Native plant community response to alien plant invasion and removal

Jara ANDREU and Montserrat VILÀ

Abstract

Given the potential ecological impacts of invasive species, removal of alien plants has become an important management challenge and a high priority for environmental managers. To consider that a removal effort has been successful requires both, the effective elimination of alien plants and the restoration of the native plant community back to its historical composition and function. We present a conceptual framework based on observational and experimental data that compares invaded, non-invaded and removal sites to quantify invaders' impacts and native plant recover after their removal. We also conduct a meta-analysis to quantitatively evaluate the impacts of plant invaders and the consequences of their removal on the native plant community, across a variety of ecosystems around the world. Our results that invasion by alien plants is responsible for a local decline in native species richness and abundance. Our analysis also provides evidence that after removal, the native vegetation has the potential to recover to a pre-invasion target state. Our review reveal that observational and experimental approaches are rarely used in concert, and that reference sites are scarcely employed to assess native species recovery after removal. However, we believe that comparing invaded, non-invaded and removal sites offer the opportunity to obtain scientific information with relevance for management.

Keywords

Exotic plants, impact, management, meta-analysis, plant abundance, reference plots, restoration, species richness

Introduction, Hypotheses and problems for Management

In many parts of the world, some alien plant species are threatening biodiversity by altering native community and ecosystem structure, function and dynamics (Vitousek et al. 1997; Parker et al. 1999; Mack et al. 2000; Ehrenfeld 2010; Powell et al. 2011). In addition, considerable socioeconomic and human welfare impacts have also been reported (Pimentel et al. 2005; Kettunen et al. 2009; Vilà et al. 2010). Given these ecological and socioeconomic impacts, management of alien plants has become an important challenge and a high priority for the conservation of native species and natural areas (Zavaleta et al. 2001; Smith et al. 2006; Swab et al. 2008).

In many natural areas invaded by alien plants, management practices include the removal of alien plants to reduce their population size or, if possible, to eradicate them (Manchester & Bullock 2000; D'Antonio & Meyerson 2002; Price & Weltzin 2003; Holmes et al. 2005). However, to consider that a removal effort has been successful requires both, the effective elimination of alien plants and the restoration of the native plant species community back to its historical composition and function (Zavaleta et al. 2001; SER 2002; Hulme 2006). In order to effectively control invasions, an assessment of the magnitude of their impacts is also required (Stinson et al. 2007). Thus, a comprehensive understanding of the success of alien plant management, would ideally involve observational and experimental comparative studies between invaded, non-invaded and removal sites, that asses the impacts of the alien plant and the resulting native species assemblage, after its removal.

Basically, three different types of comparisons can inform us on the magnitude and direction of changes of the native plant community with invasion or the removal of a particular invasive species (Figure 1). Each comparative approach will provide information about the invasion and the removal success and will give answer to different research questions or hypothesis. So far, there are many observational studies comparing

 DOI: http://dx.doi.org/10.3391/mbi.2011.2.1.08

invaded communities to their non-invaded reference counterparts (Levine et al. 2003; Comparison A in Figure 1). This approach has been used to infer alien species impact on the native community such as reduced plant richness or diversity, or reduced seedling recruitment (Gaertner et al. 2009). However, it does not demonstrate causality as the observed outcome can be confounded with site differences between invaded and non-invaded plots.

Other studies have conducted field removal experiments to eliminate the invader and compare the sites where the invasive species have been removed with invaded (unmanaged) sites (e.g. Ogle et al. 2000; Morrison 2002; Hejda & Pysek 2006; Hulme & Bremner 2006; Comparison B in Figure 1). These comparisons present substantial opportunities for demonstrating the impact of plant invasions on the native community (Díaz et al. 2003). If the invasive species is competing with native species, we expect higher richness in removal sites than in invaded ones, given that the native vegetation would be released from the use of resources by the invader. However, the outcomes of these comparisons can be confounded with short-term, local scale disturbance effects after removal. In general, these studies are purely experimental to test impact and do not have a management perspective because they do not measure the success of the removal effort.

Many times removal of alien species alone does not always lead to the reestablishment of the desirable native communities

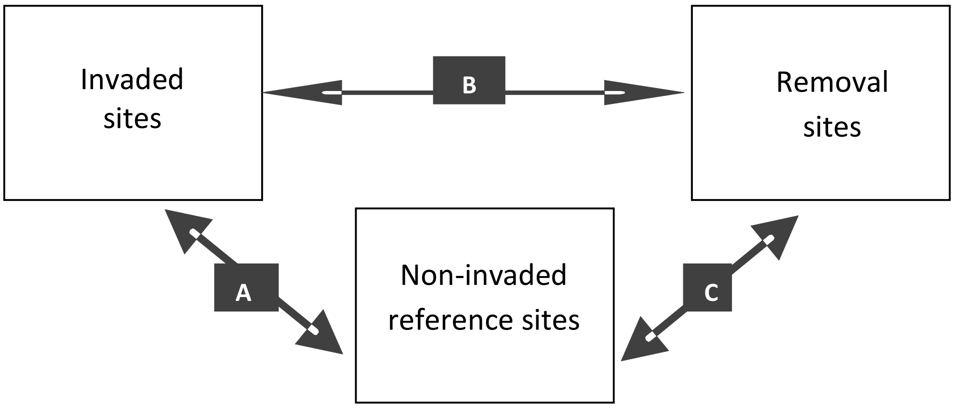

Figure 1: Schematic diagram that summarize the different types of comparison that can be used to assess the impact of an invader and the recovery of the native community after alien plant removal. (A) Observational approach, can provide a potential assessment of impacts (B) Experimental approach, can provide a causal assessment of impact, and (C) Experimental approach, provides an assessment of native community recovery after removal of the invader.

Resumen

Debido a los impactos ecológicos y socioeconómicos causados por las plantas invasoras, su gestión se ha convertido en un desafío importante y una prioridad para los gestores medioambientales. Para considerar exitosa la eliminación de una planta invasora es necesaria tanto la eliminación efectiva de la planta exótica como la restauración de la comunidad vegetal nativa. Se presenta un marco conceptual basado en datos observacionales y experimentales, que compara sitios invadidos, sitios de referencia (no invadidos y no tratados) y sitios donde se ha eliminado una planta invasora. Mediante un meta-análisis se han evaluado cuantitativamente los impactos de las plantas invasoras y las consecuencias de su eliminación en la comunidad de plantas nativas, en una gran variedad de ecosistemas de todo el mundo. Nuestros resultados confirman que la invasión por plantas exóticas es responsable de una disminución local en la riqueza y abundancia de especies nativas. También demuestran que después de la eliminación, la vegetación nativa tiene el potencial para recuperar su composición histórica y sus funciones. Finalmente, esta revisión bibliográfica ha revelado que las tres comparaciones expuestas rara vez se usan simultáneamente, y que los sitios de referencia apenas se utilizan para evaluar la recuperación de las especies nativas después de la eliminación. A pesar de ello, creemos que el uso de estas comparaciones para evaluar los impactos de la planta invasora y monitorizar las consecuencias de su eliminación es extremadamente útil para asegurar el éxito de las medidas de gestión.

Palabras clave

Plantas exóticas, impacto, gestión, meta-análisis, abundancia de plantas, parcelas de referencia, restauración, riqueza de especies.

because land-use history, seed bank availability and disturbance regime can all strongly influence the outcome of the removal effort, which might not accomplish the preferred level of recovery (Partel et al. 1998; Zavaleta et al. 2001). Thus, an increasingly common goal of ecosystem restoration is to assess whether removal sites may achieve the high levels of plant species, trait and functional group diversity found in remnant intact sites (Mason & French 2007; Stinson et al. 2007; Truscott et al. 2008). In this sense, the identification of non-invaded and non-managed reference sites and their comparison with removal sites may be crucial to assess the success of the removal effort (Chapman & Underwood 2000; Comparison C in Figure 1). A successful removal strategy would be the one in which vegetation recovers similarly to a reference community in species composition and richness (McCoy & Mushinsky 2002). This type of comparisons can be also valuable to evaluate eventual negative side-effects of removal techniques such as the proliferation of other alien species or soil erosion disturbances (Álvarez & Cushman 2002; Truscott et al. 2008).

In this study, we conducted a global literature review to quantitatively evaluate the impacts of invaders and the consequences of their removal on the native plant community, across a variety of ecosystems around the world. The response of the native plant community to removal may be an indicator of the success of the management efforts. We evaluate the magnitude and direction of change of two response variables, native plant species richness and abundance, to alien plant invasion and removal, using a meta-analytical approach (Rosenberg et al. 2000). We focused on native species richness and abundance as indicators of community level response because these are the most commonly used response variables across all reviewed papers. Meta-analysis is a technique of quantitative research synthesis that can provide a more robust method than traditional story-telling or vote-counting literature review. It also provides the opportunity to explore heterogeneity among studies and identify large-scale patterns across species and geographic regions (Steward 2010; Harrison 2011).

The framework described in Figure 1 is used as a guide to answer the following questions: (1) Does alien plant invasion decrease native species richness and abundance (Comparison A)? (2) Do alien plant removal increase native species richness and abundance (Comparison B)? and finally, (3) Does removed sites resemble to reference non-invaded sites (Comparison C)?

Methods

Literature search

To compile quantitative evidence of the response of the recipient plant community to alien plant invasion and removal, we searched for papers on the ISI Web of Knowledge (www.isiwebofknowledge.com) database on July 2009, with no restriction on publication year, using the following search term combinations: (Invasive plant OR non-native plant OR exotic plant OR alien plant) AND (restor* OR removal OR clear* OR success OR response OR rehabilitat*) AND (uninvaded OR non-invaded) OR (impact* OR invasion OR effect). Additional literature was obtained screening the reference lists from all retrieved papers. An initial set of 120 studies was evaluated in order to assess their potential for meeting the selection criteria for inclusion in the review. Studies that did not meet these criteria were omitted. The first criterion was that the focus of the study should be a particular terrestrial or riparian alien plant species, excluding all papers involving strict aquatic species. Second, we decided to include only studies in which native richness or native abundance (i.e. native cover, native density and native biomass) after invasion or removal was assessed. Studies reporting on other community indicators such as diversity, evenness, non-native richness and abundance, were too scarce for some comparisons. We also rejected articles dealing with total species richness, total diversity or total abundance, because our main goal was to focus on the response of the native community. Finally, for those articles involving alien plant removal, we discarded chemical and biological control managements; therefore, we confined our selection of studies to mechanical or manual removal techniques.

Data extraction

A total of 39 published papers involving 34 taxa met our criteria (Appendix I). Some studies investigated several species, at different sites or at different habitats, what left us with 132 cases for the meta-analysis. Eighty-seven of these cases compared native richness or abundance between non -invaded and invaded sites, 33 between removal and invaded sites and 12 between removal and non-invaded sites.

Among the alien plant species evaluated, perennial herbs (45 cases), shrubs (33 cases) and annual grasses (24 cases) were more often represented than the other life-forms. Most of the studies (36%) have been conducted in North America (36%), Europe (33%) and Australia (24%), being Mediterranean (34%) and temperate regions (30%) the most investigated.

For each response variable (i.e. native plant species richness and abundance) we recorded sample size (N), mean ( ) and statistical variation (usually SE or SD) in invaded, non-invaded and removal plots for each study. These data were extracted directly from tables or from graphs using the DATATHIEF II software (B. Thumers; http://www.datathief.org) or, in some cases, also by measuring mean and statistical variation 'manually' using a ruler. For other studies, we obtained data directly from the corresponding authors.

Meta-analysis

As a unit of analysis (i.e. the unit for calculation of effect sizes and their variances), we used pairs of plots of the following comparisons: non-invaded versus invaded (Comparison A; Figure 1), invaded versus removal (Comaprison B; Figure 1), removal versus non-invaded (Comparison C; Figure 1). For each entry of the dataset we calculated the natural log of the response ratio (Ln R) as a measure of the magnitude and direction of the effect size. Ln R is the ratio of a variable in the experimental (e) group to that of the control (c) group (Rosenberg et al. 2000). From each pair of mean values ($\overline{X}$) the effect size was calculated as:

$$\ln R = \ln\left(\frac{\overline{X}^e}{\overline{X}^c}\right)$$

where e is the experimental group and c is the control group (see below for selection of experimental and control groups). The variance of Ln R, V_{LnR} was calculated as:

$$v_{\ln R} = \frac{(s^e)^2}{N^e\left(\overline{X}^e\right)^2} + \frac{(s^c)^2}{N^c\left(\overline{X}^c\right)^2}$$

where *S* is the pooled standard deviation and N is the number of replicates per treatment.

Ln R is a unit-free index which ranges from -∞ to +∞ and estimates the effect size as a proportional change. As in classical statistical analysis, the highest effect sizes are from those studies showing large differences between control (i.e non-invaded) and experimental (i.e. invaded or removal) plots and when there is low variability within plots. Zero Ln R values imply no difference in the variable measured between control and experimental plots; positive and negative Ln R values imply a general trend following treatment (invasion or removal) for an increase and decrease, respectively. Ln R calculations and statistical analysis were conducted with the MetaWin v2.1 Software (Rosenberg et al. 2000).

The following effect sizes for native species richness and abundance were calculated:

- Comparison A: Non-invaded (control) vs. invaded (experimental) plots
- Comparison B: removal (control) vs. invaded (experimental) plots
- Comparison C: non-invaded (control) vs. removal (experimental) plots.

We tested whether effects sizes across studies were homogeneous, using the Q_{total} statistic based on a chi-squared test. A significant Q_{total} indicates that the variance among effect sizes is greater than that expected by sampling error alone (i.e. effect sizes are not equal across studies).

For each grouping category, we calculated the cumulative effect size (R+) and the 95% CI across the sample of studies, with information on the response variable. Data were analysed using random-effects models (P_{random}) which are preferable in ecological data synthesis because their assumptions are more likely to be satisfied (Rosenberg et al. 2000). A cumulative effect size (R+) is considered significant (i.e. no change with invasion or removal) when its 95% CI do not overlap zero. Confidence intervals were calculated using bias-corrected bootstrap resampling procedures (Adams et al. 1997; Rosenberg et al. 2000). The mean percentage of change in a response variable was estimated as (e^{R+} -1) x 100 (Table 1, Appendix I).

Results and Discussion

In general, across all studies, results were quite homogeneous as indicated by p-values associated to Q_{total} higher than 0.05 in most cases (Table 1). Therefore, the magnitude and direction of the effect sizes did not vary significantly across studies, making the generality of the results highly consistent.

The meta-analysis revealed an overall significant decline of native species richness and abundance after invasion. Invaded plots had lower native species richness and abundance than usually adjacent reference non-invaded plots (Fig. 2, Table 1). The same trend was found when comparing invaded versus removal plots (Fig. 2, Table 1). On average, invaded plots contained 23% fewer native species than non-invaded plots and 30% less species than removal plots (Table 1). Invaded plots were 41% less abundant in

Type of comparison	Response variable	Q_t	*P*-value	R+	df	95%-CI	% of change
Invaded vs. non-invaded	Native richness	73.40	0.008	-0.267	47	-0.363 to -0.171	-23.45
	Native abundance	46.93	0.152	-0.524	38	-0.756 to -0.292	-40.77
Invaded vs. removal	Native richness	9.60	0.651	-0.354	12	-0.557 to -0.152	-29.83
	Native abundance	89.48	**0.000**	-0.361	19	-0.515 to -0.207	-30.32
Removal vs. non-invaded	Native richness	9.43	0.223	0.005	7	-0.189 to 0.198	0.47
	Native abundance	9.03	0.108	-0.007	5	-0.563 to 0.549	-0.68

Table 1: Total heterogeneity (Q_t) with indication of P-values, mean effect sizes (R+), degrees of freedom (df) and 95%-CI for each response variable and type of comparison. Significant results of Q_t are in **bold**. The percentage of change of each response variable with invasion or removal is also indicated. See text for a detailed description of statistical analysis.

native species than non-invaded plots and 30% less abundant than in removal plots (Table 1). For none of the response variables evaluated and none of these comparisons, the CI of the mean effect size overlapped zero (Fig.2). Therefore, our review supports that alien plant species has a negative impact on species richness and abundance by replacing native species in the communities they invade (Vilà et al. 2011). Nonetheless, further research should concentrate on the mechanisms underlying alien plant invasions in order to investigate which are the factors that are ultimately responsible for this decline of native species richness and abundance (Levine et al. 2003).

Moreover, the CI for each variable overlapped between Comparison A and B suggesting that the magnitude of the impact is not significantly different between observational and removal studies. That is, whether the control plot is a non-invaded community or a community where the invader has been removed does not have an influence on the magnitude of the impact. This result indicates that although observational studies do not demonstrate causality they can be used as surrogates to test for impact. The extended time frame associated with observational studies counterbalances the logistic and man-power requirements for removal experiments, and the usually short-term monitoring afterwards (Sol et al. 2008).

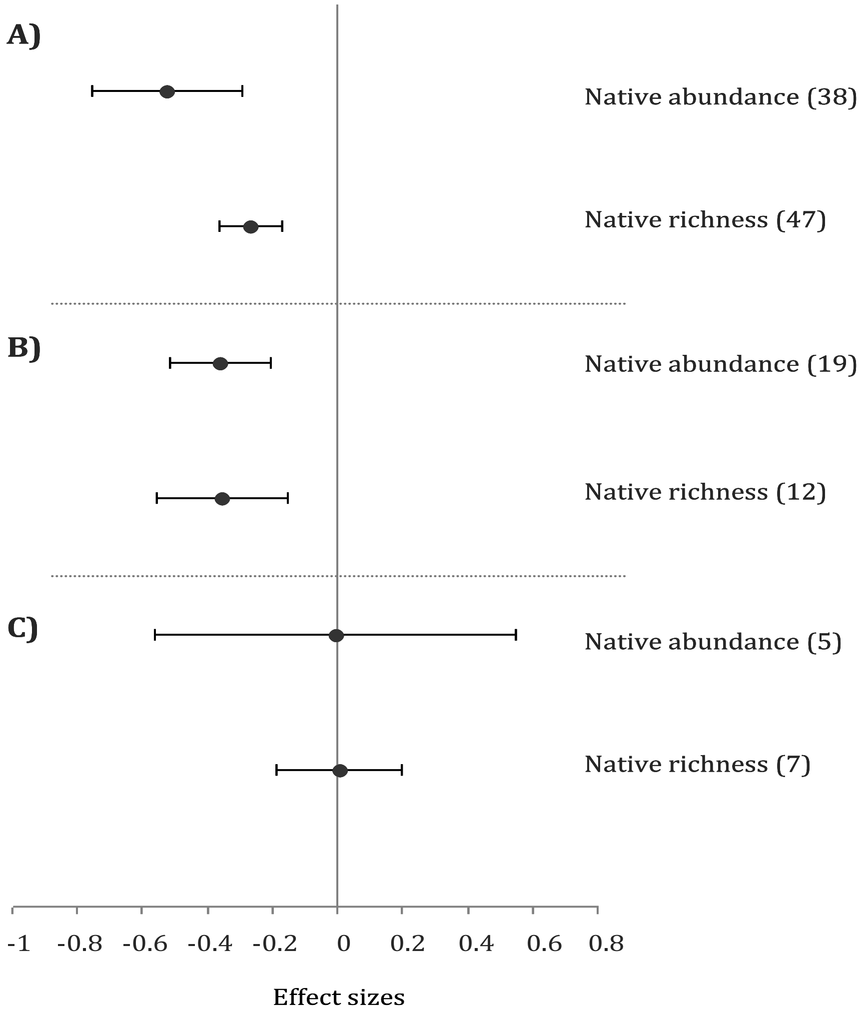

Figure 2: Mean effect size (R+) of differences in native species richness and abundance between A) invaded versus non-invaded, B) invaded versus removal and C) removal versus non-invaded plots. These comparisons are described in Fig. 1. The bars around the means denote bias-corrected 95%-bootstrap confidence intervals. A mean effect size is significantly different from zero when its 95% confidence interval do not overlap zero. Positive and negative mean effect sizes indicate, respectively, an increase or decrease of the response variable following treatment (invasion in comparisons A and B, and removal in comparisons C). The sample sizes are given next to each variable.

When comparing removal and non-invaded sites we found that after removal, native species richness and abundance reached similar values than in reference non-invaded plots as indicated by R+ values close to zero and the CI of the mean effect size overlapping zero (Fig. 2, Table 1). The magnitude and direction of the native plant community response following removal indicates that restoration of the vegetation to a pre-invasion state is feasible (Truscott et al. 2008). However, one of the consequences of invasive species removal may be to facilitate the proliferation of other invasive species (Álvarez & Cushman 2002; Ogden & Rejmánek 2005; Hulme &

Bremner 2006; Truscott et al. 2008), and to cause soil and vegetation disturbance (D'Antonio et al. 1998; Zavaleta et al. 2001). Thus, although removal increases species richness bringing the native plant community closer to non-invaded sites, an increase in the occurrence and abundance of another non-native undesired species may also occur and should be assessed. None of these side-effects could have been evaluated in this review because in the vast majority of reviewed papers information about soil and vegetation disturbance was not available and only 3 cases (Holmes et al. 2000; Mason & French 2007; Blanchard & Holmes 2008) specified non-native richness and abundance in removal and non-invaded reference sites, which resulted in the exclusion of these variables from the analysis. Nonetheless, the effective re-establishment of native species, suggested in this review, may increase the resistance of the site to re-invasion or to colonization by other non-native species.

Despite the complementarily between the three comparisons they have been rarely used in concert (only 6 papers). In fact, we found only 12 cases in the literature, meeting our inclusion criteria, which compared removal sites with non-invaded reference sites. This can be explained by the fact that, unfortunately, non-native species are often so widespread by the time they are noticed that a practical limitation of these comparisons is that such comparable non-invaded sites may be extremely rare or in some cases simply impossible to find.

Since removing invasive species requires tremendous time and effort, the potential costs and benefits of managing invaders should be assessed to better inform management and restoration decisions. Thus, it is imperative to determine which invaders have larger effects and to understand the conditions under which restoration projects are likely to succeed. Post-removal monitoring, on both the target invasive species and the invaded community, is extremely helpful because it allows documenting the success of control and provides the opportunity to restrain negative effects before they become severe (Zavaleta et al. 2001; Andreu et al. 2010). Using removal methods without thoroughly testing their effectiveness and non-target effects can lead to routine implementation of inappropriate techniques. Moreover, it is crucial to evaluate if the native vegetation is recovering in order to be able to determine whether further intervention is necessary such as active post-removal revegetation plans. The extent to which post-removal revegetation is required depends on the biology of the invasive species, the magnitude of the invasion and the length of time that the invasive species have been present (D'Antonio & Meyerson 2002).

We think that the conceptual framework presented here (Figure 1) may provide guidance for managers and can optimize restoration success. A holistic approach, based on observational and experimental studies, that evaluates both, the influence of invaders and the consequences of their removal, should be more frequently used in concert. This approach may allow managers to gain a more complete picture of the magnitude and direction of changes after its control measures, giving them an idea of the impact caused by an invasive species as well as the capacity of the native community to achieve the desired target state. The use of this comparative monitoring poses challenges to ecologists in deciding how to choose reference sites, how to select response variables, and how to sample in a way that minimizes the influence of confounding factors (Wilkins et al. 2003).

Conclusions

We have presented a conceptual framework based on observational and experimental data that compare invaded, non-invaded and removal sites to quantify invaders' impacts and native plant recover after their removal. We have quantitatively reviewed the impacts of alien plant invasions on native plant community and its response to their removal. Our results have confirmed that the invasion by alien plants is responsible for a marked local decline in native species richness and abundance, posing significant impacts to the native community. On the other hand, our quantitative approach also provides evidence that after removal, native vegetation has the potential to recover to a pre-invasion target state. Moreover, our review revealed that observational and experimental approaches are rarely used in concert, and that reference sites are scarcely employed to assess native species recovery after removal. Since the success of any alien removal operation depends, ultimately, on this recovery we believe that the comparative approach presented here is crucial because it can empirically answer fundamental ecological questions about how invasions affect native communities. Moreover it might simultaneously demonstrate how well a given removal strategy can achieve specific management goals. Therefore, we suggest that this comparative approach can make restoration efforts involving alien plant species more practical and successful, supporting science-based management decisions for the protection and restoration of biological diversity.

Acknowledgements

This study has been partially funded by the *Ministerio de Ciencia e Innovación* projects MONTES (CSD2008-00040) and RIXFUTUR (CGL2009-7515), and the Junta de Andalucía project RNM-4031.

References

Adams DC, Gurevitch J, Rosenberg MS (1997) Resampling Tests for Meta-analysis of Ecological Data. Ecology 78 (June): 1277-1283.

Alvarez ME, Cushman JH (2002) Community-level consequences of a plant invasion: Effects on three habitats in coastal California. Ecological Applications 12: 1434–1444.

Andreu J, Manzano E, Dana ED, Bartomeus I, Vilà M (2010) Vegetation response after removal of the invader *Carpobrotus spp*. in coastal dunes. Ecological Restoration 28: 440-448.

Chapman MG, Underwood AJ (2000) The need for a practical scientific protocol to measure successful restoration. Wetlands (Australia) 19: 28-49.

D'Antonio CM, Meyerson LA (2002) Exotic plant species as problems and solutions in ecological restoration: A synthesis. Restoration Ecology 10: 703-713.

D'Antonio CM, Hughes HR, Mack M, Hitchcock D, Vitousek PM (1998) The response of native species to removal of invasive exotic grasses in a seasonally dry Hawaiian woodland. Journal of Vegetation Science 9: 699 -712.

Díaz S, Symstad AJ, Chapin FS, Wardle DA, Huenneke LF (2003) Functional diversity revealed by removal experiments. Trends in Ecology and Evolution 18: 140-146.

Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. Annual Review of Ecology and Systematics 41: 59–80.

Gaertner M, Den Bree A, Hui C, Richardson DM (2009) Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. Progress in Physical Geography 33: 319–338.

Harrison F (2011) Getting started with meta-analysis. Methods in Ecology & Evolution 2: 1-10.

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

Holmes PM, Richardson DM, Esler KJ, Witkowski ETF, Fourie S (2005) A decision-making framework for restoring riparian zones degraded by invasive alien plants in South Africa. South African Journal of Science 101: 553–564.

Hulme PE (2006) Beyond control: wider implications for the management of biological invasions. Journal of Applied Ecology 43: 835–847.

Hulme PE, Bremner ET (2006) Assessing the impact of Impatiens glanduliferaon riparian habitats: partitioning diversity components following species removal. Journal of Applied Ecology 43: 43-50.

Kettunen M, Genovesi P, Gollasch S, Pagad S, Starfinger U, ten Brink P, Shine C (2009) Technical support to EU strategy on invasive species (IS) - Assessment of the impacts of IS in Europe and the EU (Final module report for the European Commission). Institute for European Environmental Policy (IEEP), Brussels, Belgium. Levine JM, Vilà M, D'Antonio CM, Dukes JS, Grigulis K, Lavorel S (2003) Mechanisms underlying the impacts of exotic plant invasions. Proceedings Royal Society of London B 270: 775-781.

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences and control. Ecological Applications 10: 689-710.

Manchester SJ, Bullock JM (2000) The impacts of non-native species on UK biodiversity and the effectiveness of control. Journal of Applied Ecology 37: 845-864.

Mason TJ, French K (2007) Management regimes for a plant invader differentially impact resident communities. Biological Conservation 136: 246-259.

McCoy ED, Mushinsky HR (2002) Measuring the success of wildlife community restoration. Ecological Applications 12: 1861–1871

Morrison JA (2002) Wetland vegetation before and after experimental purple loosestrife removal. Wetlands, 22: 159–169.

Ogden JAE, Rejmánek M (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.

Ogle CC, La Cock GD, Arnold G, Mickleson N (2000) Impact of an exotic vine Clematis vitalba (F. Ranunculaceae) and of control measures on plant biodiversity in indigenous forest, Taihape, New Zealand. Austral Ecology 25: 539–551

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamsom MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. Biological Invasions 1: 3-19

Partel M, Kalamees R, Zobel M, Rosen E (1998) Restoration of species-rich limestone grassland communities from overgrown land: the importance of propagule availability. Ecological Engineering 10: 275–286.

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

Powell KI, Chase JM, Knight TM (2011) A synthesis of plant invasion effects on biodiversity across spatial scales. American Journal of Botany 98(3): 539-548.

Price CA, Weltzin JF (2003) Managing non-native plant populations through intensive community restoration in Cades Cove, Great Smoky Mountains National Park, USA. Restoration Ecology 11: 351-358.

Rosenberg MS, Adams DC, Gurevitch J (2000) Metawin: Statistical Software for Meta-Analysis. Sinauer Associates, Sunderland, MA.

SER - Society for Ecological Restoration International Science & Policy Working Group (2004) The SER International Primer on Ecological Restoration. www.ser.org & Tucson: Society for Ecological Restoration International.

Smith RG, Maxwell BD, Menalled FD, Rew LJ (2006) Lessons from agriculture may improve the management of invasive plants in wildland systems. Frontiers in Ecology and the Environment 4 (8): 428-434.

Sol D, Vilà M, Kühn I (2008) The comparative analysis of historical alien introductions. Biological Invasions 10: 1119-1129.

Stinson K, Kaufman S, Durbin L, Lowenstein F (2007) Impacts of garlic mustard invasion on a forest understory community. Northeastern Naturalist 14: 73–88.

Stewart G (2010) Meta-analysis in applied ecology. Biology Letters 6: 78–81.

Swab RM, Zhang L, Mitsch WJ (2008) Effect of hydrologic restoration and Lonicera maackii removal on herbaceous understory vegetation in a bottomland hardwood forest. Restoration Ecology 16: 453-463.

Truscott AM, Palmer SC, Soulsby C, Westaway S, Hulme PE (2008) Consequences of invasion by the alien plant Mimulus guttatus on the-species composition and soil properties of riparian plant communities in Scotland. Perspectives in Plant Ecology, Evolution and Systematics: 10: 231–240.

Vilà M, Tessier M, Suehs CM, Brundu G, Carta L, Galinidis A, Lambdon P, Manca M, Medail F, Moragues E, Traveset A, Troumbis AY, Hulme PE (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, Basnou C, Pyšek P, Josefsson M, Genovesi P, Gollasch S, Nentwig W, Olenin S, Roques A, Roy D, Hulme PE, DAISIE partners (2010) How well do we understand the impacts of alien species on ecosystem services? A pan-European cross-taxa assessment. Frontiers in Ecology and the Environment 8: 135-144

Vila M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecology Letters 14: 702-708

Vitousek PM, D'Antonio CM, Loope LL, Rejmanek M, Westerbrooks R (1997) Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology 21 (1): 1–16

Wilkins S, Keith D, Adam P (2003) Measuring success: evaluating the restoration of a grassy eucalypt woodland on the Cumberland Plain, Sydney, Australia. Restoration Ecology 11 (4): 489–503

Zavaleta ES, Hobbs RJ, Mooney HA (2001) Viewing invasive species removal in a whole-ecosystem context. Trends in Ecology and Evolution 16: 454-459

Bio-sketch

Jara Andreu

has a degree in Biology by the Autonomous University of Barcelona (UAB, 2003), a MSc in Environmental Sciences by the Wageningen University (The Netherlands, 2005) and a PhD in Environmental Science and Technology by the Autonomous University of Barcelona (UAB, 2012). She has focused her doctoral thesis on the impact and management of exotic plants in Spain. Currently, she is working as a researcher in CREAF, coordinating an applied research about the state of the art and invasion risk by alien species in Catalonia. She also studies the most efficient management strategies to control invasive species, giving special attention to preventive methods and risk assessments.

Montserrat Vilà

Montserrat Vilà's research mainly focuses on the ecology and biogeography of biological invasions. Key topics are a) the analysis of landscape, geographic and environmental factors associated to the abundance and distribution of alien plants, b) the study of biotic factors (i.e. competition, plant-animal interactions) controlling alien plant establishment, and c) the ecological and also economic impacts of biological invasions. Main areas of study are Mediterranean ecosystems including islands.

Authors

ANDREU, Jara [1]
(Corresponding author) [1]
jara@creaf.uab.es

VILÀ, Montserrat [2]

[1] Centre for Ecological Research and Forestry Applications (CREAF), Universitat Autònoma de Barcelona. E-08193 Bellaterra, Cerdanyola del Vallès, Barcelona, Spain.

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

Appendix 1. References used to construct the dataset on native plant richness and abundance responses to alien plant invasion and removal.

A) Non-invaded versus invaded comparisons

Species	Life form	Invaded region	Biogeographical region	Invaded habitats	Variable measured	Reference
Agave americana	Shrub	Europe	Mediterranean	Coastal (sand dunes/rocky)	Abundance	Badano and Pugnaire, 2004
Agropyron cristatum	Perennial herb	North America	Temperate	Grassland	Abundance	Henderson and Naeth, 2005
Agrostis stolonifera	Perennial grass	Asia	Temperate	Riparian	Abundance	Gremmen et al., 1998
Ailanthus altissima	Tree	Europe	Mediterranean	Riparian	Richness	Vilà et al., 2006
Asparagus asparagoides	Shrub	Australia	Subtropical	Grassland	Abundance, richness	Turner et al., 2008
Bromus tectorum	Annual grass	North America	Semiarid	Grassland	Abundance	Belnap and Phillips, 2001
Bromus tectorum	Annual grass	North America	Semiarid	Grassland	Abundance	Belnap et al., 2005
Bromus tectorum	Annual grass	North America	Semiarid	Grassland	Abundance	Belnap et al., 2006
Bromus tectorum	Annual grass	North America	Mediterranean	Grassland	Abundance	Blank, 2008
Carpobrotus edulis	Perennial herb	Europe	Mediterranean	Coastal (sand dunes/rocky)	Abundance, richness	Andreu et al., 2009
Carpobrotus spp.	Perennial herb	Europe	Mediterranean	Coastal (sand dunes/rocky)	Richness	Vilà et al., 2006
Chromolaena odorata	Perennial herb	Asia	Subtropical	Forest	Richness	Muralli and Setty, 2001
Chrysanthemoides monilifera ssp. *rotundata*	Shrub	Australia	Subtropical	Coastal (sand dunes/rocky)	Richness	Mason and French, 2008
Chrysanthemoides monilifera ssp. *rotundata*	Shrub	Australia	Subtropical	Coastal (sand dunes/rocky)	Richness	Mason et al., 2007.
Cortaderia selloana	Perennial grass	Europe	Mediterranean	Oldfields	Abundance, richness	Domenech and Vilà, 2008
Cytisus scoparius	Shrub	Australia	Temperate	Forest	Richness	Wearne and Morgan, 2004
Delairea odorata	Vine	North America	Mediterranean	Shrubland	Abundance, richness	Alvarez and Cushman, 2002
Heracleum mantegazzianum	Perennial herb	Europe	Temperate	Several habitats	Richness	Pyšek and Pyšek,1995
Impatiens glandulifera	Annual herb	Europe	Temperate	Riparian	Richness	Hejda and Pyšek, 2006
Lantana camara	Shrub	Asia	Subtropical	Forest	Richness	Muralli and Setty, 2001
Lantana camara	Shrub	Australia	Semi-arid	Forest	Abundance, richness	Gooden et al., 2009
Lonicera tatarica	Shrub	North America	Temperate	Forest	Abundance, richness	Woods, 1993
Lupinus polyphyllus	Perennial herb	Europe	Temperate	Grassland	Abundance, richness	Valtonen et al., 2006
Lythrum salicaria	Perennial herb	North America	Temperate	Grassland	Richness	Treberg and Husband, 1999
Mesembryanthemum crystallinum	Annual herb	Africa	Mediterranean	Coastal (sand dunes/rocky)	Abundance	Vivrette and Muller, 1977
Mimulus guttatus	Perennial herb	Europe	Oceanic	Grassland	Richness	Trusctott et al., 2008
Orbea variegata	Perennial herb	Australia	Mediterranean	Shrubland	Abundance, richness	Dunbar and Facelli, 1999
Oxalis pes-caprae	Perennial herb	Europe	Mediterranean	Oldfields	Richness	Vilà et al., 2006
Phragmites australis	Perennial grass	North America	Temperate	Grassland	Abundance, richness	Richburg et al., 2001
Pyracantha angustifolia	Shrub	South America	Subtropical	Shrubland	Richness	Giantomasi et al., 2008
Spartina anglica	Perennial grass	North America	Temperate	Wetland/marshland	Abundance	Hacker and Dethier, 2006
Tradescantia fluminensis	Perennial herb	Pacific islands	Subtropical	Forest	Abundance	Standish et al., 2001

B) Removal versus invaded comparisons

Species	Life form	Region invaded	Biogeographical region	Invaded habitats	Variable measured	Reference
Annual grasses from the genus *Bromus*	Annual grass	North America	Subtropical	Desert	Abundance	Brooks, 2000
Bromus tectorum	Annual grass	North America	Temperate	Shrubland	Abundance	Melgoza *et al.*, 1990
Carpobrotus edulis	Perennial herb	Europe	Mediterranean	Coastal (sand dunes/rocky)	Abundance, richness	Andreu *et al.*, 2009
Chrysanthemoides monilifera ssp. *rotundata*	Shrub	Australia	Semi-arid	Coastal (sand dunes/rocky)	Richness	Mason and French, 2008
Delairea odorata	Vine	North America	Mediterranean	Riparian, shrubland	Richness	Alvarez and Cushman, 2002
Impatiens glandulifera	Annual herb	Europe	Temperate	Riparian	Richness	Hejda and Pyšek, 2006
Impatiens glandulifera	Annual herb	Europe	Temperate	Riparian	Richness	Hulme and Bremner, 2006
Lantana camara	Shrub	Australia	Semi-arid	Forest	Abundance, richness	Gooden *et al.*, 2009
Lespedeza cuneata	Perennial herb	North America	Temperate	Grassland	Abundance	Brandon *et al.*, 2004
Lupinus arboreus	Shrub	North America	Mediterranean	Shrubland	Abundance	Pickart *et al.*, 1998
Microstegium vimineum	Annual grass	North America	Temperate	Forest	Abundance, richness	Oswalt *et al.*, 2007
Microstegium vimineum	Annual grass	North America	Temperate	Forest	Abundance	Flory, 2010
Microstegium vimineum	Annual grass	North America	Temperate	Forest	Abundance, richness	Flory and Clay, 2009
Mimulus guttatus	Perennial herb	Europe	Oceanic	Grassland	Richness	Trusctott et al., 2008
Orbea variegata	Perennial herb	Australia	Mediterranean	Shrubland	Abundance, richness	Dunbar and Facelli, 1999
Tamarix spp.	Tree	North America	Temperate	Forest	Abundance, richness	Harms and Hiebert, 2006

C) Non-invaded versus removal comparisons

Species	Life form	Region invaded	Biogeographical region	Invaded habitats	Variable measured	Reference
Carpobrotus edulis	Perennial herb	Europe	Mediterranean	Coastal (sand dunes/rocky)	Abundance, richness	Andreu *et al.*, 2009
Chrysanthemoides monilifera ssp. *rotundata*	Shrub	Australia	Semi-arid	Coastal (sand dunes/rocky)	Richness	Mason and French, 2008
Lantana camara	Shrub	Australia	Semi-arid	Forest	Abundance, richness	Gooden *et al.*, 2009
Mimulus guttatus	Perennial herb	Europe	Oceanic	Grassland	Richness	Trusctott *et al.*, 2008
Orbea variegata	Perennial herb	Australia	Mediterranean	Shrubland	Richness	Dunbar and Facelli, 1999
Pinus radiata and *Hakea sericea*	Tree	Africa	Mediterranean	Forest	Abundance, richness	Holmes *et al.*, 2000

Alvarez ME, Cushman JH (2002) Community-level consequences of a plant invasion: Effects on three habitats in coastal California. Ecological Applications 12: 1434–1444.

Andreu J, Manzano E, Bartomeus I, Dana ED, Vilà M (2010) Vegetation response after removal of the invader *Carpobrotus spp.* in coastal dunes. Ecological Restoration 28(4): 440-448.

Badano EI, Pugnaire FI (2004) Invasion of *Agave* species (Agavaceae) in south-east Spain: invader demographic parameters and impacts on native species. Diversity and Distributions 10: 493–500.

Belnap J, Phillips SL (2001) Soil biota in an ungrazed grassland: Response to annual grass (*Bromus tectorum*) invasion. Ecological Applications 11: 1261–1275.

Belnap J, Phillips SL, Sherrod SK, Moldenke A (2005) Soil biota can change after exotic plant invasion: does this affect ecosystem processes? Ecology 86: 3007–3017.

Belnap J, Phillips SL, Troxler T (2006) Soil lichen and moss cover and species richness can be highly dynamic: The effects of invasion by the annual exotic grass *Bromus tectorum*, precipitation, and temperature on biological soil crusts in SE Utah. Applied Soil Ecology 32: 63–76.

Blank RR (2008) Biogeochemistry of plant invasion: a case study with downy brome (*Bromus tectorum*). Invasive Plant Science and Management 1: 226–238.

Brandon AL, Gibson DJ, Middleton BA (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.

Brooks ML (2000) Competition between alien annual grasses and native annual plants in the Mojave Desert. The American Midland Naturalist 144: 92–108.

Domenech R, Vilà M (2008) Response of the invader *Cortaderia selloana* and two coexisting natives to competition and water stress. Biological Invasions 10: 903–912.

Dunbar KR, Facelli JM (1999) The impact of a novel invasive species, *Orbea variegata* (African carrion flower), on the chenopod shrublands of South Australia. Journal of Arid Environments 41: 37–48.

Flory SL (2010) Management of *Microstegium vimineum* invasions and recovery of resident plant communities. Restoration Ecology 18:103-112.

Flory SL, Clay K (2009) Invasive plant removal method affects native community diversity responses. Journal of Applied Ecology 4: 434-442.

Giantomasi A, Tecco PA, Funes G, Gurvich DE, Cabido M (2008) Canopy effects of the invasive shrub *Pyracantha angustifolia* on seed bank composition, richness and density in a montane shrubland (Cordoba, Argentina). Austral Ecology 33: 68–77.

Gooden, B, French, K, Turner P (2009) Invasion and management of a woody plant, *Lantana camara* L., alters vegetation diversity within wet sclerophyll forest in south-eastern Australia. Forest Ecology and Management 257: 960-967.

Gremmen NJM, Chown SL, Marshall DJ (1998) Impact of the introduced grass *Agrostis stolonifera* on vegetation and soil fauna communities at Marion Island, sub-Antarctic. Biological Conservation 85: 223–231.

Harms RS, Hiebert RD (2006) Vegetation response following invasive tamarisk (*Tamarix spp.*) removal and implications for riparian restoration. Restoration Ecology 14:461–472.

Hacker SD, Dethier MN (2006) Community modification by a grass invader has differing impacts for marine habitats. Oikos 113: 279–286.

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

Henderson DC, Naeth MA (2005) Multi-scale impacts of crested wheatgrass invasion in mixed-grass prairie. Biological Invasions 7: 639–650.

Holmes P, Richardson D, Van Wilgen B, Gelderblom C (2000) Recovery of South African fynbos vegetation following alien woody clearing and fire: implications for restoration. Austral Ecology 25: 631-639.

Hulme PE, Bremner ET (2006) Assessing the impact of *Impatiens glandulifera* on riparian habitats: partitioning diversity components following species removal. Journal of Applied Ecology 43: 43–50.

Mason TJ, French K (2008) Impacts of a woody invader vary in different vegetation communities. Diversity and Distributions 14: 829–838.

Mason TJ, French K, Russell KG (2007) Moderate impacts of plant invasion and management regimes in coastal hind dune seed banks. Biological Conservation 134: 428–439.

Melgoza G, Nowak RS, Tausch RJ (1990) Soil-water exploitation after fire competition between *Bromus tectorum* (cheatgrass) and 2 native species. Oecologia 83: 7–13.

Muralli KS, Setty RS (2001) Effect of weeds *Lantana camara* and *Chromelina odorata* growth on the species diversity, regeneration and stem density of tree and shrub layer in BRT sanctuary. Current Science 80: 675–678.

Oswalt CM, Oswalt SN, Clatterbuck WK (2007) Effects of *Microstegium vimineum* (Trin.) A. Camus on native woody species density and diversity in a productive mixed-hardwood forest in Tennessee. Forest Ecology and Management 242: 727–732.

Pickart AJ, Miller LM, Duebendorfer TE (1998) Yellow bush lupine invasion in northern California coastal dunes: I. Ecological impacts and manual restoration techniques. Restoration Ecology 6: 59-68.

Pyšek P, Pyšek A (1995) Invasion by *Heracleum mantegazzianum* in different habitats in the Czech Republic. Journal of Vegetation Science: 711–718.

Richburg JA, Patterson WA, Lowenstein F (2001) Effects of road salt and *Phragmites australis* invasion on the vegetation of a western Massachusetts calcareous lake-basin fen. Wetlands 21: 247–255.

Standish RJ, Robertson AW, Williams PA (2001) The impact of an invasive weed *Tradescantia fluminensis* on native forest regeneration. Journal of Applied Ecology 38: 1253–126.

Treberg MA, Husband BC (1999) Relationship between the abundance of *Lythrum salicaria* (purple loosestrife) and plant species richness along the Bar River, Canada. Wetlands 19: 118–125.

Truscott AM, Palmer SC, Soulsby C, Westaway S, Hulme PE (2008) Consequences of invasion by the alien plant *Mimulus guttatus* on the-species composition and soil properties of riparian plant communities in Scotland. Perspectives in Plant Ecology, Evolution and Systematics 10: 231–240.

Turner PJ, Scott JK, Spafford H (2008) The ecological barriers to the recovery of bridal creeper (*Asparagus asparagoides* (L.) Druce) infested sites: Impacts on vegetation and the potential increase in other exotic species. Austral Ecology 33: 713–722.

Valtonen A, Jantunen J, Saarinen K (2006) Flora and lepidoptera fauna adversely affected by invasive *Lupinus polyphyllus* along road verges. Biological Conservation 133: 389–396.

Vilà M, Tessier M, Suehs CM, Brundu G, Carta L, Galanidis A, Lambdon P, Manca M, Medail F, Moragues E, Traveset A, Troumbis AY, Hulme PE (2006) Local and regional assessments of the impacts of plant invaders on vegetation structure and soil properties of Mediterranean islands. Journal of Biogeography 33: 853–861.

Vivrette NJ, Muller CH (1977) Mechanism of invasion and dominance of coastal grassland by *Mesembryanthemum crystallinum*. Ecological Monographs 47: 301–318.

Wearne LJ, Morgan JW (2004) Community-level changes in Australian subalpine vegetation following invasion by the non-native shrub *Cytisus scoparius*. Journal of Vegetation Science 15: 595–604.

Woods KD (1993) Effects of invasion by *Lonicera tatarica* L on herbs and tree seedlings in 4 New-England forests. The American Midland Naturalist 130: 62–74.