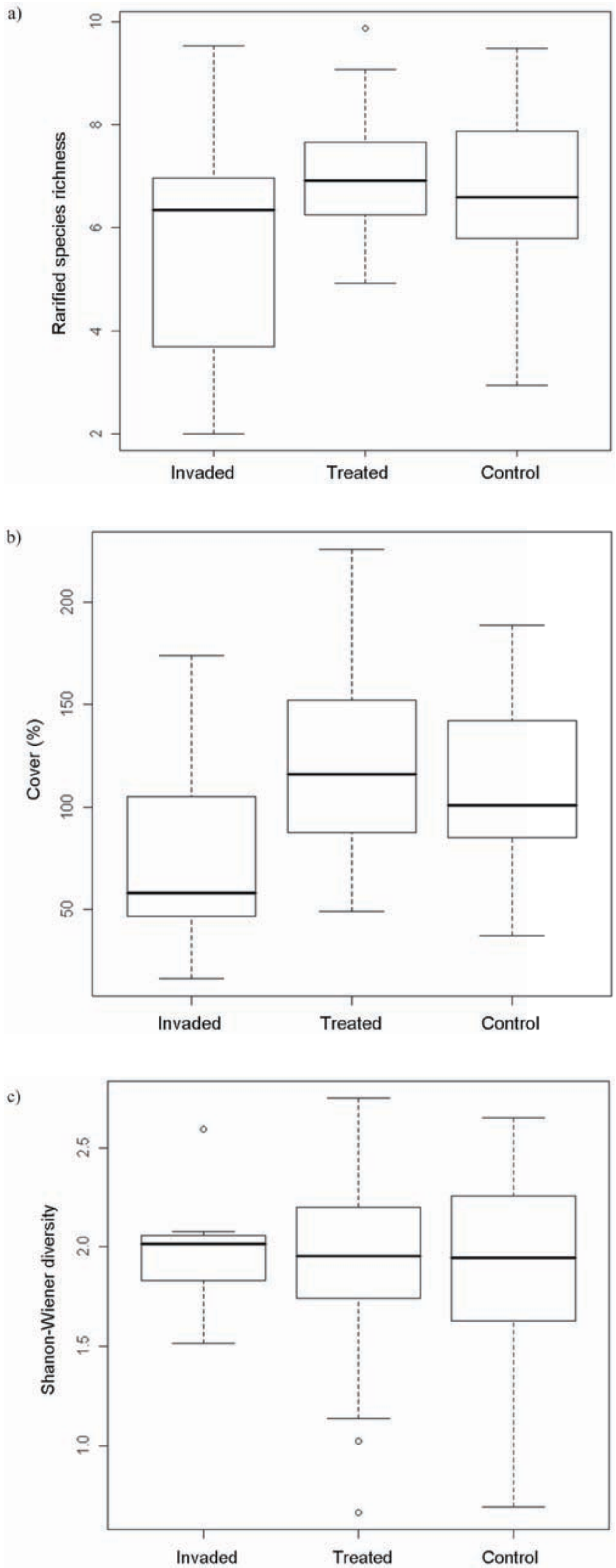

Figure 3. Boxplots of native plant response to *Carpobrotus* removal in invaded, control, and treated plots in six coastal sites in Andalucía, Spain, measured by a) rarefied species richness; b) total native species cover; and c) Shannon-Wiener species diversity. The box itself contains 50% of the data (75th percentile indicated by the upper edge, the median by the center line, and the 25th percentile by the lower edge), with outliers as open circles and maximum/minimum value at the terminus of the vertical line.

diversity, indicating that regeneration after *Carpobrotus* removal results in coastal dune communities similar to reference native communities. Nonetheless, we have to be cautious when interpreting these results, mostly in the case of total native species cover between treated and invaded plots ($p = 0.07$); the limited power of our statistical analysis ($\beta = 0.67$) could prevent us from detecting possible significant differences among treatments.

Native Species Composition

Despite the lack of changes in total native species cover and diversity, there were some changes in species composition. The Sorensen Similarity Index between control and treated plots was, on average, 0.77 ± 0.034, which provides additional support for the idea that regeneration after *Carpobrotus* removal results in coastal dune communities similar to reference native communities.

In Figure 4, percent cover of the different Raunkier functional groups have been compared between treated and control plots (Figure 4a) and between treated and invaded plots (Figure 4b). Only two of the five functional groups responded significantly to *Carpobrotus* removal. Cover of therophytes was significantly greater in treated plots than in control and invaded plots. This observed increase in annual plants suggests that the coastal dunes that were treated are in an early successional stage. Other studies have shown responses of annual plants following removal of invasive species (McCarthy 1997, Carlson and Gorchov 2004, Crimmins and McPherson 2008), which increases light, soil temperature, and resource availability, favoring the germination of species in the seed bank, such as annuals (D'Antonio and Meyerson 2002). However, cover of chamephytes (excluding *Carpobrotus*) was lower in treated plots than in control plots, and no significant differences were found between treated and invaded plots (Figure 4a, also see online appendix at uwpress.wisc.edu/journals/journals/er_suppl.html).

This can be explained by the fact that chamephytes grow more slowly than therophytes and need more time to reestablish. As no significant differences in other functional groups were found between treated and control plots, we expect that natural community dynamics will lead them to become more mature communities with a more homogeneous relative cover of different life forms.

Without taking into account graminoids, a total of 107 species were found in our plots. Of these, 63 were never found in invaded plots, 27 of which appeared only in treated plots and 11 only in control plots. Another 43 species out of the 107 were not present in control plots, and only 11 species were never found in treated plots, of which 7 were present only in control plots.

The relative cover of particular species differed between treatments (Figure 5). For example, water medick (*Medicago littoralis*), *Cyperus capitatus*, buckhorn plantain (*Plantago coronopus*), and whitebuttons (*Anacyclus clavatus*) were poorly represented in control plots and appeared very frequently in treated plots (Figure 5a).

On the contrary, creta trefoil (*Lotus creticus*), curry plant (*Helichrysum italicum*), *Helichrysum stoechas*, and *Rumex tingitanus* have higher relative cover in the control than in the treated plots (Figure 5a). In fact, neither *Helichrysum* was ever found in invaded plots, probably because they are associated with stable and undisturbed sites. There were also differences between invaded and treated plots. For instance, *Malcolmia littorea*, Geraldton carnation weed (*Euphorbia terracina*), and Engels gras (*Armeria pungens*) were more represented in invaded than treated plots, while *Cyperus capitatus* was as abundant in invaded as in treated plots (Figure 5b).

Only four of the 107 species were non-native. These were American century plant (*Agave americana*), Cape weed (*Arctotheca calendula*), salt heliotrope (*Heliotropium curassavicum*), and Bermuda buttercup (*Oxalis pes-caprae*). No significant differences were found between the total cover of non-native species in treated (4.78 ± 3.32), control (4.08 ± 2.25), and invaded (8 ± 6.33) plots (Kruskal-Wallis H = 0.95, df = 2, p = 0.620). Many studies have documented an increase in undesirable invasive species following disturbances (Burke and Grime 1996, Pickart et al. 1998, Zavaleta et al. 2001, Mason and French 2007, Crimmins and McPherson 2008). Such secondary invasions following control efforts can be problematic for ecological restoration (Hartman and McCarthy 2004, Hulme and Bremner 2006). The lack of such findings in our short-term study is, therefore, encouraging from a community management perspective.

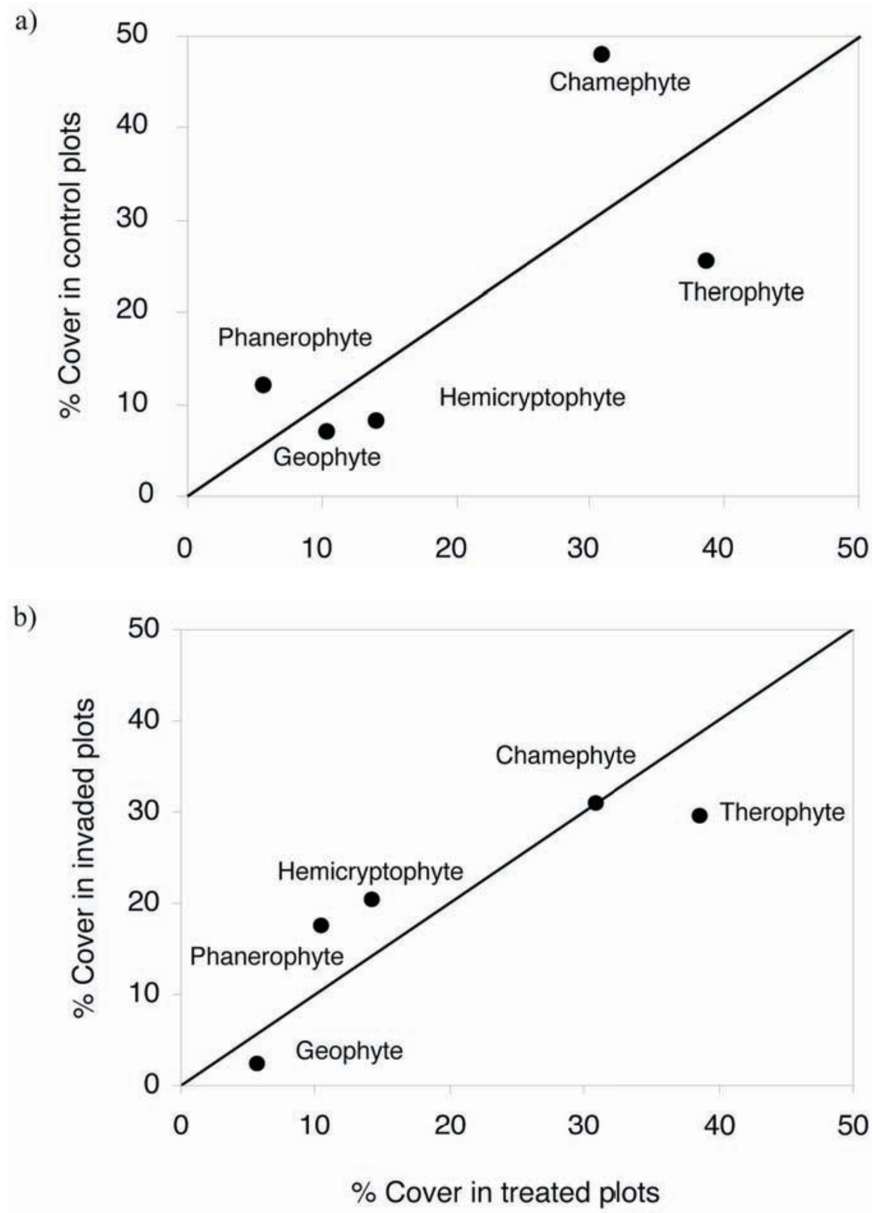

Figure 4. Raunkier life-form cover as a function of treated plots for a) control and b) invaded plots. Proximity to the line of unity indicates lack of difference from the treated plots for the life-form group.

Conclusions and Management Implications

When eradicating *Carpobrotus* it is important to remove any remnants, as any remains left in place soon

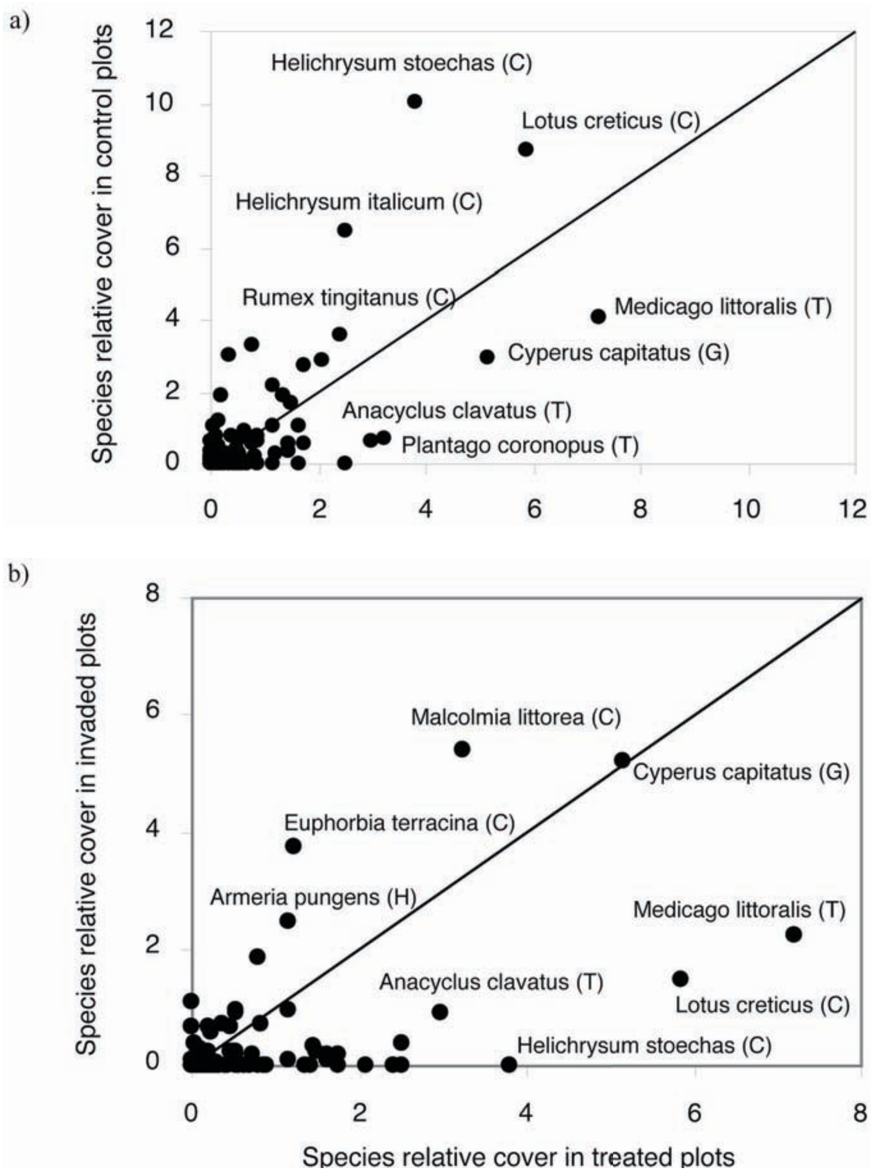

Figure 5. Individual native species relative cover as a function of treated plots for a) control and b) invaded plots. Raunkier life-form category is indicated in parentheses: T = Therophyte, C = Chamephyte, G = Geophyte, H = Hemicryptophyte.

become an active focus of regeneration (Fraga et al. 2006), which was demonstrated by the very low densities of large recruits, probably resprouts, one year after pulling (Figure 2). Our research revealed that hand-pulling greatly reduced *Carpobrotus*; however, successful control will likely require perseverance and a commitment to long-term planning, implementation, and monitoring (Pickart et al. 1998, Manchester and Bullock 2000). Moreover, regional eradication would be needed in order to prevent new invasions from neighboring populations (Pickart and Sawyer 1998).

Our findings suggest that native species could easily establish after *Carpobrotus* removal, particularly annual plants. However, with just one year of growth, these species are not able to occupy all bare ground (Díaz et al. 2003). In addition, comparisons between treated and control plots showed that management has resulted in coastal dunes with vegetation similar to reference native communities.

Some studies suggest that native species recovery after non-native species removal requires several years. This could also be true for *Carpobrotus* and, therefore, our findings for these communities should not yet be regarded as definitive, since the managed sites are still in an early successional stage. Although repeated sampling is necessary to determine whether any observed pattern of community response is transient or stable (Sax and Brown 2000), these findings can be applied to achieve cost-effective removal strategies that accomplish overall restoration goals.

Overall, our results revealed that removal of *Carpobrotus* is not facilitating invasion by non-natives and that recovery of native species is high. This suggests that if seeds of native species are present, natural reestablishment is possible. Natural regeneration would be cheaper in these coastal dune communities than seeding after *Carpobrotus* removal. Thus although planting desired native species is a potential scheme to facilitate the native recovery of a community, it is an expensive method and we do not consider it necessary in our case.

Acknowledgments

We thank Núria Gassó and Corina Basnou for statistical advice and useful comments. We also thank A.J. Pickart and two anonymous reviewers for helpful comments on a previous version of the manuscript. This study has been partially funded by the Consejería de Medio Ambiente de Andalucía (NET852690), the 6th Framework Programme of the European Commission's ALARM project (GOCE-CT-2003-506675; see www.alarmproject.net and Settele et al. 2005), and the MONTES project of CONSOLIDER (CSD2008-00040).

References

Albert, M.E. 1995. Morphological variation and habitat association within the *Carpobrotus* species complex in coastal California. MS thesis. University of California, Berkeley.

Albert, M.E., C.M. D'Antonio and K.A. Schierenbeck. 1997. Hybridization and introgression in *Carpobrotus* spp. (Aizoaceae) in California: I. Morphological evidence. *American Journal of Botany* 84:896–904.

Andreu, J., M. Vilà and P.E. Hulme. 2009. An assessment of stakeholder perceptions and management of noxious alien plants in Spain. *Environmental Management* 43:1244–1255.

Bartomeus, I. and M. Vilà. 2009. Breeding system and pollen limitation of two supergeneralist alien plants invading Mediterranean shrublands. *Australian Journal of Botany* 57:1–8.

Bourgeois, K., C.M. Suehs, E. Vidal and F. Médail. 2005. Invasional meltdown potential: Facilitation between introduced plants and mammals on French Mediterranean islands. *Ecoscience* 12: 248–256.

Brandon, A.L., D.J. Gibson and B.A. Middleton. 2004. Mechanisms for dominance in an early successional old field by the invasive non-native *Lespedeza cuneata* (Dum. Cours.) G. Don. *Biological Invasions* 6:483–493.

Burke, M.J.W. and J.P. Grime. 1996. An experimental study of plant community invasibility. *Ecology* 77:776–790.

Carlson, A.M. and D.L. Gorchov. 2004. Effects of herbicide on the invasive biennial *Alliaria petiolata* (garlic mustard) and initial responses of native plants in a southwestern Ohio forest. *Restoration Ecology* 12:559–567.

Conser, C. and E.F. Connor. 2009. Assessing the residual effects of *Carpobrotus edulis* invasion, implications for restoration. *Biological Invasions* 11:349–358.

Crawley, M.J. 2002. *Statistical Computing: An Introduction to Data Analysis Using S-Plus.* Chichester UK: Wiley.

Crimmins, T.M. and G.R. McPherson. 2008. Vegetation and seedbank response to *Eragrostis lehmanniana* removal in semi-desert communities. *Weed Research* 48:542–551.

D'Antonio, C.M. 1990. Seed production and dispersal in the non-native, invasive succulent *Carpobrotus edulis* (Aizoaceae) in coastal strand communities of central California. *Journal of Applied Ecology* 27:693–702.

___. 1993. Mechanisms controlling invasion of coastal plant communities by the alien succulent *Carpobrotus edulis*. *Ecology* 74:83–95.

D'Antonio, C.M. and B.E. Mahall. 1991. Root profiles and competition between the invasive, exotic perennial, *Carpobrotus edulis*, and two native shrub species in California coastal scrub. *American Journal of Botany* 78:885–894.

D'Antonio, C.M. and L.A. Meyerson. 2002. Exotic plant species as problems and solutions in ecological restoration: A synthesis. *Restoration Ecology* 10: 703–713.

D'Antonio, C.M., D.C. Odion and C.M. Tyler. 1993. Invasion of maritime chaparral by the introduced succulent *Carpobrotus edulis*. *Oecologia* 95:14–21.

Díaz, S., A.J. Symstad, F.S. Chapin, D.A. Wardle and L.F. Huenneke. 2003. Functional diversity revealed by removal experiments. *Trends in Ecology & Evolution* 18:140–146.

Fournier, P. 1952. *Dicotylédones*. Vol. 2 of *Flore illustrée des Jardins et des Parcs: Arbres, Arbustes et Fleurs de Pleine Terre.* Paris: P. Lechevalier.

Fraga, P., I. Estaun, J. Olives, G. Da Cunha, A. Alarcon et al. 2006. Eradication of *Carpobrotus* (L.) N.E. Br. in Minorca. IUCN Species Survival Commission case study report.

Gotelli, N.J. and R.K. Colwell. 2001. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4:379–391.

Hartman, K.M. and B.C. McCarthy. 2004. Restoration of a forest understory after the removal of an invasive shrub, Amur honeysuckle (*Lonicera maackii*). *Restoration Ecology* 12:154–165.

Hejda, M. and P. Pyšek. 2006. What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation? *Biological Conservation* 132:143–152.

Hulme, P.E. and E.T. Bremner. 2006. Assessing the impact of *Impatiens glandulifera* on riparian habitats: Partitioning diversity components following species removal. *Journal of Applied Ecology* 43:43–50.

Hurlbert, S.H. 1971. Nonconcept of species diversity: A critique and alternative parameters. *Ecology* 52:577–586.

Mack, R.N., D. Simberloff, W.M. Lonsdale, H. Evans, M. Clout and F.A. Bazzaz. 2000. Biotic invasions: Causes, epidemiology, global consequences and control. *Ecological Applications* 10:689–710.

Manchester, S.J. and J.M. Bullock. 2000. The impacts of non-native species on UK biodiversity and the effectiveness of control. *Journal of Applied Ecology* 37:845–864.

Mason, T.J. and K. French. 2007. Management regimes for a plant invader differentially impact resident communities. *Biological Conservation* 136:246–259.

McCarthy, B.C. 1997. Response of a forest understory community to experimental removal of an invasive nonindigenous plant (*Alliaria petiolata*, Brassicaceae). Pages 117–130 *in* J.O. Luken and J.W. Thieret (eds), *Assessment and Management of Plant Invasions*. New York: Springer-Verlag.

McKinney, M.L. and J.L. Lockwood. 1999. Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution* 14:450–453.

McNeely, J. 2001. Invasive species: A costly catastrophe for native biodiversity. *Land Use and Water Resources Research* 1(2):1–10.

Ogden, J.A.E. and M. Rejmánek. 2005. Recovery of native plant communities after the control of a dominant invasive plant species, *Foeniculum vulgare*: Implications for management. *Biological Conservation* 125:427–439.

Ortega Alegre, F. and G. Ceballos. 2006. Control de species exóticas invasoras: Actuaciones. *Medio Ambiente* 54:30–39. www.juntadeandalucia.es/medioambiente/contenidoExterno/Pub_revistama/revista_ma54/ma54_32.html

Pavlovic, N.B., S.A. Leicht-Young, K.J. Frohnapple and R.Grundel. 2009. Effect of removal of *Hesperis matronalis* (dame's rocket) on species cover of forest understory vegetation in NW Indiana. *American Midland Naturalist* 161:165–176.

Pickart, A.J., L.M. Miller and T.E. Duebendorfer. 1998. Yellow bush lupine invasion in northern California coastal dunes: I. Ecological impacts and manual restoration techniques. *Restoration Ecology* 6:59–68.

Pickart, A.J. and J.O. Sawyer. 1998. *Ecology and Restoration of Northern California Coastal Dunes.* Sacramento: California Native Plant Society.

Pimentel, D., R. Zuniga and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52:273–288.

Raunkier, C. 1977. Biological types with reference to the adaptation of plants to survive the unfavorable season. Chapter 1 *in* F.N. Egerton (ed), *Life Forms of Plants and Statistical Plant Ecology*. Reprint of the 1934 English translation from the original 1904 article (in Danish). New York: Arno Press.

Sanders, H.L. 1968. Marine benthic diversity: A comparative study. *American Naturalist* 102:243–282.
Sanz-Elorza, M., E.D. Dana and E. Sobrino. 2004. Atlas de las plantas alóctonas invasoras en España. Madrid: Dirección General para la Biodiversidad, Ministerio de Medio Ambiente.
Sax, D.F. and J.H. Brown. 2000. The paradox of invasion. *Global Ecology & Biogeography* 9:363–371.
Settele, J., V. Hammen, P. Hulme, U. Karlson, S. Klotz et al. 2005. ALARM: Assessing LArge-scale environmental Risks for biodiversity with tested Methods. *GAIA* 14:69–72.
Smith, R.G., B.D. Maxwell, F.D. Menalled and L.J. Rew. 2006. Lessons from agriculture may improve the management of invasive plants in wildland systems. *Frontiers in Ecology and the Environment* 4:428–434.
Suehs, C.M., F. Médail and L. Affre. 2004. Invasion dynamics of two alien *Carpobrotus* (Aizoaceae) taxa on a Mediterranean island: I. Genetic diversity and introgression. *Heredity* 92:31–40.
Swab, R.M., L. Zhang and W.J. Mitsch. 2008. Effect of hydrologic restoration and *Lonicera maackii* removal on herbaceous understory vegetation in a bottomland hardwood forest. *Restoration Ecology* 16:453–463.
Traveset, A., G. Brundu, L. Carta, I. Mprezetou, P. Lambdon et al. 2008. Consistent performance of invasive species within and among islands of the Mediterranean basin. *Biological Invasions* 10:847–858.
Vidra, R.L., T.H. Shear and J.M. Stucky. 2007. Effects of vegetation removal on native understory recovery in an exotic-rich urban forest. *Journal of the Torrey Botanical Society* 134:410–419.
Vilà, M. and C.M. D'Antonio. 1998. Hybrid vigor for clonal growth in *Carpobrotus* (Aizoaceae) in costal California. *Ecological Applications* 8:1196–1205.
Vilà, M., M. Tessier, C.M. Suehs, G. Brundu, L. Carta et al. 2006. Local and regional assessment of the impacts of plant invaders on vegetation structure and soil properties of Mediterranean islands. *Journal of Biogeography* 33:853–861.
Vilà, M., E. Weber and C.M. D'Antonio. 1998. Flowering and mating system in hybridizing *Carpobrotus* (Aizoaceae) in coastal California. *Canadian Journal of Botany* 76:1165–1169.
Wisura, W. and H.F. Glen. 1993. The South African species of *Carpobrotus* (Mesembryanthema - Aizoaceae). *Contributions to the Bolus Herbarium* 15:76–107.
Zavaleta, E.S., R.J. Hobbs and H.A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology & Evolution* 16:454–459.

Jara Andreu, Centre for Ecological Research and Forestry Applications, Universitat Autònoma de Barcelona, E-08193 Bellaterra, Barcelona, Catalonia, Spain, 34-954232340, Fax: 34-954621125, jara@creaf.uab.es

Esperanza Manzano-Piedras, Estación Biológica de Doñana (EBD-CSIC), Avda. Américo Vespucio, s/n, Isla de La Cartuja, 41092 Sevilla, Spain

Ignasi Bartomeus, Centre for Ecological Research and Forestry Applications, Universitat Autònoma de Barcelona, E-08193 Bellaterra, Barcelona, Catalonia, Spain.

Elías D. Dana, Programa Andaluz para el Control de Especies Invasoras, EGMASA–Consejería de Medio Ambiente, Junta de Andalucía, Avda. Américo Vespucio, 5, Isla de La Cartuja, 41092 Sevilla, Spain

Montserrat Vilà, Estación Biológica de Doñana (EBD-CSIC), Avda. Américo Vespucio, s/n, Isla de La Cartuja, 41092 Sevilla, Spain

---