

SPECIAL FEATURE

FACILITATION IN PLANT COMMUNITIES

The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems

Lorena Gómez-Aparicio*

Instituto de Recursos Naturales y Agrobiología (IRNAS, CSIC), PO Box 1052, Sevilla 41080, Spain

Summary

1. Traditionally, techniques of plant manipulation during restoration have focused on the reduction of competition by ‘problematic’ existing vegetation. However, the increasing recognition of facilitation as a main process regulating the composition of communities has brought a change in the practice of restoration towards a better awareness of the benefits inherent to conserving neighbouring vegetation.

2. Here, I provide the results of a meta-analysis of published studies that have manipulated interactions among plants with the objective of restoring degraded terrestrial systems. I created four different data sets corresponding to the variables most commonly used to measure plant performance (i.e. emergence, survival, growth and density), and asked whether the benefits of facilitation as a restoration tool vary depending on the study duration, the life-form of the neighbour and target species, and the ecosystem type.

3. Neighbour effects varied strongly among performance estimators. Positive effects were frequently found for emergence and survival, whereas neutral or negative interactions predominated for growth and density.

4. No clear support existed for a relationship between study duration and neighbour effect.

5. The life-form of the interacting species, particularly of neighbours, largely influenced the interaction outcome. Herbs had strong negative effects, especially on other herb species, whereas shrubs had large facilitative effects, especially on trees.

6. Semiarid and tropical systems showed in general more positive neighbour effects than wetlands and particularly mesic temperate systems, where negative interactions predominated. However, these results were largely influenced by the over-representation of herb species in wetlands and temperate habitats, survival facilitation being found in all systems when only woody species were considered.

7. *Synthesis.* Pre-existing vegetation can have large impacts on species establishment in degraded habitats. Inhibition predominates in herbaceous communities typical of early-successional stages, whereas facilitation prevails in communities dominated by shrubs and trees. Even productive systems (e.g. mesic temperate habitats) appear suitable for the application of facilitation as a restoration tool of woody communities. Whereas restoring herbaceous communities seems largely reliable on removal techniques, augmenting populations of nurse shrubs and trees should be considered a promising strategy for restoring woody late-successional communities.

Key-words: competition, degraded systems, establishment, facilitation, growth, life-forms, nurse plants, plant–plant interactions, restoration, succession

Introduction

As human impacts on ecosystems world-wide intensify, the restoration of degraded habitats increasingly becomes an urgent

*Correspondence author. E-mail: lorenag@irnase.csic.es

task and a difficult challenge (Choi *et al.* 2008; Hobbs & Cramer 2008). Stimulated by this need, the science of restoration ecology has experienced a major advance in the last 20 years, and numerous techniques have been proposed as tools to improve the physicochemical and biological properties of degraded systems (Perrow & Davy 2002; Van Andel & Aronson 2006). Among these techniques, the manipulation of the plant community appears to be one of the most effective ways to simultaneously overcome the abiotic and biotic barriers that usually limit the recovery of degraded areas. Plants alter surface wind and fluvial flows, ameliorate stressful micro-environmental conditions and are a source of organic matter that improves soil fertility, therefore restoring the abiotic environment in a natural, self-sustaining way (Davy 2002; Whisenant 2002). As a result of this modifying activity, established vegetation can facilitate the incorporation of new individuals into the community, according to a model of succession by facilitation (Connell & Slatyer 1977). However, it is also possible that once earlier colonists are established, they arrest the incorporation of new individuals according to a model of succession by inhibition (Connell & Slatyer 1977). The balance between these positive and negative plant interactions will condition the rate and direction of successional change, and its manipulation can therefore be used to influence the development or regression of a degraded system towards the target community (Siles *et al.* 2008).

Traditionally, the most popular techniques of plant manipulation during restoration have focused on the reduction of competition by 'problematic' existing vegetation. Thus, before seeding or planting desired species, neighbours were eliminated with different treatments such as fire, herbicides, grazing, or by manual or mechanical removal (Jordan 1988; Clewell & Lea 1990; Savill *et al.* 1997). However, the renewed interest in positive plant interactions in mainstream ecology and the accumulating evidence of facilitation as the dominant interaction in many situations (Callaway 2007; Brooker *et al.* 2008) have initiated a change in the practice of restoration towards a better awareness of the benefits inherent to conserving neighbouring vegetation (Byers *et al.* 2006; Padilla & Pugnaire 2006; Halpern *et al.* 2007). Thus, in Mediterranean post-fire shrublands pioneer shrubs have been shown to act as nurse plants that benefit the establishment of late-successional woody species (Gómez-Aparicio *et al.* 2004; Castro, Zamora & Hódar 2006; Siles *et al.* 2008). In semiarid rangelands, where typical restoration approaches included shrub removal to promote herbaceous forage production for livestock grazing, more recent studies have focused on using established shrubs to enhance herbaceous production and diversity (Huber-Sannwald & Pyke 2005). Similarly, whereas weed suppression has been usually considered necessary in wetland restoration, some doubts have started to rise about the need of weed control in all situations (McLeod, Reed & Wike 2001).

Despite the increasing number of facilitation examples in restoration practice, it is still not clear when and where existing vegetation should be removed or promoted. For example, in tropical abandoned pastures, grasses and shrubs have been found to compete with trees for resources in some situations

(Sun & Dickinson 1996; Holl 1998; Griscom, Ashton & Berlyn 2005), but to buffer harsh abiotic conditions and facilitate tree recruitment in others (Aide & Cavellier 1994; Vieira, Uhl & Nepstad 1994; Holl 1999). The consequence of such conflicting results are passive management recommendations such as "being cautious about assuming that removing non-tree vegetation will benefit forest regrowth until more is known" (Duncan & Chapman 2003a,b) or the need of "more research before shrubs are introduced on a wide scale to help restore abandoned pastures" (Holl 1998). Clearly, being passive implies not exploiting the large potential that managing plant interactions has to accelerate the recovery of degraded systems. The outcome of plant interactions is highly variable because it implies a balance of positive and negative effects that may change depending on several factors such as the characteristics of the species interacting or the environmental conditions (Callaway & Walker 1997; Armas & Pugnaire 2005; Maestre *et al.* 2009). Therefore, if we are to take an active restoration approach, efforts should be made to improve our understanding of which species and habitats are more likely to benefit from a management based on releasing competition and which ones from a management based on promoting facilitation.

In this study I present the results of a meta-analysis that aims to assess the generality of the effects of manipulated plant interactions in degraded terrestrial systems. A meta-analysis provides a useful tool for extracting general results from a suite of individual studies (Gurevitch & Hedges 2001), and therefore is employed here to explore whether the experience accumulated over the past few decades can be used to formulate specific recommendations about the use of facilitation as a restoration tool. Although different words with somewhat different meanings are frequently used in ecological restoration (i.e. restoration, rehabilitation, reclamation, remediation), here I used the term 'restoration' to refer broadly to the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed (Society for Ecological Restoration International Science & Policy Working Group 2004). I focused the meta-analysis on four main questions. First, I asked whether the benefits of facilitation as a restoration tool vary depending on the plant performance estimator (i.e. emergence, survival, growth, density). Understanding how restoration practices can differentially affect demographic parameters is important to appropriately weigh the costs and benefits of the restoration (Gillespie & Allen 2004). Second, I asked whether the benefits of facilitation vary depending on the duration of the study. Because competition has been shown to increase with ontogeny (Miriti 2006; Quero *et al.* 2008; Armas & Pugnaire 2009), I would expect the net effect of established neighbours to become increasingly negative as study duration increases. Third, I asked whether the benefits of facilitation vary depending on the life-form (i.e. herb, shrub, tree) of the neighbour and target species. If so, I further explored the existence of interdependence between neighbour and target life-forms, looking for particular pair combinations that were more likely to render positive interactions. Knowledge of the extent to which a certain species group may facilitate the establishment of another group would be valuable in formulating

assembly rules for ordering the introduction of species into a site (Gómez-Aparicio *et al.* 2004; Siles 2008). Finally, I asked whether the benefits of using established vegetation as nurse plants vary among ecosystem types (i.e. semiarid, tropical, wetland, mesic temperate). Because positive plant interactions are expected to be especially common under high abiotic stress (Bertness & Callaway 1994; see discussion in Maestre, Valladares & Reynolds 2005, 2006a; Lortie & Callaway 2006), facilitation could be a more useful restoration tool in stressful systems such as water-limited habitats than in more productive ones such as wetlands or mesic temperate habitats.

Materials and methods

DATA BASE

I focused on published studies that explicitly explored the role of plant interactions (both positive and negative) in the restoration of degraded terrestrial ecosystems. Studies were located by searching keywords in an electronic data base (ISI Web of Science 1945–2008) for combinations of two groups of terms: (i) 'facilitation', 'competition', 'positive interaction', 'negative interaction', 'interference' or 'nurse', and (ii) 'restoration', 'rehabilitation', 'reclamation', 'remediation', 'revegetation', 'reforestation' or 'afforestation'. More studies were found within the reference lists of the gathered papers. A study was considered valid for the meta-analysis if it met the following criteria: (i) the study had to be quantitative and the data reported in a usable form; (ii) the study had to be conducted under natural conditions in the field (glasshouse experiments were excluded); and (iii) the study had to evaluate the effect of neighbours on the performance of target species or group of species. Performance of the target species growing in the vicinity of a neighbour was compared with that of plants growing in open areas (without neighbours) or in areas where neighbours had been removed. Studies where the influence of neighbours was reduced (e.g. canopy thinning) but not eliminated (i.e. no pure 'open treatment' existed) were not considered. When several removal methods were tested (e.g. mowing versus herbicide), only the data from the most effective method was considered. Studies that used burning as a removal method were not included due to the several side-effects of fire (e.g. on soil structure and nutrient content; Certini 2005). Studies that simulated the presence of neighbours (i.e. artificial shade) instead of using real plants were not included.

Suitable studies were grouped in four different data sets, depending on the plant performance estimator quantified: emergence, survival, growth (measured as biomass or height) and density (measured as number of individuals or cover per a given area). If repeated measures were taken in a study, only the results obtained at the end of the experiment were used. If more than one publication presented results from the same field plots (e.g. Castro *et al.* 2002, 2004), I relied upon data from the most recent paper. In cases in which the neighbour treatment was crossed with additional treatments that implied explicit manipulation of the environment (i.e. fertilizer addition), I included only the ambient treatment. In cases in which articles described several combinations of nurse and target species, or where the same experiment was conducted in several sites or years, each combination was treated as a separate study. I decided to include several studies from the same paper because, although it tends to reduce the overall heterogeneity in effect sizes, excluding multiple results from a paper can underestimate effect sizes (Gurevitch & Hedges 1999; Karst *et al.* 2008). When data were only reported in graphical form, I used the data-grabbing software TechDig v2.0 (Jones 1998).

META-ANALYSIS

The meta-analysis involves two steps. First, the results from each study are used to calculate a biologically relevant effect size, and second, effect sizes are statistically summarized to estimate a weighted average for the sample of studies (average effect size) and to test hypotheses. Here, I used two different measures of effect size: the odds ratio metric for categorical data (emergence and survival) and the response ratio for continuous data (growth and density).

Emergence and survival data were summarized in 2×2 contingency tables, with columns representing treatments (with versus without neighbours) and rows the possible outcomes (emerged versus not emerged, alive versus dead). An odds ratio (OR) metric was obtained for each study, calculated as the ratio of the odds of emergence or survival in the presence of neighbours (experimental treatment) to the odds of emergence or survival in their absence (control treatment). There were some studies where all individuals emerged or survived or not emerged or survived, and because this could produce odds ratio values that require division by 0, the odds ratios were calculated adding 1 to the number of individuals in each category for every study (Hyatt *et al.* 2003; Maestre, Valladares & Reynolds 2005, 2006a). Values of the natural log of the odds ratio ($\ln(\text{OR})$) higher than 0 indicate a positive effect of neighbours on performance (facilitation), whereas values lower than 0 indicate a negative effect of neighbours (competition).

The effect size of neighbours for growth and density data was calculated using the natural log of the response ratio ($\ln(\text{RR})$) and its associated variance ($v_{\ln \text{RR}}$). The response ratio (RR) is the ratio of the mean outcome in the experimental group to that of the control group. The response ratio was preferred over the more traditional Hedge's d because it better estimates the actual difference in mean performance among treatments, whereas the Hedge's d (based on standard deviation units) can yield large effect sizes even when the absolute difference among means is small (Morris *et al.* 2007). The estimate of $\ln(\text{RR})$ and $v_{\ln \text{RR}}$ for each study is based on means, SDs, and replicate numbers for control and treatments (Hedges, Gurevitch & Curtis 1999). If standard errors (SEs) were reported, they were transformed according to the equation: $\text{SD} = \text{SE} (n^{1/2})$. As for odds ratios, positive $\ln(\text{RR})$ values indicate facilitation and negative values competition.

The effect of neighbours was first assessed for each of the four entire data sets. The total heterogeneity of each meta-analysis, Q_T , was calculated to analyse whether the variance among effect sizes was greater than expected by sampling error (Rosenberg, Adams & Gurevitch 2000). Q_T is a weighted sum of squares comparable to the total sum of squares in ANOVAs, and it is tested against a chi-squared distribution with $n-1$ degrees of freedom. Then, I evaluated the homogeneity of results among groups (Q_M , variance explained by the model), which were created to respond to the specific questions posed in the study. The percentage of variation in effect sizes explained by each grouping variable was estimated as Q_M/Q_T (Rosenberg, Adams & Gurevitch 2000). One continuous and four categorical grouping variables were selected. The continuous variable was 'study duration', and its effect was explored using weighted least-squares regression adjusted for meta-analysis (Rosenberg, Adams & Gurevitch 2000). The duration effect was only assessed for survival and growth (variables measured mainly in experimental seedlings and rarely in natural vegetation) because emergence was always assessed a few months after sowing, and density was in many cases a one-time estimation of cover or abundance of natural vegetation. The four categorical grouping variables were: (i) neighbour life-form (i.e. herb, shrub and tree). Herbaceous species were further

subdivided into grasses versus forbs, and annuals versus perennials; (ii) target life-form (i.e. herb, shrub and tree). As for neighbours, herbaceous species were subdivided into grasses versus forbs, and annuals versus perennials; (iii) neighbour–target combination (i.e. herb–herb, herb–shrub, herb–tree, shrub–herb, shrub–shrub, shrub–tree, tree–herb, tree–shrub and tree–tree); and (iv) ecosystem type (i.e. semiarid, tropical, wetland and mesic temperate). The semiarid category was used in the broad sense to include different types of water-limited ecosystems (arid, semiarid, Mediterranean), since preliminary analysis did not show differences among them. Also based on a preliminary data exploration, wet and dry tropical systems were merged into a single tropical category. To control for possible correlation among grouping variables (e.g. woody species were more common in semiarid and tropical studies than in wetland and mesic temperate ones, and the opposite was true for herbs), I also examined ecosystem effects considering only woody species. Differences in mean effect sizes among groups were calculated using random-effects models, which allows for the possibility that studies differ not only by sampling error (as fixed-effects models do), but also by a random component in effect sizes among studies (Gurevitch & Hedges 2001). Bias-corrected bootstrap 95% confidence intervals (CIs) were calculated for each effect size (Rosenberg, Adams & Gurevitch 2000). If the 95% CI did not overlap with zero, then effects were significant at $P < 0.05$.

Sensitivity analyses were used to control dependence between data and confirm that the trends detected were not affected by a few large

studies (Gates 2002; Lortie & Callaway 2006). For this, I performed additional analyses at the study level by pooling all experimental cases within a same study and calculating a single (cumulative) effect size (for similar approaches see Xiong & Nilsson 1999; Verdú & Traveset 2005; or Clark *et al.* 2007). The possibility of publication bias (i.e. the greater possibility of publishing significant results) was tested by calculating the Rosenthal's fail-safe number, that is, the number of studies with an effect size of zero that would be necessary to add to the meta-analysis to nullify its overall effect size. I also used funnel plots as a graphical method to assess publication bias and conducted Spearman rank correlation tests to analyse the relationship between the standardized effect size and the standardized variance across studies. Significance of this test indicates that larger effect sizes are more likely to be published than smaller effects. All the meta-analyses were conducted using MetaWin v2.0 (Rosenberg, Adams & Gurevitch 2000).

Results

EMERGENCE

A total of 14 studies met the selection criteria, yielding 62 suitable cases (see Appendix S1 in Supporting Information). On average, neighbours had a neutral effect on emergence (i.e. 95% CI crossed zero; Fig. 1a). The test of the overall heteroge-

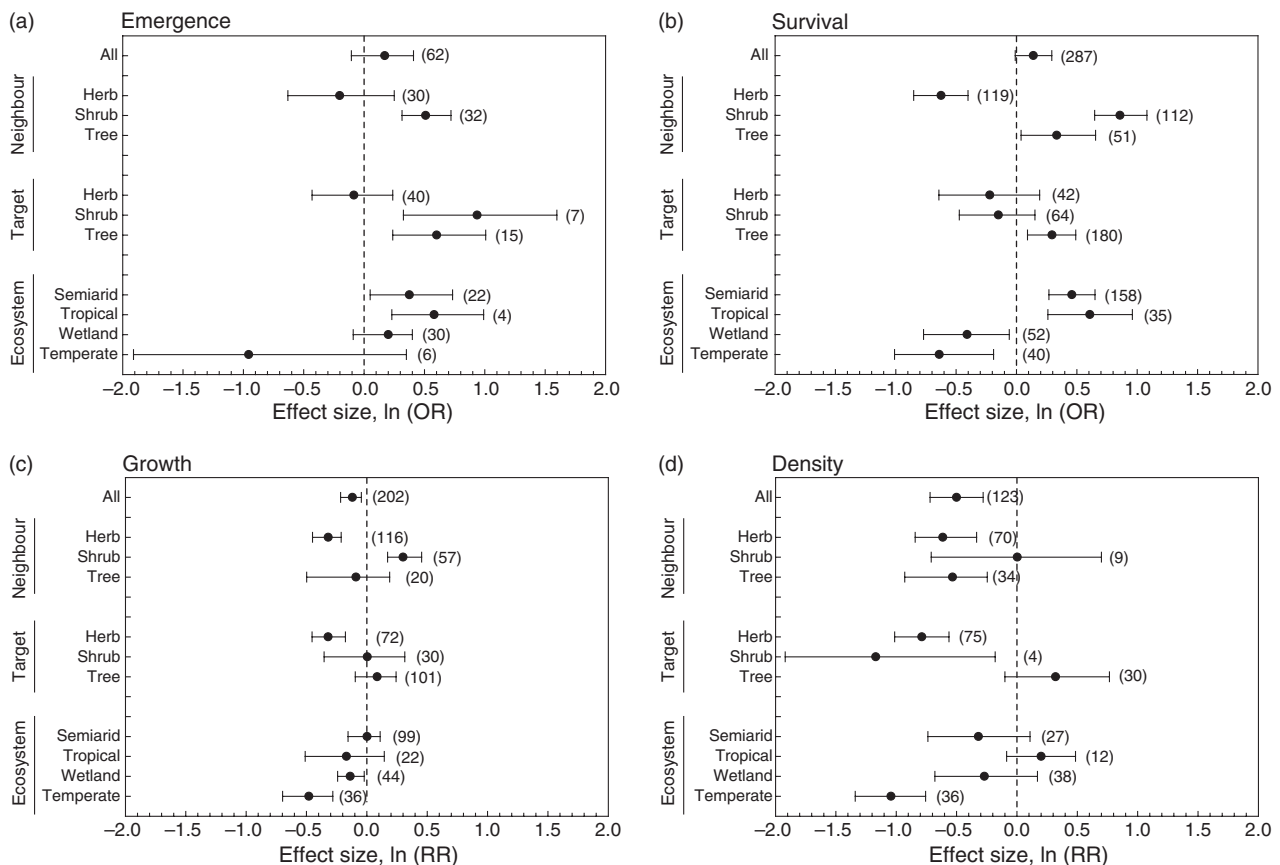


Fig. 1. Mean effect sizes by categorical grouping variable (neighbour life-form, target life-form, neighbour–target combination and ecosystem type) for emergence (a), survival (b), growth (c) and density data (d). Error bars are 95% bootstrapped confidence intervals. The number of cases is shown in parentheses. Significant neighbour effects are indicated by confidence intervals that do not overlap zero. Not enough data were available to calculate an effect size for the effect of neighbour trees on target emergence.

Table 1. Summary of random models analysing differences among groups in neighbour effects for each of the four performance estimators (emergence, survival, growth and density). Data presented are degrees of freedom (d.f.) and the P -values of Q analyses. Q_M = heterogeneity explained by the model (between-group heterogeneity), Q_E = residual error variance (within-group heterogeneity). Q_M/Q_T = fraction of the total heterogeneity explained by the model

Comparison	d.f.	Q_M	Q_E	Q_M/Q_T	P -value among groups
Emergence					
Neighbour (N)	1, 59	8.31	51.97	0.14	0.003
Target (T)	2, 59	6.00	39.35	0.13	0.04
N–T pairs	5, 55	33.65	54.29	0.38	<0.0001
Ecosystem	3, 58	14.85	83.29	0.15	0.002
Survival					
Neighbour (N)	2, 279	72.73	224.48	0.25	<0.0001
Target (T)	2, 283	8.11	266.87	0.03	0.02
N–T pairs	7, 264	85.39	222.52	0.28	<0.0001
Ecosystem	3, 281	39.22	284.27	0.12	<0.0001
Growth					
Neighbour (N)	2, 190	38.05	218.43	0.15	<0.0001
Target (T)	2, 199	8.65	211.62	0.04	0.01
N–T pairs	7, 185	36.33	181.61	0.17	<0.0001
Ecosystem	3, 197	15.99	223.72	0.07	0.001
Density					
Neighbour (N)	2, 110	5.07	162.15	0.03	0.06
Target (T)	2, 115	37.25	153.49	0.19	<0.0001
N–T pairs	7, 111	79.19	155.53	0.34	<0.0001
Ecosystem	3, 115	21.51	152.13	0.12	<0.0001

neity was not significant ($Q_T = 43.09$, d.f. = 61, $P = 0.95$). However, significant among-group differences appeared for the four categorical grouping variables ($P < 0.05$ in all cases; Table 1). Among neighbour life-forms, herbs had a neutral effect on emergence, whereas the effect of shrubs was positive (there were not enough cases available to calculate a tree effect; Fig. 1a). Among target groups, herbs showed a neutral response, whereas the response of shrubs and trees was largely positive (Fig. 1a). However, when herbs were subdivided into grasses and forbs, the response varied from positive in grasses to negative in forbs (Fig. 2a). When neighbour and target groups were analysed in pairs to explore interdependence, herbs were found to have a negative effect on themselves but a positive effect on shrubs and trees, whereas shrubs had positive effects on the three groups, especially on trees (Fig. 3a). Among ecosystem types, the effect of neighbours was significantly positive in semiarid and tropical habitats, whereas no significant effect was found for wetlands or mesic temperate systems (Fig. 1a). The small sample size precluded exploring differences among ecosystem types considering only woody species.

SURVIVAL

A total of 57 studies met the selection criteria, yielding 287 suitable cases (see Appendix S2). Across all studies, the presence of

neighbours had a neutral effect on survival (Fig. 1b). The test of the overall heterogeneity was not significant ($Q_T = 250.11$, d.f. = 286, $P = 0.95$). However, large significant differences in neighbour effects appeared for all continuous and categorical grouping variables ($P < 0.05$ in all cases; Fig. 4a, Table 1). There was a significant negative relationship between the duration of the study and the effect size (Fig. 4a). Regarding the neighbour life-form, herbs had a large negative effect on survival, whereas trees and particularly shrubs had a positive effect (Fig. 1b). Within herbs, grasses had a much larger negative effect than forbs, whereas only marginal differences appeared between annuals and perennials (Table 2; Fig. 2b). Among target groups, herbs and shrubs showed a neutral response to neighbours, whereas the response of trees was positive (Fig. 1b). No differences appeared among the different target subgroups of herbs (Table 2; Fig. 2b). When neighbour and target groups were analysed in pairs, herbs were found to have a significant, large negative effect on themselves and on trees, but not on shrubs. Shrubs had a positive effect on the three groups, especially on trees, and trees had a positive effect only on themselves (Fig. 3b). The neighbour effect was positive in semiarid and tropical systems, and negative in wetland and mesic temperate habitats (Fig. 1b). However, when analyses were repeated considering only woody species, differences among ecosystem types disappeared ($Q_M = 2.65$, d.f. = 3, 158, $P = 0.44$), and positive neighbour effects were found in all systems (lnOR (95% CI) semiarid = 0.75 (0.50–0.98); tropical = 0.40 (0.09–0.73); wetland = 0.69 (0.41–1.07); mesic temperate = 0.61 (0.13–1.30)).

GROWTH

A total of 54 studies met the selection criteria, yielding 202 suitable cases (see Appendix S3). Across all studies, the presence of neighbours had a small negative effect on the growth of target species (Fig. 1c) and the data set showed significant internal heterogeneity ($Q_T = 257.57$, d.f. = 201, $P = 0.006$). There was not a significant relationship between the effect size and the duration of the study (Fig. 4b). Among neighbour groups, although the effect size was small in all cases, it varied from negative for herbs, through neutral for trees, to positive for shrubs (Fig. 1c). Within herbs, annual neighbours had a larger negative effect than perennials (Fig. 2c). Among target species, only herbs showed a significant negative response to neighbours (Fig. 1c). When neighbour and target groups were analysed in pairs, herbs had the largest negative effects on themselves, followed by trees, whereas the effects on shrubs were not significant. Shrubs had a neutral effect on herbs, and a positive effect on themselves and especially on trees. Contrary to shrubs, trees had a negative effect on herbs and a neutral effect on themselves (Fig. 3c). Among ecosystem types, the neighbour effect varied from not significant for semiarid and tropical systems, to negative for wetland and particularly mesic temperate systems (Fig. 1c). Differences among ecosystems remained when only woody species were considered ($Q_M = 12.64$, d.f. = 3, 71, $P = 0.005$).

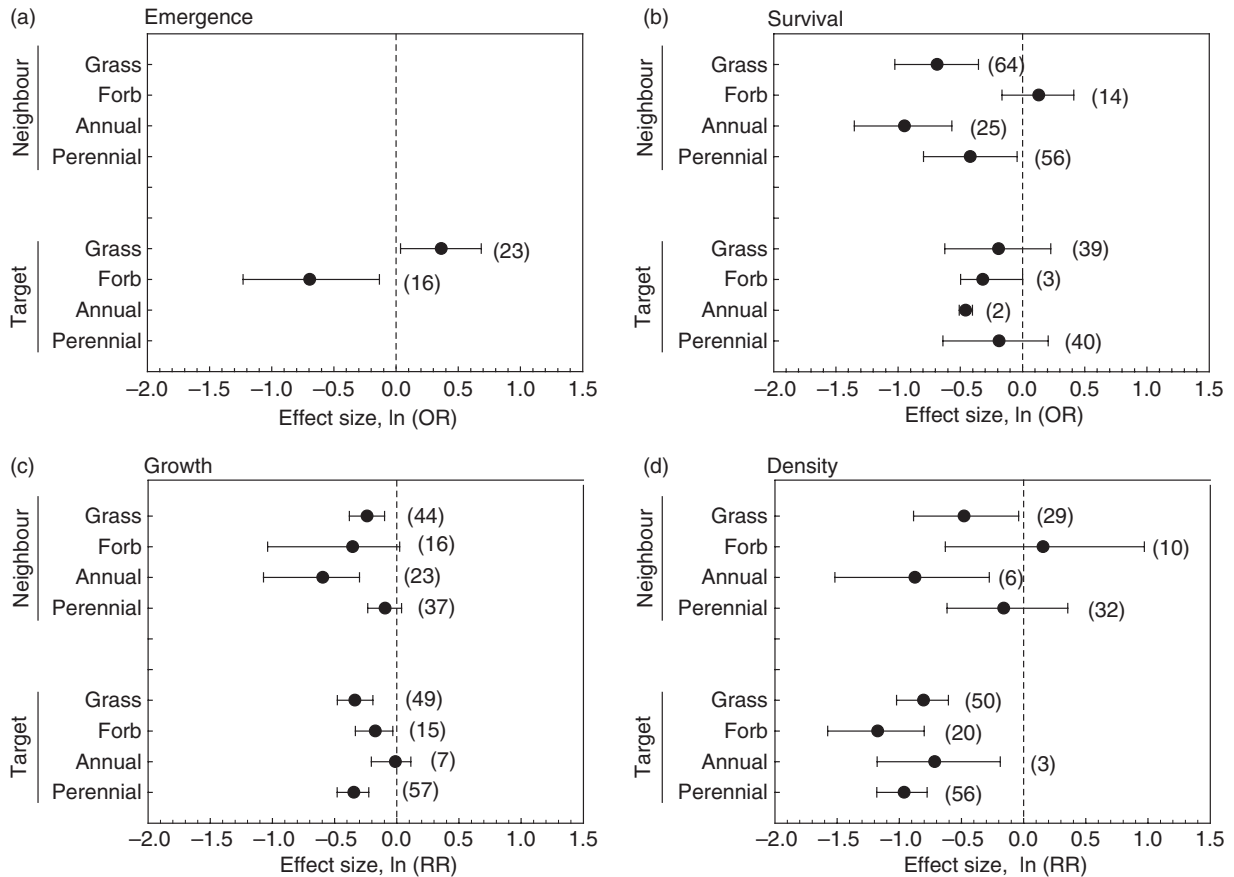


Fig. 2. Mean effect sizes by grouping variable of herbaceous species (grass versus forb, annual versus perennial) for emergence (a), survival (b), growth (c) and density data (d). Error bars are 95% bootstrapped confidence intervals. Number of cases is shown in parentheses. Significant neighbour effects are indicated by confidence intervals that do not overlap zero. The small sample size for emergence data only allowed the calculation of effect sizes for target grasses and forbs.

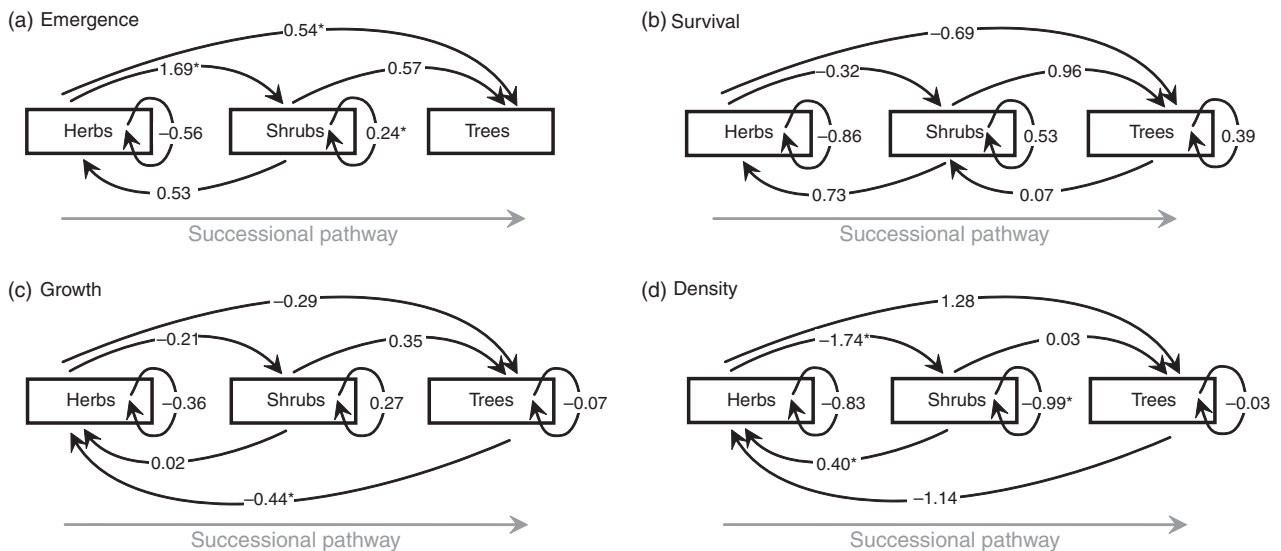


Fig. 3. Diagram describing the magnitude of the interactions among different combinations of neighbour and target life-forms that represent different successional stages. The grey arrow indicates the successional pathway from an early-successional herb community to a late-successional tree community. Data are ln(OR) for survival and emergence, and ln(RR) for growth and density. Significant effect sizes (i.e. 95% bootstrapped confidence intervals did not overlap zero) are highlighted in bold. Only the neighbour-target interactions for which there were more than two experimental cases available are represented. Small sample sizes (i.e. effect sizes calculated using less than five experimental cases) are indicated by an asterisk (*).

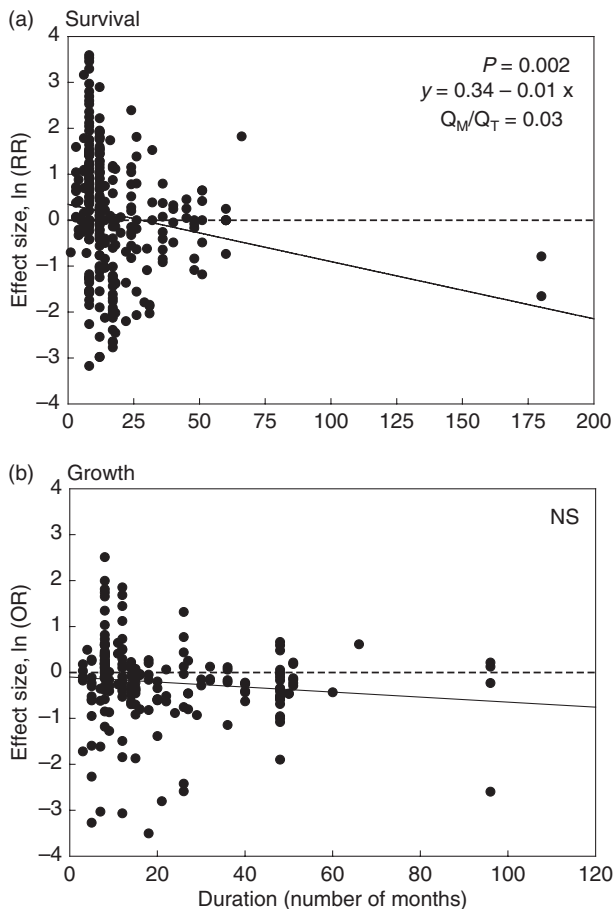


Fig. 4. Relationship between mean effect size and study duration (in number of months) for survival (a) and growth (b). Each point represents an experimental case. Q_M/Q_T is the amount of total heterogeneity in the data due to variation in effect sizes explained by the model.

DENSITY

A total of 40 studies met the selection criteria, yielding 123 suitable cases (see Appendix S4). Across all studies, the presence of neighbours had a moderate negative effect on the density of target species (Fig. 1d). The data set presented significant internal heterogeneity ($Q_T = 157.87$, d.f. = 122, $P = 0.008$). Among neighbour groups, herbs and trees had a negative effect on target density, whereas the effect of shrubs was neutral (Fig. 1d). However, the statistical differences among the three groups were only marginally different (Table 1). There were no differences among herbaceous subgroups in their neighbour effects (Table 2; Fig. 2d). The response of target groups to the presence of neighbours was negative for herbs and shrubs and neutral for tree species (Fig. 1d). No differences appeared in the response of the different herb subgroups considered (Table 2; Fig. 2d). When neighbour and target groups were analysed in pairs, herbs had large negative effects on shrubs and on themselves, but positive effects on trees. Shrub effects were not significant for any of the three groups, and trees had significant (negative) effects only on herbs (Fig. 3d). Among ecosystems, the effect of neighbours was significantly different from zero only in mesic temperate systems,

Table 2. Summary of random models analysing differences in neighbour effects among groups of herbaceous species for each of the four performance estimators (emergence, survival, growth and density). Herbaceous species were classified as grasses (G) versus forbs (F), and as annuals (A) versus perennials (P). Data presented are degrees of freedom (d.f.) and the P -values of Q analyses. Q_M = heterogeneity explained by the model (between-group heterogeneity), Q_E = residual error variance (within-group heterogeneity). Q_M/Q_T = fraction of the total heterogeneity explained by the model. Due to the small sample size for emergence data, only the target grass versus forb comparison was conducted

Comparison	d.f.	Q_M	Q_E	Q_M/Q_T	P -value among groups
Emergence					
Target					
G–F	1, 37	11.17	37.55	0.23	0.0008
Survival					
Neighbour					
G–F	1, 76	5.01	42.78	0.10	0.05
A–P	1, 79	3.17	58.05	0.05	0.07
Target					
G–F	1, 40	0.01	24.09	0.00	0.90
A–P	1, 40	0.05	23.96	0.00	0.82
Growth					
Neighbour					
G–F	1, 60	0.82	106.53	0.01	0.36
A–P	1, 60	15.34	108.19	0.17	<0.0001
Target					
G–F	1, 62	0.52	28.44	0.02	0.47
A–P	1, 62	1.43	27.59	0.05	0.23
Density					
Neighbour					
G–F	1, 37	2.40	48.19	0.05	0.12
A–P	1, 36	2.46	48.11	0.05	0.12
Target					
G–F	1, 68	3.13	80.09	0.04	0.07
A–P	1, 57	0.38	61.31	0.01	0.53

where they had a large negative effect on target density (Fig. 1d). These differences among systems remained when only woody species were considered in the analysis ($Q_M = 19.06$, d.f. = 3, 45, $P = 0.0003$).

ASSESSMENT OF INDEPENDENCE AND PUBLICATION BIAS

At the study level, the results for the overall meta-analysis and the comparisons among neighbour and target life-forms were similar to those obtained when considering each experimental case separately. The smaller sample size resulted, however, in generally lower significance of the tests (see Appendices S5–S7). Differences among ecosystem types, on the contrary, disappeared at the study level, indicating that consistent results within a few large studies masked some of the variation that was present in results among studies. As at the experimental case level, positive neighbour effects on survival were found in all systems when only woody species were considered at the study level, whereas neutral or negative effects were found for growth and density (data not shown). The negative relationship between study duration and the survival effect size also

disappeared at the study level ($Q_M = 1.76$, d.f. = 56, $P = 0.18$), indicating the existence of bias probably induced by a few larger studies that found strong positive short-term neighbour effects.

Fail-safe numbers tended to be large compared to the number of cases included in the meta-analysis. Rosenthal (1979) suggested that if the fail-safe number was larger than five times the sample size plus 10, it was safe to conclude that results were robust regarding publication bias. This was true for all response variables (emergence fail-safe number = 667.4; survival fail-safe number = 679.6; growth fail-safe number = 9759.4; density fail-safe number = 7360.9). Scatter plots of effect size against sample size of the four data sets (not shown) exhibited a typical funnel shape, indicating that studies with small sample sizes (and generally low precision) showed a larger scatter around the true effect value than studies with larger sample sizes (and higher precision). Accordingly, the Spearman rank correlation tests between effect size and variance were not significant for any of the four performance estimators ($R_s = -0.04$, $P = 0.74$ for emergence; $R_s = 0.01$, $P = 0.82$ for survival; $R_s = -0.11$, $P = 0.10$ for growth; $R_s = 0.03$, $P = 0.78$ for density). Overall, these results suggest that there was little publication bias in the studies included in the review and that the meta-analyses outputs were robust.

Discussion

Restoration strategies of degraded terrestrial systems usually centre on accelerating changes in species composition (Pyke & Archer 1991; Whisenant 1999; Walker, Walker & Hobbs 2007). One of the most popular tools to accelerate successional dynamics is the deliberate introduction of the desired species into the system, overcoming in this way a major constraint in the restoration of degraded habitats represented by the lack of seed dispersal (Van Wieren 2002; Howe & Miriti 2004). Accordingly, the large majority of the studies included in this meta-analysis involved the seeding or planting of target species. Results shown here indicate that understanding the complexity of how these introduced target species will interact with the pre-established neighbouring vegetation can largely influence the success of restoration. Thus, although low-magnitude or non-significant neighbour effects were found when all studies were pooled together, strong significant patterns emerged when interaction outcomes were explored among different life-forms of neighbours and targets that represent differential successional stages in diverse ecosystem types. Specifically, even under the most parsimonious data analysis (i.e. at the study level), woody species (particularly shrubs), but not herbs, appeared as excellent candidates to use as nurses in the restoration of all type of systems, including those not considered stressful at a global scale (e.g. mesic temperate habitats).

THE IMPORTANCE OF THE PERFORMANCE ESTIMATOR AND THE STUDY DURATION

A first important result of this review is that the effect of neighbours was clearly dependent on the variable used to estimate

target performance, a conclusion in agreement with previous studies on plant interactions (Goldberg *et al.* 1999, 2001; Hastwell & Facelli 2003; Maestre, Valladares & Reynolds 2005, 2006a). Neighbouring vegetation had in general stronger positive effects on emergence and survival of introduced species than on their growth or density, for which neutral or negative interactions predominated. A similar pattern of variation from facilitation of emergence and survival to inhibition of growth has been repeatedly found in the literature in all types of systems (De Steven 1991a,b; Callaway *et al.* 1996; Suding & Goldberg 1999; Walker & Powell 1999; Foster 2002), indicating that the environmental conditions that maximize early establishment are not necessarily those that maximize biomass production. This type of life-stage conflicts (*sensu* Schupp 2007) adds complexity to the restoration of vegetation, indicating that any given treatment will imply some cost in terms of plant performance. However, because seedling survival in degraded systems is quite low (more than half of the reviewed studies showed survival percentages < 20%) and recruitment limitation is a key determinant of long-term community dynamics (Grubb 1977; Hurt & Pacala 1995), vegetation management during the first years of a restoration program should probably focus on maximizing emergence and survival, despite the potential costs in terms of growth.

Contrary to what was expected, no support was found for an increase of competition with study duration. However, such lack of support for ontogenetic shifts in plant interactions was probably influenced by the nature of the data set, dominated by short-term studies focused on small seedlings during short periods of time. More than half of the 84 papers that analysed neighbour effects on survival and/or growth lasted 2 years or less, and only three studies lasted longer than 5 years. Because growth rates and resource demand are usually low in seedlings and increase with plant size or age (Kitajima & Fenner 2000; Coomes & Allen 2007), an increase of competition with study duration could have been expected if older age classes or long-term studies were better represented in the review. Unfortunately, the short duration of the studies allows us to discuss the benefits of using facilitation to maximize early establishment in degraded systems, but not to understand its long-term contribution to vegetation dynamics. More long-term research is urgently required, either by promoting long-term monitoring (despite its logistical problems) or by using promising alternatives such as modelling (e.g. Siles *et al.* 2008).

THE IMPORTANCE OF THE NEIGHBOUR AND TARGET LIFE-FORMS

A second main result of this review is that the neighbour life-form strongly influenced the interaction outcome to a much larger extent than the life-form of the target species. The neighbour effect varied from very negative in herbs to strongly positive in shrubs (Fig. 1). Moreover, among herb groups, grasses had a larger negative effect than forbs, supporting previous studies that show grasses to be stronger competitors than forbs (Goldberg *et al.* 2001; Pywell *et al.* 2003). Grasses have fibrous roots and a large root : shoot ratio, which allow them to com-

pete efficiently for soil resources (Caldwell & Richards 1986). This is probably a main reason why the few restoration studies that have found benefits in using grasses as nurse plants were either conducted in systems where facilitation is largely non-resource mediated (e.g. reduced salinity or structural support in wetlands; Egerova, Proffitt & Travis 2003; McKee, Rooth & Feller 2007) or under extreme low-resource conditions that prevent rapid grass growth (e.g. mine tailings (Choi & Wali 1995) or semiarid steppes (Maestre *et al.* 2001)).

Shrubs appeared by far as the most promising life-form to use as nurse plants in restoration activities. On the one hand, shrubs are not as strong competitors as early-successional grasses for below-ground resources due to differences in allocation patterns (e.g. lower root : shoot ratio, higher inversion in unproductive tissues as stems) and in architecture (e.g. higher rooting depth, which promotes niche partitioning with seedlings; Aerts, Boot & van der Aart 1991; Jackson *et al.* 1996; Köchy & Wilson 2000). On the other hand, they are not as strong competitors as trees for above-ground resources due to their general smaller size, providing frequently a moderate shade intermediate between the too high irradiance levels of open habitats and the limiting deep shade of closed forests (Harrington & Johns 1990; Puerta-Piñero, Gómez & Valladares 2007). As a result, shrubs offer the benefits of proximity (e.g. microclimate amelioration, increased soil fertility) at minimum costs in terms of competitive effects.

Although the role of the target life-form was not as determinant of the interaction outcome as that of the neighbour life-form, targets also differed in their response to pre-established vegetation, which was generally negative in herbs and positive in trees (Fig. 1). These differences are related to the way the two main components of the facilitative response of a target species – competitive-response ability and stress tolerance – may vary among life-forms with different successional roles. The facilitative response is expected to increase with increasing competitive-response ability and decreasing stress tolerance (Brooker & Callaghan 1998; Liancourt, Callaway & Michalet 2005). Herbs are generally light-demanding early-successional species, with high resource consumption rates that make them highly sensitive to competition by neighbours (i.e. poor competitive-response ability). Comparatively, trees are late-successional life-forms with a conservative use of resources (i.e. large competitive-response ability) and lower tolerance to stress, as suggested by their higher seedling mortality rates and regeneration niches frequently linked to nurse species (Gómez-Aparicio *et al.* 2004; Valiente-Banuet *et al.* 2006; Mendoza *et al.* 2009; Padilla *et al.* 2009). Therefore, the use of pre-established vegetation as nurse plants will be a more efficient restoration tool when the target species are woody plants, particularly trees (with strong facilitative response), than when they are herbaceous species.

RESTORATION MANAGEMENT BASED ON KEY NEIGHBOUR–TARGET COMBINATIONS

Beyond the general trends in the effects and responses of the different life-forms, results shown here also indicate that taking

into account the interdependence among neighbour and target life-forms would benefit the design of restoration activities. For example, the restoration of late-successional forests could benefit from the finding that herb species have much weaker negative effects on shrubs than on trees (Fig. 3). Most current initiatives to recover forest canopies imply the direct introduction of the target tree species into the early-successional habitat that is to be restored, usually with high economic and ecological costs (e.g. intensive site preparation for herb removal, high mortality of both planted and natural seedlings; Rey Benayas *et al.* 2005; Devine, Harrington & Leonard 2007; Hovick & Reinartz 2007). This meta-analysis indicates that a two-phase restoration strategy, where shrubs are sown or planted into the herb layer in a first stage and tree species later introduced under the shrub cover, should be considered as an alternative to the direct introduction of trees. It would not only overcome the problem of the strong inhibition of tree species by herbs, but it would also take advantage of the large positive effects of shrubs on trees. Reforestation schemes with a similar multi-phase approach have been recently proposed for Mediterranean (Gómez-Aparicio *et al.* 2004; Siles 2008) and tropical forests (Cabin *et al.* 2002). Mimicking the sequential stages of the successional process (i.e. herb-shrub-tree) and avoiding successional jumps is probably the most natural, cheap and secure way to recover late-successional woody communities.

Moreover, the fact that tree species had an overall positive (survival) or neutral (growth, density), but not negative, effect on other trees indicate that not only shrubs but also trees can be considered as nurses in the restoration of forest communities. This result supports the benefits of one of the most extensively applied methods to catalyze the restoration of degraded forests: the use of nurse plantations. Fast-growing conifers have been used since the 19th century to promote the establishment of more valuable late-successional hardwoods in the temperate zone (Vallauri, Aronson & Barbero 2002; Pausas *et al.* 2004) and also more recently throughout the tropics (Ashton *et al.* 1997; Parrotta, Turnbull & Jones 1997; Feyera, Beck & Luttge 2002). The most important drawback of nurse plantations is that they require intensive post-planting management (e.g. thinning), since their beneficial effects usually disappear as the tree stand develops (Otsamo 1998; Dulohery, Kolka & McKevlin 2000; McNamara *et al.* 2006). Unfortunately, such post-planting management is not always conducted, rendering large monospecific and dense stands that become more of a problem than a solution (Gómez-Aparicio *et al.* 2009). If managed actively, however, nurse plantations can have the advantage of producing economic benefits (i.e. wood, fruits) that compensate for or even exceed restoration costs.

FACILITATION: A RESTORATION TOOL FOR ALL SYSTEMS?

Current conceptual models about the effect of abiotic conditions on the facilitation–competition balance suggest that positive interactions should be particularly common in harsh, limiting environments, while competition dominates in more fertile, mesic and stable habitats (Bertness & Callaway 1994;

Callaway & Walker 1997). Accordingly, a recent review of 296 nurse–protégé interactions conducted by Flores & Jurado (2003) found more than half of these interactions to occur in arid and semiarid communities. Based on these results, I anticipated the benefits of facilitation to be larger in the restoration of severe environments (i.e. water-limited systems) than on more productive habitats (i.e. wetlands or mesic temperate systems). However, the results of the meta-analysis supported this expectation only partially. Although effect sizes tended to be more positive for semiarid and tropical systems than for wetlands and particularly mesic temperate habitats, these results can not be considered conclusive due to problems of interdependence. And even more importantly, when analyses were run considering only woody species (i.e. correcting for the over-representation of herb species in wetland and temperate studies), neighbour effects on survival turned positive in all systems. These two results together indicate that positive neighbour effects are not necessarily restricted to systems catalogued as ‘stressful’ at a global scale and that the dominant interaction is not governed only by the severity of the abiotic environment, but also (and very importantly) by other factors such as the life history of the interacting species (see also Maestre *et al.* 2009).

The fact that facilitation of woody species was found in all systems should be interpreted taking into account that this review focused on degraded habitats, where, by definition, the conditions for establishment of native species are limiting and numerous stressful factors exist for neighbours to ameliorate. The probability of finding facilitative effects of neighbours in a particular site has been shown to depend on the position of that site within the target species’ niche (Choler, Michalet & Callaway 2001; Liancourt, Callaway & Michalet 2005; Chu *et al.* 2008). The further a site is from the fundamental niche optimum, the more likely facilitation will be. Thus, it is possible that the occurrence of positive interactions in all types of degraded habitats, even in those where positive interactions are not usually considered important (e.g. temperate systems), is influenced by a much higher probability of finding woody species outside their fundamental niche optima in degraded than in well-conserved natural systems, where much of the basic ecological theory is developed.

CONCLUDING REMARKS

An important challenge in restoration ecology is to find rules that are general enough to be widely applicable and easily transferable to managers, but specific enough not to be useless (Temperton & Hobbs 2004). This meta-analysis represents an effort to learn from the accumulated experience in order to identify general rules that can be used for the management of plant interactions involving different types of species and degraded systems. However, because meta-analyses are conditional on the set of studies included, the analyses presented here had some clear limitations to assess this aim. First, the quantity of data available was only moderate in most cases and rather low for some performance estimators (e.g. emergence) and among-group comparisons, which restricted the

statistical power of the analyses, especially at the study level. An analysis including more studies would therefore be desirable before conclusions could be considered definitive. A second important drawback was the short duration of most studies, which forces the conclusions of this review to be applicable only in the short-term.

Despite these limitations, the results shown here clearly indicate that pre-existing vegetation can have large impacts on the success of species establishment in degraded systems, with inhibition predominating in herbaceous communities typical of early-successional stages and facilitation in communities dominated by shrubs and trees. Accordingly, whereas restoring early-successional herbaceous communities seems to necessarily rely on removal techniques, augmenting populations of facilitator shrubs and trees should be considered as a promising strategy for restoring degraded shrublands and forests (Holl *et al.* 2000; Su & Zhao 2003; King 2008). Introduced nurses can nucleate forest recovery at several isolated points and promote patch formation through both abiotic (e.g. resource trapping) and biotic (e.g. attraction of seed dispersers) feedback dynamics (Aerts *et al.* 2006a). Probably, the cheapest and easiest way to trigger this process of nucleation would be to first introduce shrubs that catalyze natural succession and to later introduce, under their canopies, those tree species that are not able to colonize spontaneously. Restoration approaches that promote rapid revegetation and minimize cost and effort are urgently needed, especially for developing countries that have few resources at their disposal and lack incentives to restore degraded forests (Brown & Lugo 1994; Aerts *et al.* 2006b; McKee, Rooth & Feller 2007). Incorporating facilitation into the mainstream of practical ecology can clearly contribute to achieving this aim.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of studies included in the meta-analysis of emergence data.

Appendix S2. List of studies included in the meta-analysis of survival data.

Appendix S3. List of studies included in the meta-analysis of growth data.

Appendix S4. List of studies included in the meta-analysis of density data.

Appendix S5. Summary of random models analysing differences among groups in neighbour effects at the study level.

Appendix S6. Mean effect sizes (calculated at the study level) by categorical grouping variable for emergence (a), survival (b), growth (c) and density data (d).

Appendix S7. Diagram describing the magnitude of the interactions (calculated at the study level) among different neighbour and target life-forms that represent different successional stages.

Appendix S8. References included in Appendices S1–S4 and not cited in the main text.

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